Predicting species richness of ectoparasites of wild rodents from the Río de la Plata coastal wetlands, Argentina

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Predicting species richness of ectoparasites of wild rodents from the Río de la Plata coastal wetlands, Argentina

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Abstract
The richness of ectoparasite species associated with Sigmodontinae rodents (Cricetidae) from different sites located in the coastal wetlands of the Río de la Plata in Argentina was predicted by a model with three components: (1) habitat type, considered analogous to rodent species; (2) average ectoparasite species richness on each rodent species, and (3) average number of rodent species parasitized by each ectoparasite species. The model, based on rodent information (number of species and total number of captured rodents) and the environmental gradient, has a reasonably good fit for the observed data as well as independent data from different localities. The model is predictive and robust, and it could be a useful tool for epidemiological and biodiversity management strategies. Furthermore, the model could be adapted to other habitats if a suitable estimate of an environmental gradient is found, and it could be also possible to adapt it to other host taxa.

Keywords Ectoparasites · Rodents · Model · Species richness · Argentinean wetlands

Introduction

Total species richness of free-living individuals at a regional scale (i.e., γ-diversity) is characterized by using a model that combined the mean species richness of local communities (i.e., α-diversity) multiplied by the magnitude of change in species composition between local communities (i.e., β-diversity), usually along an environmental gradient (Whittaker 1967): $\gamma = \alpha \cdot \beta$, where γ-diversity and α-diversity are expressed in terms of number of species, while β-diversity is dimensionless and calculated dividing γ-diversity by α-diversity (Whittaker 1972). However, β-diversity is a complex concept constrained by environmental gradients (Qian et al. 2005) and historical processes (Nekola and White 1999; Qian et al. 2005; Baselga 2010), and linked to structural

patterns of host-parasite food webs as well as metacommunities (Tuomisto 2010).

Schluter and Ricklefs (1993) proposed the following expression for β-diversity: the quotient between the number of different habitats each one inhabited by a local community, R, and the mean number of habitats in which each species is present, b. Then, γ-diversity is $\gamma = \alpha (R/b)$ (Schluter and Ricklefs 1993). This expression has a more direct ecological meaning since it reflects the mean richness of local communities, α; the environmental heterogeneity based on the number of different habitats, R; and an indicator of the average niche breadth of the species, b. If all local communities were inhabited by exclusive species (i.e., $b = 1$), total species richness equals the sum of species richness of all local communities (i.e., $\gamma = \alpha \cdot R$), and all variation in species composition among communities will be caused by species replacement. In the absence of species replacement across habitats, all variation in species composition is due to differences in species richness (Ulrich and Almeida-Neto 2012), and in this case the average niche breadth of the species, b, is greater than one.

In a study on fleas parasitizing different rodent species, the population of each rodent species was considered analogous to a habitat type, and individual hosts were considered analogous to different patches of the same habitat type (Krasnov et al. 2003). Rodent species may have qualitative and quantitative differences: the greater the population host density, the

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greater the probability that parasite individuals will contact a host (May and Anderson 1978). In this context, and considering similar environmental conditions, it is expected that a local rodent population with a great density will exhibit greater α-diversity than another local host population with lower density.

The ectoparasites of sigmodontine rodents (Cricetidae) belong to different arthropod taxa which differ in their biology (Marshall 1981). In previous studies, we recorded 25 ectoparasites (lice, fleas, mites, and ticks) from four sigmodontine species captured at six sites of the Río de la Plata coastal wetlands. In addition, independent studies provided information on ectoparasites from rodents from different localities of Buenos Aires Province (Castro et al. 1987; Nava et al. 2003; Colombo et al. 2013). Our objective is to develop a model to predict the richness of ectoparasites of sigmodontines at each site based on (1) the total number of captured rodents, (2) the specific richness of the rodents, and (3) an indicator of the environmental gradient.

