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Relative importance of environment, human activity and spatial situation in determining the distribution of terrestrial mammal diversity in Argentina

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Abstract

Aim The partition of the geographical variation in Argentinian terrestrial mammal species richness (SR) into environmentally, human and spatially induced variation.

Location Argentina, using the twenty-three administrative provinces as the geographical units.

Methods We recorded the number of terrestrial mammal species in each Argentinian province, and the number of species belonging to particular groups (Marsupialia, Placentaria, and among the latter, Xenarthra, Carnivora, Ungulates and Rodentia). We performed multiple regressions of each group's SR on environmental, human and spatial variables, to determine the amounts of variation explained by these factors. We then used a variance partitioning procedure to specify which proportion of the variation in SR is explained by each of the three factors exclusively and which proportions are attributable to interactions between factors.

Results For marsupials, human activity explains the greatest part of the variation in SR. The purely environmental and purely human influences on all mammal SR explain a similarly high proportion of the variation in SR, whereas the purely spatial influence accounts for a smaller proportion of it. The exclusive interaction between human activity and space is negative in carnivores and rodents. For rodents, the interaction between environment and spatial situation is also negative. In the remaining placental groups, pure spatial autocorrelation explains a small proportion of the variation in SR.

Main conclusions Environmental factors explain most of the variation in placental SR, while Marsupials seem to be mainly affected by human activity. However, for edentates, carnivores, and ungulates the pure human influence is more important than the pure spatial and environmental influences. Besides, human activity disrupts the spatial structure caused by the history and population dynamics of rodents and, to a lesser extent, of carnivores. The historical events and population dynamics on the one hand, and the environment on the other, cause rodent SR to vary in divergent directions. In the remaining placental groups the autocorrelation in SR is mainly the result of autocorrelation in the environmental and human variables.

Keywords
Mammal diversity, species richness, spatial structure, human influence, variation partitioning, Argentina.

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Resumen

Objetivo Descomponer la variación geográfica de la riqueza específica de los mamíferos terrestres argentinos en las siguientes partes: variación inducida por el ambiente, variación inducida por la actividad humana y variación debida a la localización espacial.

Localización Argentina, utilizando las 23 provincias administrativas como unidades geográficas.

Métodos Se ha registrado el número de especies de mamíferos terrestres en cada provincia argentina, y el número de especies pertenecientes a grupos particulares (Marsupialia, Placentaria y, dentro de estos últimos, Xenarthra, Carnivora, Ungulados y Rodentia). Se han realizado regresiones múltiples de la riqueza específica de cada grupo sobre variables ambientales, humanas y espaciales, para determinar las proporciones de la varianza explicadas por estos factores. Después se utilizó un procedimiento de partición de la varianza para especificar qué proporción de la variación de la riqueza específica explica cada uno de los tres factores exclusivamente, y qué proporciones se pueden atribuir a interacciones entre factores.

Resultados Para los marsupiales, la actividad humana explica la mayor parte de la variación de la riqueza específica. La influencia puramente ambiental y la puramente espacial explican una proporción similarmente alta de la variación de la riqueza específica de la totalidad de mamíferos terrestres, mientras la influencia puramente espacial explica una proporción más pequeña. La interacción exclusiva entre la actividad humana y el espacio es negativa en carnívoros y roedores. Para los roedores, la interacción entre ambiente y situación espacial es también negativa. En los restantes grupos de placentados, la autocorrelación espacial pura explica una proporción pequeña de la variación de la riqueza específica.

Conclusiones principales Los factores ambientales explican la mayor parte de la variación de la riqueza específica de placentados, mientras los marsupiales parecen ser principalmente afectados por la actividad humana. Sin embargo, para los desdentados, carnívoros y ungulados la influencia humana pura es más importante que las influencias espacial y ambiental puras. Además, la actividad humana rompe la estructura espacial causada por la historia y dinámica poblacional de los roedores y, en menor medida, de los carnívoros. Los eventos históricos y la dinámica poblacional, por una parte, y el ambiente, por la otra, hacen que la riqueza específica de los roedores varíe en direcciones divergentes. En los demás grupos de placentados la autocorrelación de la riqueza específica se debe principalmente a autocorrelación en las variables ambientales y humanas.

