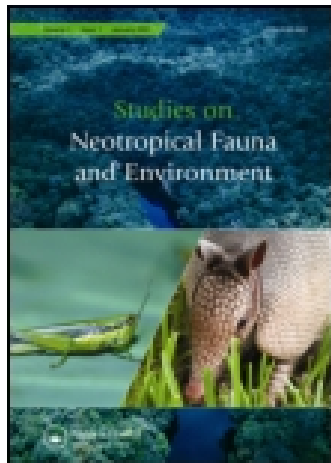


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ORIGINAL ARTICLE

Spatial and temporal variation of terrestrial rodent assemblages in Cholila, Chubut Province, Argentina

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We examined spatial and temporal variation of the sigmodontine rodent assemblage in Cholila, Chubut Province, Argentina, from spring 2003 to spring 2006. Rodent populations were sampled in shrublands, forests, pastures and peridomestic habitats. Species–habitat associations were evaluated as well as richness, species diversity and evenness. The assemblage was composed of 11 species, but three species dominated the assemblage varying spatially and temporally, depending on the habitat. Temporal fluctuations in abundance of these dominant species probably accounted for observed evenness and diversity fluctuations.

Keywords: assemblage changes; habitats; seasons; years; Argentina

Introduction

In Argentina, sigmodontine rodents have received much attention due to their epidemiological importance. The colilargo (*Oligoryzomys longicaudatus*) is the major reservoir of Andes hantavirus (ANDV), which is the etiological agent of hantavirus pulmonary syndrome (HPS) in southern Argentina and Chile (López et al. 1996; Levis et al. 1997, 1998; Padula et al. 2000). *Oligoryzomys longicaudatus* has a large geographic range (Porcasi et al. 2005) and it occurs in multiple habitat types including disturbed habitats (cultivated field borders and peridomestic settings), as well as pasture, shrublands and forests (Pearson 1983, 2002; Monjeau et al. 1998; Pardiñas & Cirignoli 2000; Pardiñas et al. 2003; Piudo et al. 2005). Rodent assemblages vary in composition among these habitats. Most studies of rodent communities in different Patagonian areas of Argentina (Pearson & Pearson 1982; Kelt et al. 1994; Pearson 1995; Kelt 1996; Guthmann et al. 1997; Monjeau et al. 1997; 1998; 2011; Pardiñas et al. 2003; Piudo et al. 2005, 2011; Andreo et al. 2012) have been done in short time periods (only a year or, if more than a year, in only one season). Polop et al. (2010) examined spatial heterogeneity in the Andean region of Chubut Province (Cholila) recording more than 10 species, but they did not focus on assemblage differences and changes over time.

Long-term studies are important to understand spatial and temporal variation in rodent community structure and species coexistence (M'Closkey 1972;

Kaufman et al. 1995). In addition, community structure may affect disease transmission within the community as well as human risk of exposures (Mills 2005). The goal of this study was to describe and compare the composition of the sigmodontine rodent assemblage by habitat and season at a study site in the Andean region of Chubut Province, in order to examine functional relations that explain assemblage composition.

Materials and methods

Study area

The study was performed from November 2003 to December 2006 in Cholila (42°31' S; 71°27' W), Andean region, Chubut Province (for a description of the study area, see Polop et al. 2010). Rodent populations were sampled in four types of habitat: shrublands, forests, pastures, and peridomestic areas. Shrubbylands were characterized by native species, such as *Berberis buxifolia*, *Acanthostyles buniifolius*, *Rhamnus lycioides* and *Schinus patagonicus*, and exotic species, such as *Rosa* spp. Forests were dominated by *Nothofagus antarctica*, *N. dombeyi*, *Austrocedrus chilensis*, and *N. pumilio* (above 1200 m), some with *Chusquea culeou* in the understory. Pastures were defined as habitats where the vegetation did not exceed 50 cm height and were dominated by gramineous plants. Peridomestic areas included environments with some human use around habitations.