Materials and methods

Study area

The study area is located in a wetland on the coastal plain of the Río de la Plata and comprises a 2–9-km wide area with a flat to flat-concave relief. The phreatic water level is at less than a meter below the surface and can rise at lower areas during rainy periods creating several wetlands. Much of the area is between 0 and 3 m and it lies between a slight elevation along the coastal bank and a ravine sub-parallel to the coastline, so the drainage network is poorly developed. The area is subject to frequent flooding, especially with easterly-southeasterly winds, causing the river to rise, process known as sudestada. The sudestada events occur more frequently between March and October and have variable effects depending on the intensity and persistence of the wind and the simultaneous occurrence with the maximum height of the tidal wave. Rain is less important and affects the persistence of the flood (Hurtado et al. 2006). During 1951–2000, there were 298 sudestada events, with an average of almost six events per year (Servicio de Hidrografía Naval, Argentina). The water level during the sudestadas varied between 1.64 and 3.04 m, and 80% of the events lasted 60 h or less. Frequency and intensity of floods were identified as the environmental gradient that explains the presence of the main vegetation units, despite the small topographic differences among sites (Dascanio et al. 1996). The common names for these units are Matorral Ribereño (coastal scrubland), Pajonal (reeds), and Selva Marginal (riverside forest), and their floristic-physiognomic characterization and spatial location were determined by Cabrera (1949). See Supplementary 1 for the description of habitat types.

Capturing rodents and collecting ectoparasites

Rodents were captured at six sites with the following codification, geographic location, and vegetation units: the PC site, located in the Municipal Reserve of Punta Colorada (34°45′S, 58°5′W, Berazategui), in the Selva Marginal area. PLV and PLN sites, located in the Integral Natural Reserve of Punta Lara (34°47′S, 58°1′W, Ensenada): PLV, in the Selva Marginal; PLN, in the Pajonal. The site BB, in Balneario Bagliardi (34°53′S, 57°52′W, Berisso), in Matorral Ribereño area. The site PB, in the resort of Palo Blanco (34°52′S, 57°52′ W, Berisso), in the area of Matorral Ribereño; and the site LB, in La Balandra resort (34°56′S, 57°45′W, Berisso), in Pajonal (Fig. 1). In each sampling, rodents were captured alive using Shermann traps baited with oats and arranged in two parallel grids, 5 m apart from each other. Traps remained in the camp overnight. Ectoparasites were collected by brushing the fur of the hosts, preserved in vials with alcohol 96%, and prepared following conventional techniques for their identification at optic microscope (Lareschi et al. 2003).

### Site elevation as an indicator of the environmental gradient

The topographic elevation of the kth site, $E_{(k)}$, was considered as an indicator of the environmental gradient given by the frequency and intensity of floods and by the shelter and food resources offered by the different vegetation units. To estimate the elevation of each capture site, we measured the height between the central area in which the traps were set out and the surface of the Río de la Plata or adjacent areas depending on each site (Santiago River or drainage channels nearby). The river behaves as a micromareal system characterized by amplitudes generally smaller than 1 m (Kokot and Codignotto 2005), and at the same time we measured the site's elevation, we recorded the height of the river at the La Plata port relative to the zero level of the tide gauge of the mareograph (information provided by the Servicio de Hidrografía Naval Puerto La Plata). The addition of these two values provided the site's elevation relative to 0 m.

The model

Inspired by the Schluter and Ricklefs (1993) model, we predicted the ectoparasite species richness in the kth site, $S_{(k)}$, by means of the number of rodent species, i.e., the number of habitat types, $R_{(k)}$; the mean number of ectoparasite species per host species, i.e., the average species richness per habitat type, $\alpha_{(k)}$; and the mean number of rodent species in which was registered each ectoparasite species, i.e., the average