Palabras clave
Diversidad de mamíferos, riqueza específica, estructura espacial, influencia humana, partición de la varianza, Argentina.

INTRODUCTION

Species richness (SR) at local, regional and global scales is an important feature of nature that varies according to different geographical patterns. The assessment of the causes that govern these patterns is of interest to both biologists and environmental managers and has become a central issue in biogeography (Lubchenco *et al.*, 1991). Mammals are suitable for studies on patterns of species diversity, as their taxonomy and distributions are relatively well known. They have ecological and economic importance, are appealing to the general public – many of them being flagship species whose conservation benefits from broad public support – and they justify conservation measures because several mammal species have become extinct and many are endangered. In addition, mammals could serve as a model system on which to base initial policy and management decisions, as some of their diversity patterns and conservation problems can be generalized to other taxonomical groups (Ceballos & Brown, 1995).

Several studies have focused the explanation of mammal SR patterns on the geographical variation in environmental factors (e.g. Simpson, 1964; Fleming, 1973; Wilson, 1974; Owen, 1988, 1990; Kelt, 1999). However, the biogeography of the current mammal fauna is complicated by human activity, which often brings about extinctions, alterations of ranges, and introductions, both deliberate and accidental (Dobson, 1994). In particular, the introduction of mammal livestock may be disruptive for wild mammal distributions, each domestic species differentially affecting different groups of wild species. Consequently, the assessment of the human impacts on wild mammal communities is important to establish effective strategies for the conservation of biodiversity. Human influences on land mammal distribution or coenotic structure have been considered in some studies (e.g. Philips, 1936; Kirkland, 1977; Grant *et al.*, 1982; Pizzolotto *et al.*, 1991; Douglass *et al.*, 1992; Halle, 1993; Amarena *et al.*, 1994; Dobson, 1994; Barbosa *et al.*, 2001).

Species richness at a given locality is, in addition, influenced by the SR at surrounding localities because of contagious biotic processes such as reproduction and migration. This results in spatial autocorrelation in the data, which violates the assumption of most standard statistical tests that observations are independent. However, spatial structuring as a result of autocorrelation is functional in natural systems and not the result of some random, noise-generating process, and therefore should be integrated in geographical studies rather than ignored or eliminated (Legendre & Fortin, 1989; Legendre, 1993).

Autocorrelation in mammal species diversity is, thus, caused by historical events, the species' own population dynamics, and by external factors, both environmental and human, that are spatially autocorrelated as well. Borcard *et al.* (1992) and Legendre (1993) proposed methods for measuring the fraction of the variation in species data that can be explained by the spatial structure of the data, the fraction explainable by environmental variables, and the fraction of shared variation among spatial and environmental components. Several studies have employed such methods to quantify the environmental and the spatial influences on species' or groups of species' distributions and on SR patterns (Borcard *et al.*, 1992; Borcard & Legendre, 1994; Mandrak, 1995; Heikkinen & Birks, 1996; O'Connor *et al.*, 1996; Lobo *et al.*, 2001). Vaughn & Taylor (2000) included a third component, the availability of host fish, in a study of freshwater mussel distribution and abundance in south central USA, and Barbosa *et al.* (2001) included the influence of human activity in an analysis of otter distribution in Spain.

Our aim is to assess the relative importance of environmental, human, and spatial influences on the geographical variation of terrestrial mammal SR in Argentina, and to evaluate their differential influence in several groups of mammal species.

METHODS

Study area

Argentina covers an area of almost 2.8 million square kilometres and comprises most of America's 'southern cone', being the second largest country in South America and the eighth largest in the world. The topography and climate of Argentina vary significantly, with the high Andean mountains and their arid foothills in the west, subtropical climate in the marshes and dense forests of the northeast, temperate climate in the vast grasslands of the Pampas in the middle part of the country, and cold, arid climate in the southern, windswept plateau of Patagonia. The middle third of the country, which includes the capital Buenos Aires, contains most of the population, as well as most of the economic activity and agricultural and livestock production. The main environmental problems (urban and rural) are soil degradation, desertification, air and water pollution, and those derived from the extensive introduction of domestic species.