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Rodent trapping and processing

Twenty-four lines of snap traps and live capture traps were placed in each of three habitats (forest, pasture, and peridomestic) and 15 in the shrubland habitats each season. For a detailed description of the rodent trapping and processing see Polop et al. (2010). Handling of rodents followed standardized safety guidelines recommended by the Centers for Disease Control and Prevention (Mills et al. 1995).

Data analysis

The abundance of each rodent species in each habitat was estimated by RDI as

$$\text{RDI} = \frac{\text{number of captures}}{(\text{number of traps} \times \text{number of nights}) - a} \times 100, \quad (1)$$

where a is the number of shut/sprung traps without animals (Castillo et al. 2003).

Species–habitat associations were tested, as suggested by Mills et al. (1991), by deriving an expected number of captures of each species in each habitat by multiplying the proportion of trap-nights in a specific habitat by the total number of individuals of each species captured. This expected value was compared to the observed number of captures in a particular habitat and χ^2 values for each species derived. Deviations of observed values from expected values were standardized as percentages of expected values. Significant deviations from expected associations were tested by the use of 95% Bonferroni confidence intervals (Byers et al. 1984; Mills et al. 1991). The null hypothesis in this analysis is that the four different habitat types have the same probability of capture for every species.

Species diversity (H), richness (S) and evenness (J) indices were used to characterize the assemblage for each habitat and season and to compare them. Following Jost (2006) diversity was estimated with the conversion of Shannon–Wiener entropy index to true diversity [$H' = \exp(-\sum pi \ln pi)$], where pi is the proportion of the total sample belonging to the i th species. We quantified evenness (J) as [$H'/\ln(\text{Richness})$] and defined richness as the number of species.

The diversity index was compared among habitats (shrublands, pastures, forests and peridomestic areas) in seasonal trapping sessions using repeated-measures ANOVA (spring 2003, summer 2004, autumn 2004, winter 2004, spring 2004, summer 2005, autumn 2005, winter 2005, spring 2005, summer 2006, autumn 2006, winter 2006, and spring 2006). We considered

each trap line as a unit of spatial replication in each habitat, and each trapping session (season) was the repeated measure factor. The F statistics for within-subject factors (and their interactions) were inflated in repeated-measures ANOVA when the sphericity assumption was not met (Von Ende 2001); thus the Greenhouse–Geisser corrected probability was used when interactions were statistically significant. In all cases the normality assumption was tested by the Kolmogorov–Smirnov test, and variance homogeneity was tested by Bartlett's test (Sokal & Rohlf 1981). We had to apply log transformation to the data in order to solve problems with heterogeneity of variances (Underwood 1997).

Results

Composition of sigmodontine rodent assemblages in different environments

During the study period 2537 individuals were captured with a total effort of 85,800 trap nights. The greatest trap success was in shrubland (1381 individuals), followed by forest (735 individuals), peridomestic environments (232 individuals) and pasture (189 individuals). The assemblage was comprised of 11 small rodent species: *Oligoryzomys longicaudatus*, *Abrothrix longipilis*, *A. olivaceus*, *Geoxus valdivianus*, *Loxodontomys micropus*, *Reithrodon auritus*, *Irenomys tarsalis*, *Chelemys macronyx*, *Akodon iniscatus*, *Akodon* sp. and *Mus musculus*. One marsupial, *Dromiciops gliroides*, belonging to the order Microbiotheria, was also captured.

Species–habitat associations

Three species made up 89% of the rodent assemblage: *O. longicaudatus* was the most abundant species captured (62%), followed by *A. longipilis* (14%), and *A. olivaceus* (13%). The other nine species were poorly represented (Table 1). *Oligoryzomys longicaudatus* was most abundant in shrubland and forest habitats followed by *A. longipilis*. In pastures, *O. longicaudatus* was less abundant than *A. olivaceus*; and together with *M. musculus* dominated peridomestic habitats (Table 1). All species except *G. valdivianus*, *I. tarsalis* and *A. iniscatus* showed significant associations with at least one habitat (all $\chi^2 \geq 10.6$, $p \leq 0.014$, $df = 3$). *Oligoryzomys longicaudatus* and *A. longipilis* were associated with shrubland and forest, and to a lesser extent *R. auritus*, *A. olivaceus* and *L. micropus* with shrublands. Moreover, *A. olivaceus* was associated with pastures and *C. macronyx* with forests; *M. musculus* was the only species significantly associated with peridomestic areas.