Fig. 1 The study area located at a wetland on the coastal plain of the Río de la Plata, Buenos aires Province, Argentina. The sampling sites: PC = Municipal Reserve of Punta Colorada (Berazategui county), PLV and PLN = Integral Natural Reserve of Punta Lara (Ensenada county), BB = Balneario Bagliardi (Berisso county), PB = Palo Blanco resort (Berisso county), LB = La Balandra resort (Berisso county)
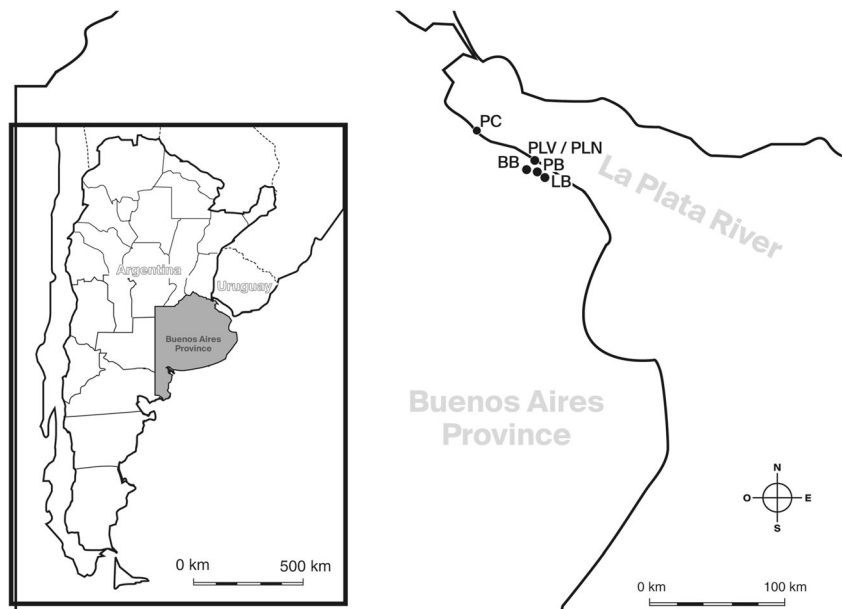
niche breadth of the ectoparasite species, $b_{(k)}$. In turn, $\alpha_{(k)}$ was estimated by means of the logarithmic accumulation curve (Soberón and Llorente 1993) of ectoparasite richness as a function of sample size whose slope was expressed in terms of the elevation of the site $E_{(k)}$, and $b_{(k)}$ in terms of the proportion of ectoparasites "using" $r = 1,..,R_{(k)}$ rodent. Symbolically, $S_{(k)} = R_{(k)} \cdot f[n_{(k)}, E_{(k)}]/g[R_{(k)}]$, where f represents the expression that estimates $\alpha_{(k)}$ and g represents the expression that estimates $b_{(k)}$. The total number of rodent species at the kth site was symbolized as $R_{(k)}$. The mean number of ectoparasite species per host species, $\alpha_{(k)}$, was estimated in two ways: directly from field data and indirectly as a function of the number of captured rodents and the elevation of the site.

The direct estimation of $\alpha_{(k)}$

We consider the presence-absence dichotomy on a given host. In the kth site, we registered the ectoparasite species richness in the rth rodent species, $S_{(r, k)}$, and then calculated $\alpha_{(k)}$ as $\alpha_{(k)} = \sum_{r = 1, 4} S_{(r, k)}/R_{(k)}$, where $R_{(k)}$ represents the total number of rodent species in the site.

The indirect estimation of $\alpha_{(k)}$

For the rth host species and the kth site, we estimated the richness of ectoparasite species, $\alpha_{(r, k)}$, as a function of host density, $n_{(r, k)}$, by means of the logarithmic model (Soberón and Llorente 1993) with a previous randomization of the samples, i.e., captured rodents. The model was as follows: $\alpha_{(r, k)} = c_{(r, k)} + m_{(r, k)} \cdot \text{Ln}[n_{(r, k)}]$, where $c_{(r, k)}$ represents the richness of ectoparasites when only one rodent was captured, and $m_{(r, k)}$ represents the increase rate in richness according to the increase in the number of rodents. The logarithmic model is a non-asymptotic model, and in our case for a large number of rodents (i.e., $n_{(r, k)} > 200$) the maximum possible ectoparasite richness value was considered equal to the maximum registered at all sites (see above). Both coefficients, $c_{(r, k)}$ and $m_{(r, k)}$, were adjusted using numeric techniques with the Solver tool from the Excel de Microsoft® software.

In order to generate a function as generalized as possible, different host species at the kth site were considered as replicates: the average number of individuals per rodent irrespective of the rodent species was calculated as $n(k) = [\sum r = 1,..4\, n(r, k)]/R(k)$, and both coefficients are only function of the site and symbolized as $c_{(k)}$ and $m_{(k)}$. To introduce explicitly the effect of the environmental gradient, we plotted both coefficients as the dependent variable, on the elevation of the corresponding site as the independent variable, and selected the linear regression equations, $c_{(k)} = A_1 + M_1 \cdot E_{(k)}$, and $m_{(k)} = A_2 + M_2 \cdot E_{(k)}$, with the highest coefficient of determination. If the regression was significant, we then replaced the corresponding coefficient in the logarithmic model. Particularly, if $M_2 > 0$, the slope of the logarithmic model will increase as the elevation increases, and given the same number of rodents, the ectoparasite richness will be higher in more elevated sites.