Argentina is divided into twenty-three political-administrative provinces, which we used as territorial units. The use of political divisions in biogeographical research is sometimes criticized because patterns and processes responsible for biological diversity are supposed not to recognize such artificial boundaries. However, provincial limits are not totally arbitrary, but rather are partly based on natural borders, so they may be suitable to detect natural phenomena. In fact, Baroni-Urbani & Collingwood (1976) were able to obtain different distribution types for British ants using vice-counties as geographical units; and Márquez *et al.* (2001) found that administrative provinces were the best lattice for obtaining biotic regionalizations for Spanish ferns when compared with river basins, natural regions, physiographical and geological regions, and mountains and plains. Furthermore, Ceballos & Brown (1995) pointed out that the application of biodiversity conservation measures is usually conducted at an administrative (regional or national) level and, in order to focus attention and resources effectively, biological studies should aim at affecting policy and management decisions at levels where they can be developed and implemented. In addition, the human activity patterns that affect biodiversity often are shaped by political limits, and statistical data on human variables are usually available on a political-unit basis only.

The variables

We recorded the total number of indigenous non-volant terrestrial mammal species in each Argentinian province. As different mammal groups can show different SR patterns (see Simpson, 1964; Fleming, 1973; Wilson, 1974; Owen, 1988, 1990; Kelt, 1999), we also recorded the number of species belonging to particular groups: Marsupialia, Placentaria, and among the latter, Xenarthra, Carnivora, Ungulates, and Rodentia. Lagomorphs and Primates were not included in the analysis of separate groups because of their very low SR

Table 1 Number of indigenous non-volant terrestrial mammal species in each Argentinian province. ALL, all mammals; PLA, Placentaria; MAR, Marsupialia; XEN, Xenarthra; CAR, Carnivora; UNG, Ungulates; ROD, Rodentia (data completed from Galliari *et al.*, 1996)

Province	ALL	PLA	MAR	XEN	CAR	UNG	ROD
Jujuy	75	70	5	9	16	6	37
Salta	92	84	8	14	15	5	48
Formosa	61	56	5	12	14	7	20
Catamarca	46	46	0	3	9	3	31
Tucumán	68	65	3	4	17	8	35
Santiago del Estero	36	35	1	6	12	3	13
Chaco	47	45	2	5	8	7	22
Misiones	77	63	14	8	17	7	27
La Rioja	34	33	1	3	8	2	20
San Juan	25	24	1	4	5	3	12
Córdoba	45	43	2	4	8	3	27
Santa Fe	41	38	3	5	9	2	20
Corrientes	35	32	3	2	10	2	18
Entre Ríos	48	43	5	6	13	3	20
Mendoza	43	38	5	5	9	2	22
San Luis	26	23	3	4	6	2	11
La Pampa	43	38	5	5	8	1	24
Buenos Aires	49	44	5	7	10	3	24
Neuquén	50	46	4	2	10	3	31
Río Negro	48	44	4	2	8	3	31
Chubut	43	41	2	3	7	2	29
Santa Cruz	33	32	1	4	10	3	15
Tierra del Fuego	23	20	3	0	8	3	9
Total	255	229	26	18	28	14	164

values. Data on the mammal SR in the Argentinian provinces and their source are shown in Table 1.

Our aim was not to determine which particular variables mostly affect mammal SR in Argentina, but rather to ascertain the relative contributions of environment, human activity and spatial situation in accounting for SR variation. So, we used a number of variables thought to be representative of these three factors and bound to affect terrestrial mammal distribution, and found available on a provincial basis. We recorded, for each province, the values of ten environmental variables, related to climate, orography and habitat diversity; twelve human variables, related to population density, agriculture, forestry, and livestock; and nine spatial variables: latitude, longitude, and the other seven factors of a cubic trend-surface polynomial of both spatial terms. Latitude and longitude describe linear spatial trends while quadratic, cubic and interaction terms can model more complex patterns such as patches, peaks and valleys of diversity (Borcard *et al.*, 1992; Legendre, 1993; Borcard & Legendre, 1994). The thirty-one variables used and their source are shown in Table 2.