Table 1. Rodent assemblage composition, expressed as number of individuals by species captured and percentages, by habitats (pooling together seasons and years) in Cholila, Chubut Province, Argentina (spring 2003–spring 2006).

Species	Forest		Shrubland		Pasture		Peridomestic	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
<i>Oligoryzomys longicaudatus</i>	414	66.2	686	69.4	38	31.15	54	30.68
<i>Abrothrix longipilis</i>	115	18.4	151	15.28	7	5.74	8	4.55
<i>Abrothrix olivaceus</i>	59	9.44	103	10.43	50	48.98	17	9.66
<i>Loxodontomys micropus</i>	20	3.20	28	2.83	1	0.82	—	—
<i>Akodon</i> sp.	2	0.32	2	0.20	9	7.38	—	—
<i>Akodon iniscatus</i>	—	—	1	0.10	7	5.74	—	—
<i>Reithrodon auritus</i>	3	0.48	7	0.71	4	3.28	—	—
<i>Mus musculus</i>	1	0.16	1	0.10	5	4.10	97	55.11
<i>Chelemys macronyx</i>	6	0.96	6	0.61	1	0.82	—	—
<i>Irenomys tarsalis</i>	5	0.80	—	—	—	—	—	—
<i>Geoxus valdivianus</i>	—	—	3	0.30	—	—	—	—

Changes in species richness, diversity and evenness of the assemblage

Species richness varied among habitats and seasons, ranging from one to eight species, with shrubland having the highest number of species, followed by forest, and peridomestic habitat. In most seasons, individuals belonging to five or more species were captured in shrubland, and four to five species were most often recorded in forest, whereas only 2–4 and 2–3 species were most frequently captured in pastures and peridomestic areas, respectively (Figure 1). Shrubland, forest and pasture habitats showed high species richness values in summer, decreasing through

spring (Figure 1). The opposite occurred in peridomestic areas, in which the highest richness was registered in spring, autumn and winter (Figure 1). In most seasons, diversity indices were highest for shrubland. For forest, H' was highly variable and highest in summer 2004 and autumn 2005. Pastures and peridomestic areas had low values in general (Figure 2). However, there were seasons when pasture (summer 2004 and autumn 2005) and peridomestic areas (autumn and spring 2005 and autumn 2006) showed higher values (Figure 2). Repeated-measures ANOVA found significant differences in diversity (H') by habitat and by season ($p < 0.001$), after the sphericity test was applied (Table 2).