Statistical analyses

The distributions of the variables were tested for normality by means of a Kolmogorov–Smirnov test, with the aim of eliminating from subsequent analyses those variables whose distribution was significantly ($P < 0.001$) different from normal.

We performed a multiple linear regression of each mammal group's SR on all the recorded variables. The variables excluded from the models as a result of collinearity problems were eliminated from subsequent analyses. We then regressed each group's SR onto each of the three groups of variables (environmental, human and spatial) in turn, to determine the proportions of the variation in SR that were explainable by the environment (*Env*), by human activity (*Hum*) and by spatial situation (*Spa*), respectively.

The effects of different factors on the distribution of SR may coincide or counteract one another (Borcard *et al.*, 1992), so the sum of the amounts of variation explainable by each group of variables usually differs from the total amount explained by the three groups together. With the linear multiple regression of SR on the three groups together we obtained the total amount of variation explained by our variables (*Env*U*Hum*U*Spa*). Then, in order to specify which proportion of the variation in mammal SR is explained by each of the three factors exclusively and which proportions are attributable to interactions between factors, we performed a variance partitioning procedure as follows. We regressed SR on the environmental and human variables simultaneously, so obtaining the amount of variation explained by both these factors together (*Env*U*Hum*); in a similar way, we determined the amounts of variation explained by environment and space together (*Env*U*Spa*), and by human activity and space together (*Hum*U*Spa*). Then the proportion of the variation explained exclusively by the environment (E) was obtained with the following

Table 2 Environmental, human and spatial variables used to partition the variation in terrestrial mammal species richness in the Argentinian provinces (source: Instituto Geográfico Militar, 1997)

Environmental variables
MT: Mean annual temperature
HT: Mean temperature of the hottest month
CT: Mean temperature of the coldest month
TR: Annual temperature range
MP: Mean annual precipitation
PR: Annual precipitation range
MA: Mean altitude
AR: Altitude range
LR: Latitude range
SA: Surface area
Human variables
PD: Population density
CA: Cropland area (%)
FP: Forestry production
LD: Livestock density
SD: Sheep density
SP: Sheep proportion (number of sheep/total livestock)
CD: Cattle density
CP: Cattle proportion
HD: Horse density
HP: Horse proportion
SD: Swine density
SP: Swine proportion
Spatial variables
La: Mean latitude
Lo: Mean longitude
LaLo: Latitude × longitude
La^2: Latitude^2
Lo^2: Longitude^2
La^2Lo: Latitude^2 × longitude
$LaLo^2$: Latitude × longitude^2
La^3: Latitude^3
Lo^3: Longitude^3

subtraction: *Env*U*Hum*U*Spa* – *Hum*U*Spa*. The proportions explained exclusively by human activity (*H*) and by spatial situation (*S*) were obtained in a similar way. The amount of variation attributable exclusively to the interaction (or simultaneous influence) of environment and human activity (*EH*) was obtained with the subtraction *Env*U*Hum*U*Spa* – *Spa* – *E* – *H*. The amount of variation attributable exclusively to the interactions between environment and space (*ES*) and between human activity and space (*HS*) were calculated in a similar way, and the amount attributable to interactions between the three factors together (*EHS*) was obtained with the subtraction *Env*U*Hum*U*Spa* – E – *H* – *S* – *E* – *ES* – *HS*.

RESULTS

None of the variables' distributions were found to be significantly different from the normal distribution. *HT*, *SD*, *SP*, *CD*, *Lo*, *LaLo*, La^2, Lo^2, and La^2Lo were excluded from the linear regressions as a result of multicollinearity problems, and were consequently eliminated from the following analyses.

Figure 1 represents, for all mammals, Marsupialia, and Placentaria, the observed values of SR and the expected values according to environmental conditions (*Env*), human activity (*Hum*) and spatial structure (*Spa*), as well as the proportion of the variation in SR explained by each of the three factors. Environmental factors explain most (nearly 73%) of the variation in all mammal SR, whereas human activity and spatial situation can explain *c.* 40% each. However, this pattern reflects that of placentals, which comprise most mammal species. For marsupials, human activity, mainly measured by livestock abundance, explains the greatest part (72.3%) of the variation in SR, while environmental conditions explain nearly 60% of this variation and spatial situation explains the smallest part (26.6%).

In Fig. 2, we represent the observed and expected values of SR and the percentages of variation explained by each factor for the four subgroups of Placentaria (Xenarthra, Carnivora, Ungulates and Rodentia). Environmental factors also explain most (between 57.3% and 74.9%) of the variation in SR for the four placental subgroups. Human activity explains the second greatest part for carnivores and for rodents, while spatial location explains the second greatest part for edentates (Xenarthra) and for ungulates.

The results of the variation partitioning for each mammal group are shown in Figs 3 and 4. Purely environmental and purely human influences on all mammal SR explain a similar proportion of the variation (between 21% and 22%), whereas the pure spatial influence accounts for a smaller (16%) proportion of the variation. Significant proportions of the variation are explained simultaneously by environment and space independently of human activity (19.3%) and by environment and human activity independently of space (19.4%). The exclusive interaction between human activity and space is negative, which means that human activity counteracts the spatial structure of mammal SR. This negative interaction does not present in marsupials but does in placentals, and then in carnivores and rodents.

For rodents, the pure influences of the environment and of spatial situation are important and the exclusive interaction between them is negative, which suggests that the historical events and the population dynamics of rodents condition the geographical variation of SR independently from the environment. In the remaining placental groups, pure spatial autocorrelation explains a small proportion of the variation in SR, which means that the autocorrelation in SR is mainly the result of autocorrelation in the environmental and human variables that condition it.

DISCUSSION

According to Ruggiero *et al.* (1998) Argentina is nearly enclosed by isolines of environmental resistance to mammals, a concept closely related to faunal turnover that measures the loss of biotic resemblance occurring from any point in the rest of South America; in this way, it constitutes a natural territory within which to analyse changes in mammal species