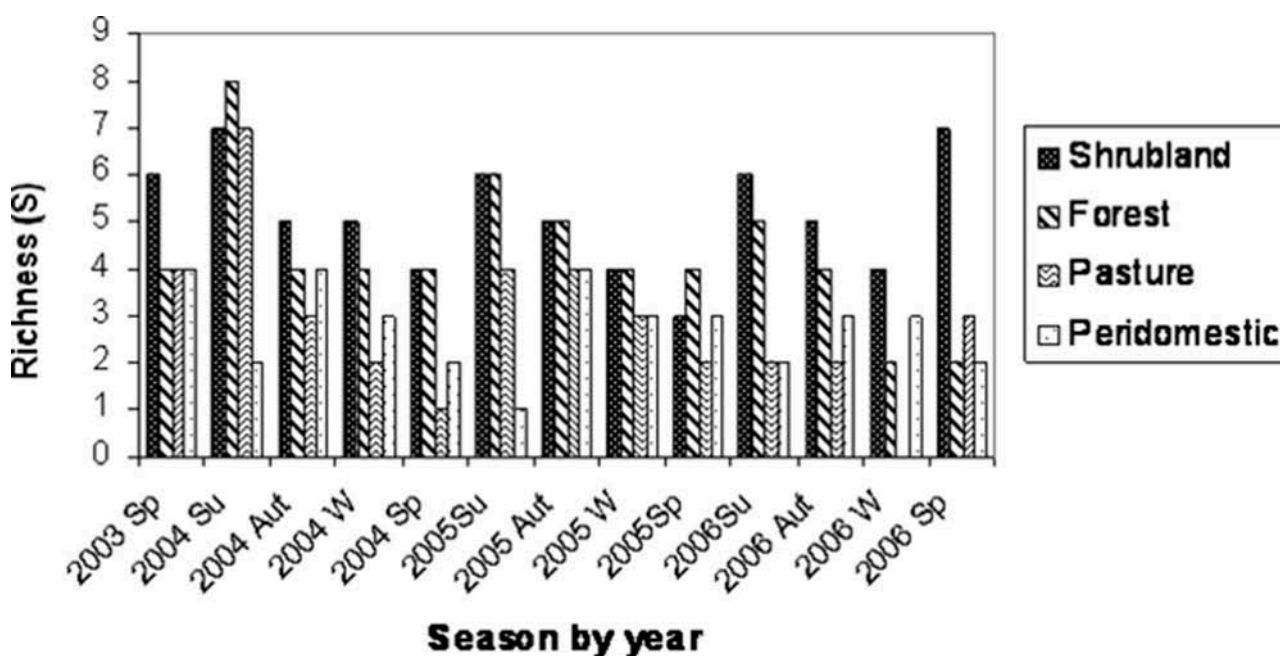


Figure 1. Richness (S) of rodent assemblage by habitat, season and years in Cholila, Chubut Province, Argentina (spring 2003–spring 2006).

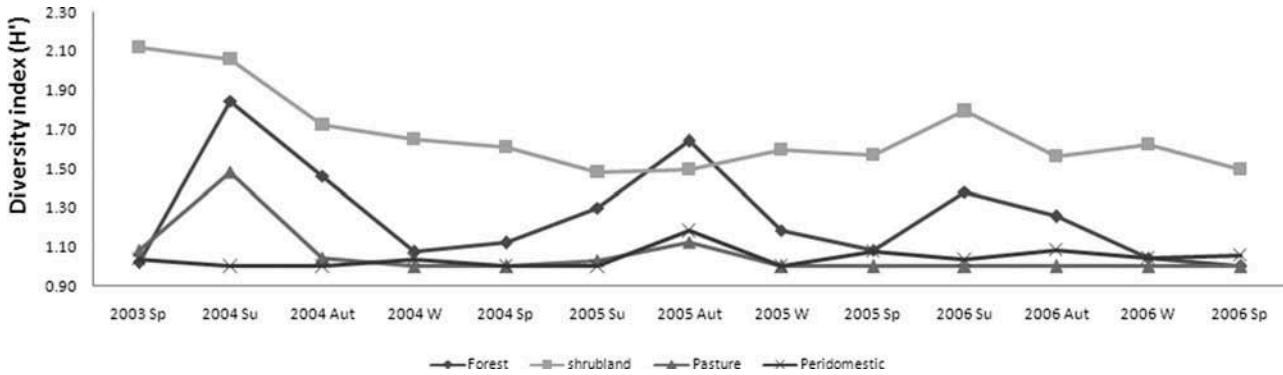


Figure 2. Diversity index (H') of rodent assemblage by habitat, season and years in Cholila, Chubut Province, Argentina (spring 2003–spring 2006).

Table 2. Repeated-measured ANOVA table for assemblage diversity index compared among habitat and seasons of the years (repeated measure factor) in Cholila (spring 2003–spring 2006).