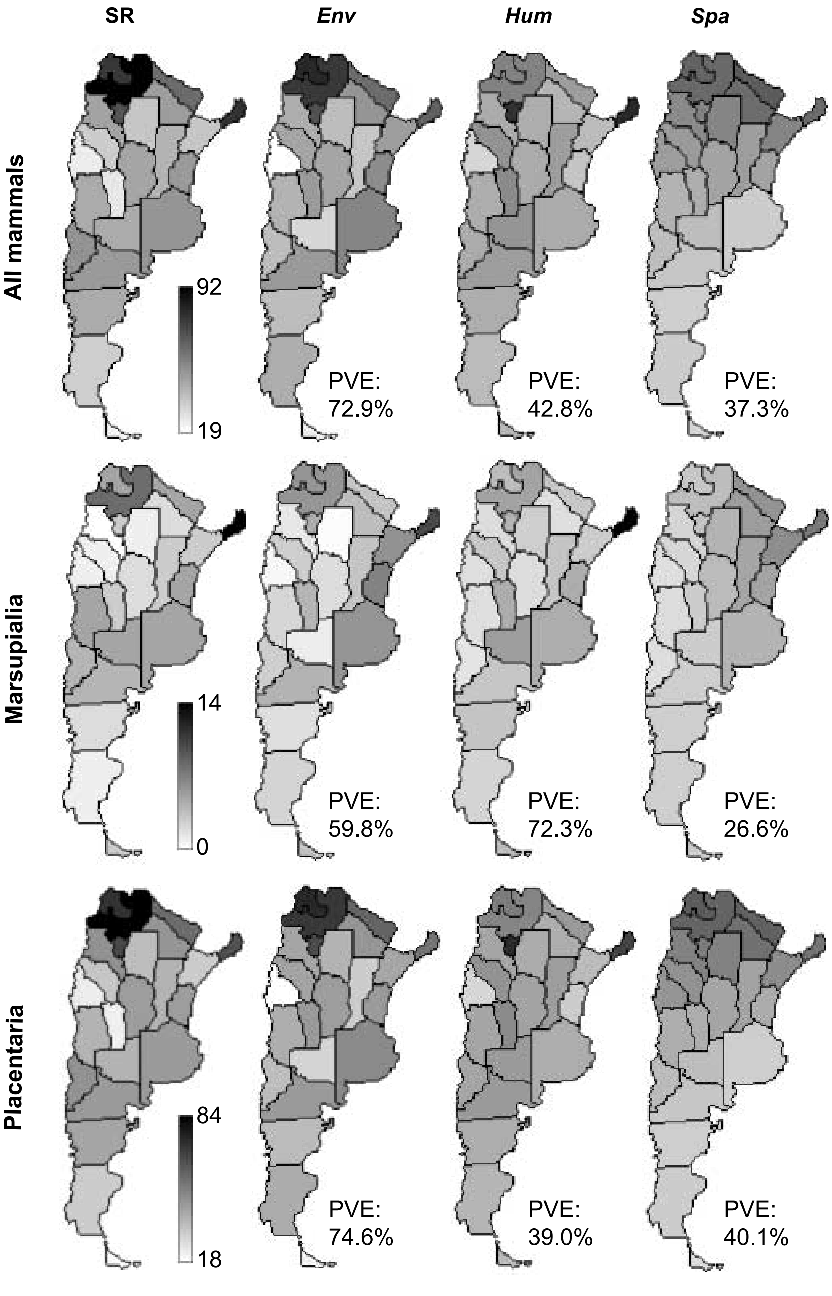

Figure 1 Species richness (SR) values for Argentinian terrestrial mammals by province, and expected values according to the environmental conditions (*Env*), human influence (*Hum*) and spatial structure (*Spa*). PVE: proportion of the SR variation explained by each factor.

diversity. Different groups of mammal species show distinct geographical trends affected by different factors in Argentina. This kind of difference has been reported elsewhere. For example, Fleming (1973) detected different latitudinal trends in species diversity for carnivores and for small mammal species in USA and Panama; similarly, Owen (1988, 1990) found different patterns of diversity for carnivores and rodents in Texas, even when the same mechanism was supposed to act upon both groups of species. Environmental factors have been customarily considered as the primary causes of these variations. Wilson (1974) obtained a positive correlation between quadruped diversity and topographic relief in North America; Abramsky & Rosenzweig (1984) related the variation in rodent species diversity with differences in productivity; Olff *et al.* (2002) considered that gradients of precipitation, temperature, and soil fertility might explain the distribution of large mammal herbivore diversity.

The variation in mammal SR explained by pure spatial structure reflects available species pools, because of colonization or other historical events, and biotic processes that have led to non-random distribution patterns (Schluter & Ricklefs, 1993; Vaughn & Taylor, 2000). For instance, a species may be absent from a particular region not because of local conditions or biotic interactions, but simply