Effect	df	MS	F	Significant difference (p)	Greenhouse-Geisser corrected probability
Habitat (H)	3	2.73	107.31	0.00000	
Error	77	0.025			
Seasons (S)	12	0.150	5.95	0.00000	
H × S	36	0.070	2.77	0.00000	0.00010*
Error	924	0.0253			

Note: MS: mean square.

Therefore temporal and spatial diversity were not independent. The a posteriori (Tukey) test showed no pattern through the study with respect to diversity differences among habitats. However, significant differences were detected between shrublands in spring 2003 and all other habitats ($p < 0.05$). In 2004, shrubland was significantly different from other habitats and

seasons ($p < 0.05$) except for forest and pasture in summer 2004 and for forest in autumn 2005 ($p > 0.05$). Other significant differences were detected between shrubland in summer 2006 and the rest of the habitats ($p < 0.05$) except for forest in summer 2004 and autumn 2005 ($p > 0.05$).

In shrublands, evenness was stable (Figure 3) from spring 2003 to spring 2004, but variable in the other two years. In forest, evenness was relatively stable with minor variation until autumn 2006. In pastures, evenness increased from spring to autumn, with no records in winter. Evenness in peridomestic areas had no distinct pattern.

Discussion

Assemblage composition

The 11 species captured over the course of this study were species expected based on distribution, there were no new records for the study site. The rodent assemblage composition resembles other assemblages in similar sites of Patagonia (Piudo et al. 2005). The

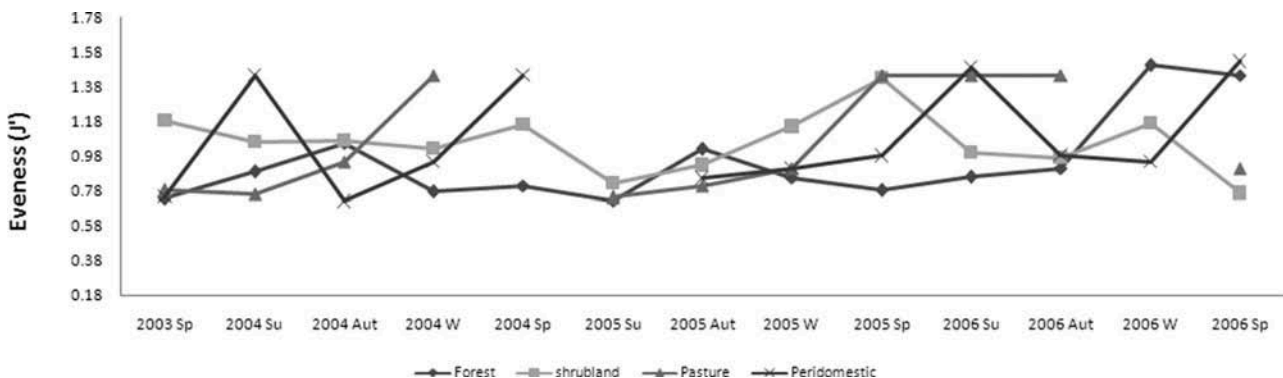


Figure 3. Evenness (J') of rodent assemblage by habitat, season and years in Cholila, Chubut Province, Argentina (spring 2003–spring 2006).

species richness of small terrestrial rodents at our study area was similar to the species richness recorded in the forest–steppe transition zone of other provinces (Monjeau et al. 1997, 2011; Pardiñas et al. 2003; Piudo et al. 2005).

Species richness and diversity per habitat

Differences in species richness and diversity in the rodent assemblage among different habitats of south-western Patagonia appear to be related to the structure and composition of vegetation and to anthropogenic disturbance. However, species richness may also be determined by ecological interactions as well as the evolutionary and biogeographic history of the study area.