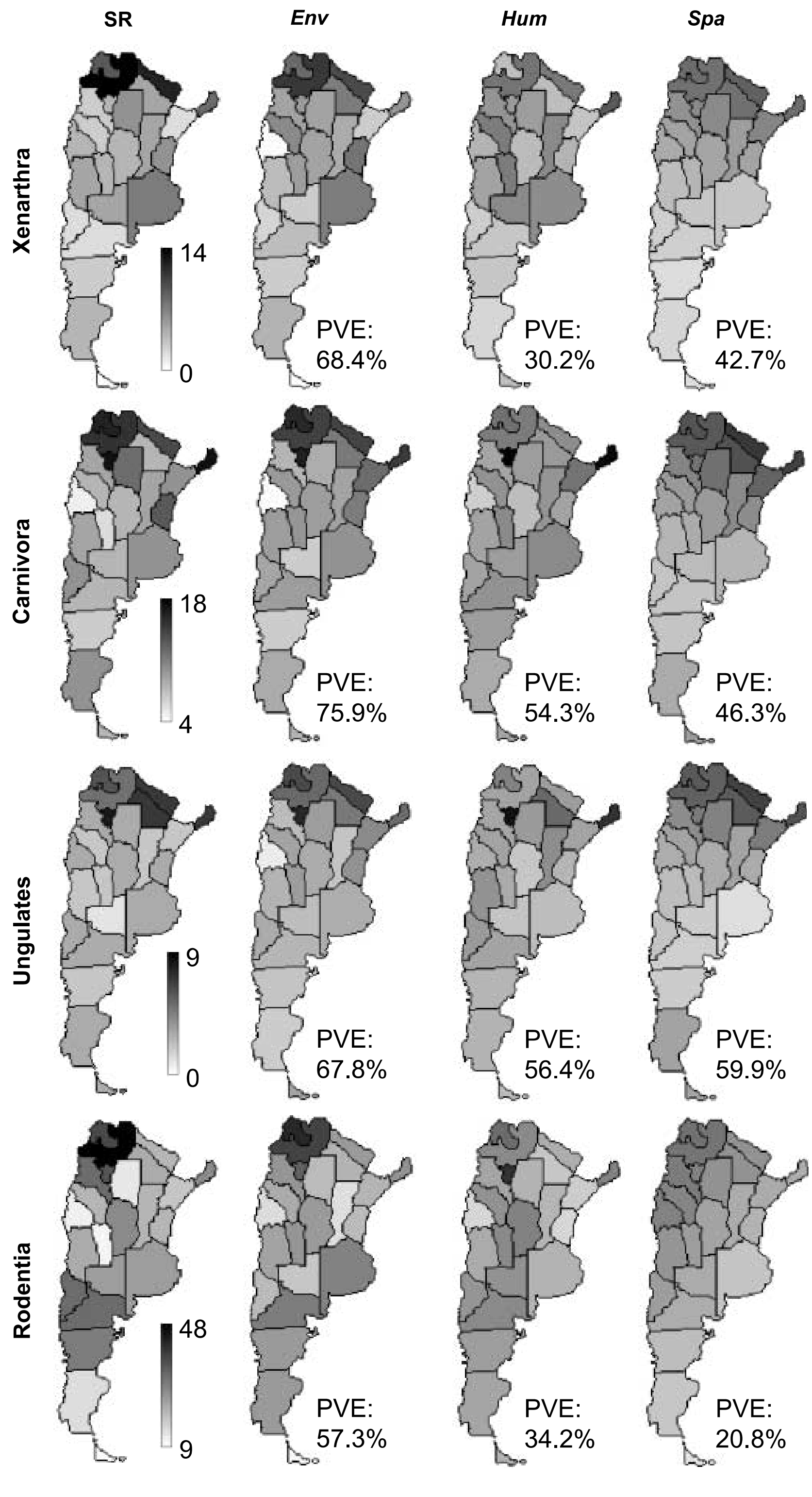

Figure 2 Species richness (SR) values for Placentaria subgroups by province, and expected values according to the environmental conditions (*Env*), human influence (*Hum*) and spatial structure (*Spa*). PVE: proportion of the SR variation explained by each factor.

because it has not yet arrived at the region. Conversely, a species may be present at a locality due to proximity to a suitable region rather than to favourable local conditions. Consequently, after accounting for the environmental and human influences on mammal SR, the remaining correlation between spatial situation and SR may be attributable to historical events and the population dynamics of the species. The relatively high proportion of variation in SR of all mammals and of placentals that is attributable to historical events and their population dynamics is, in effect,

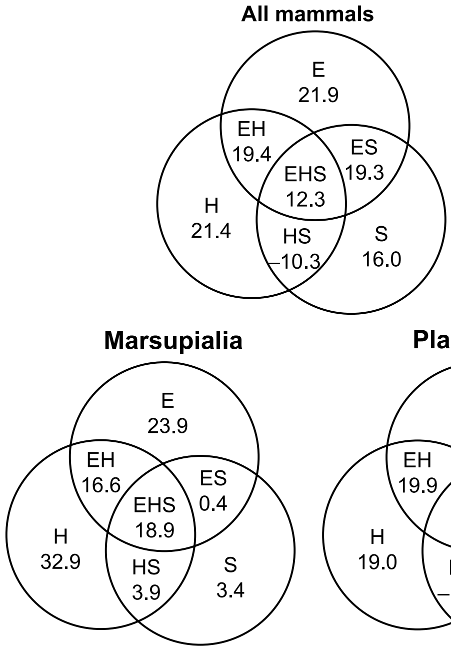

Figure 3 Variation partitioning of terrestrial mammal species richness in the Argentinian provinces. Values shown in the diagrams are the percentages of variation explained exclusively by environmental conditions (*E*), human activity (*H*), spatial structure (*S*), and by the interactions between these components (*EH*, *ES*, *HS*, *EHS*).

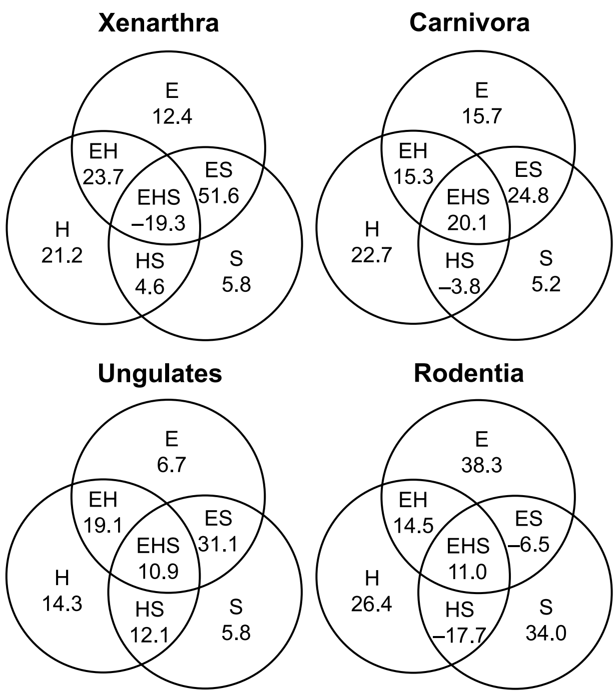

Figure 4 Variation partitioning of Placentaria subgroups' species richness in the Argentinian provinces. Values shown in the diagrams are the percentages of variation explained exclusively by environmental conditions (*E*), human activity (*H*), spatial structure (*S*), and by the interactions between these components (*EH*, *ES*, *HS*, *EHS*).

the result of the high value shown by rodents. For marsupials and each of the remaining groups of placentals, less than 6% of the variation is purely spatial (see Figs 3 and 4). Ruggiero (1994) found that while the geographical range sizes of South American marsupials, edentates, and artiodactyls have lognormal distributions, rodents have a significantly high proportion of species with smaller geographical ranges; this might hinder the dilution of the effects of historical events on local rodent SR.

The most remarkable difference between marsupials and placentals is the role of human activity. Marsupials seem to be mainly affected by this factor, while for placentals it is the least important (Fig. 1). However, for edentates, carnivores, and ungulates the pure human influence is more important than the pure spatial and environmental influences (Fig. 4). Besides, human activity is an important factor for rodents as well, and the interaction between human and spatial influences is negative for this group and for carnivores, indicating that human activity disrupts the spatial structure caused by the history and population dynamics of rodents and, to a lesser extent, of carnivores.

Interaction between environment and space, excluding human influence, is the most important component of the explained variation in SR of placentals (Fig. 3) and, among these, of edentates, carnivores, and ungulates (Fig. 4). This might mean that the spatial structure in these groups is mainly the result of the effect of environmental factors that are spatially structured. This is not the case of rodents, for which the interaction between environment and space is negative, i.e., environment and space cause rodent SR to vary in divergent directions.

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