The higher diversity of small rodents in forest and shrublands is probably due to the higher complexity of these habitats, whereas the simpler habitats, pastures and peridomestic environments, had few species. Rosenzweig & Winakur (1969) found that differences in richness and diversity in rodent assemblages of two arid regions of Arizona were related to the complexity of the vegetation. Thus, structurally simple habitats such as pastures and peridomestic areas seem to have fewer species. On the other hand, lower species diversity in the rodent assemblage registered in pasture and peridomestic areas could also be due to anthropogenic habitat changes as suggested by other authors (Ostfeld & Keesing 2000a, 2000b; Daszak et al. 2001; Schmidt & Ostfeld 2001).

Specific habitat associations

The association of rodent species with particular habitats is likely the result of environmental differences among habitats. *Oligoryzomys longicaudatus* is known to feed heavily on fruits of *Rosa* spp. in forests and shrublands year-round (Sbriller & Sepúlveda 2007; Polop et al. forthcoming), and Andreo et al. (2012) suggested that shrubland provided this species with both refuge and food resources. Regarding the other rodent species, our results are similar to Pearson (1983) who found *A. longipilis* to be associated mainly with forest and shrubland habitats, and *A. olivaceus* with shrubland and pasture habitats. Meserve (1981) recorded that *A. longipilis* and *A. olivaceus* are primarily insectivorous, although *A. olivaceus* may be characterized as omnivorous because it consumed a wide range of seeds, foliage and arthropods during the year at a study site in Fray Jorge National Park (Chile). The diets of *L. micropus* and *C. macronyx* have not been studied so far. Knowing the trophic niches and which other resources are important for the rodent species of the assemblage would contribute to our understanding

of their association with a particular habitat. We have an ongoing study at the same sites, to identify those factors.

Abundance

Rare species generally require more trapping time to capture. We consider that our sampling design, including sample size, was adequate and that all species had the same likelihood of being captured (Polop 2011; Andreo 2012). In our site this would suggest that *G. valdivianus*, *L. micropus*, *R. auritus*, *I. tarsalis*, *Ch. macronyx*, and *A. iniscatus* are really much rarer than *O. longicaudatus*, *A. longipilis* and *A. olivaceus*. Similar results were recorded by Piudo et al. (2005, 2011). However, in northern, central, and some southern areas of Argentina, abundance of hantavirus host species in rural peridomestic habitats were similar or higher than those in open field habitats (Calderón et al. 1999; Piudo et al. 2005), suggesting higher risk to human exposure to these species in peridomestic settings. We did not find this to be the case in our study; differences may due to the characteristics of peridomestic environments in each study site.

Assemblage variations in richness, diversity and evenness

The variation recorded in both diversity and evenness in all the studied habitats suggests, as proposed by Piudo et al. (2011), that temporal fluctuations in abundance of the three dominant species (*O. longicaudatus*, *A. longipilis* and *A. olivaceus*), especially *O. longicaudatus*, caused the evenness and diversity fluctuations in most habitats. *Oligoryzomys longicaudatus* has a high population growth rate (Polop 2011), thus its populations may increase more rapidly than those of species with lower growth rates. As a consequence, habitats with high proportions of this species tend to have decreased diversity (Huston 1979). Polop (2011) detected a correlation between climatic conditions (spring and summer rainfall and winter minimum temperature) and *O. longicaudatus* abundance that could explain high abundances in this species for the period 2003–2006. Thus, the lack of a pattern along the study period with respect to diversity differences among habitats might be related to the species' response to climatic differences among years, probably acting indirectly through primary productivity, the onset of vegetative growth, and the production of seeds and fruits, thereby affecting food and refuge resources.

On the other hand, natural habitats (forest and shrubland) were generally more stable in evenness than disturbed or anthropic habitats (pasture and

peridomestic) because this index has a direct relation to the abundance of each species, included in the diversity (H') of the assemblage. Thus, this index would show the different dynamic of assemblage due to different processes acting, as dispersal patterns of the species that compose it. When the population of one species increases in abundance, it may reduce the relative abundance of other species populations, without necessarily changing total community abundance, resulting in lower evenness and diversity, as Brady & Slade (2001) proposed for species of rodents that are syntopic in an old-field habitat in northeastern Kansas.

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