The mean number of rodent species on which each ectoparasite species was recorded, $b_{(k)}$

A highly host-specific parasite exploits a single host species whereas host-opportunistic parasites exploit several different host species. Consequently, from an ecological perspective, host specificity represents a component of the breadth of a parasite's ecological niche, i.e., the one reflecting the diversity of resources it uses (Futuyma and Moreno 1988; Krasnov et al. 2011). In our model, b represents the mean number of

rodent species that are a resource for an ectoparasite species. Coefficient b takes values in the interval $[1, R]$, and as mentioned before, if $b = 1$, all ectoparasites recorded are host specific, whereas if $b = R$, all ectoparasites are host generalists. However, rodent's ectoparasites exhibit a different range of hosts: lice and some mites are host specific; ticks, chiggers, and several fleas are generalists; whereas other parasites are associated to two or three rodent species. So, we estimated b based on the host range of ectoparasites.

The direct estimation of $b_{(k)}$

In the kth site, we recorded the total number of rodent species in which the jth ectoparasite species was recorded, $r_{(j, k)}$, and calculated: $b_{(k)} = [\sum_{j = 1,...,S(k)} r_{(j, k)}]/S_{(k,)}$.

The indirect estimation of $b_{(k)}$

The direct estimate of $b_{(k)}$ presumes to know the ectoparasite richness $S_{(k)}$, a value that we wish to estimate for a new site by using the model. Since closely related host species may harbor similar parasite faunas (Muñoz et al. 2006), we suppose that different assemblages of rodents inhabiting temperate regions would exhibit a similar or the same proportion of specific, moderately generalist or extreme generalist ectoparasite species, independently of the identity of those species.

So, in the kth site, we estimate $j_{(r, k)}$, the proportion of ectoparasite species that were collected from $r = 1,..,R_{(k)}$ rodent species and estimated $b_{(k)}$ as: $b_{(k)} = \sum_{r = 1,...,R(k)} [j_{(r, k)} \cdot r]$. Sites PB and BB allowed us to calculate $b_{(k)}$ when $R_{(k)} = 2$. Sites LB, PLN, PLV, and PC and all sites considered together (coded T6) allowed us to calculate $b_{(k)}$ when $R_{(k)} = 4$. For other sites where $R_{(k)} > 4$, the fourth term of the summation is calculated as: $j_{(4, k)} \cdot (4 + R_{(k)})/2$, and $b_{(k)}$ calculates as: $b_{(k)} = \sum_{r = 1,..., 3} [j_{(r, k)} \cdot r] + [j_{(4, k)} \cdot (4 + R_{(k)})/2]$.

Increasing the number of rodents increases the probability of recording ectoparasite species with low prevalence, so we regressed $j_{(r, k)}$ for $r = 1,..,4$ on the mean number of individuals per rodent species, $n_{(k)}$. Different sites were considered as replicates. Sites LB, PLN, PLV, PC, and T6 (four rodent species captured) were used. If the regressions were significant, they were used to replace the corresponding $j_{(r, k)}$.

Statistical analysis

The total number of rodents and the ectoparasite species richness as predictor variables at each site were analyzed in each case by two-way ANOVA without replication, using the six sites and the four rodent species and predictive variables. We used Levene's test to assess equality of variances and the Shapiro-Wilk W test for normality, in the software StatSoft® Statistica. Values were compared using Duncan's multiple comparisons test. The null hypothesis stated that possible differences in the total number of rodents and ectoparasite richness did not differ from what was expected only by chance. We calculated regression equations using the least square method and chose those with the highest determination coefficient, r^2. To validate the model, we compared ectoparasite species richness at the different sites with a χ^2 test. For all tests, $p < 0.05$ were considered significant.

Capturability of the rodents was calculated taking into account the accumulated number of traps at each site as $100 \times$ (total number of rodents captured)/(total number of traps). We also calculate the prevalence $100 \times$ (number of hosts parasitized/number of hosts examined); the ectoparasite richness on the jth rodent species at the kth site, $\alpha_{(j, k)}$; and the total richness of ectoparasites at the kth site, $S_{(k)}$, as well as the incidence (number of sites where the ectoparasite was recorded) (Bush et al. 1997).

Results

The rodent-ectoparasite system

At the six sites of the Río de la Plata wetlands, 510 sigmodontines of the following species were captured: *Scapteromys aquaticus* Thomas, *Oxymycterus rufus* Thomas, *Oligoryzomys flavescens* (Waterhouse), *Akodon azarae* (Fischer), *Deltamys kempi* Thomas, and *Holochilus brasiliensis* (Demarest) (Sigmodontinae), as well as five individuals of *Rattus* sp. (Murinae) (Table 1). The first four species were dominant and represented 98.83% of the total, while the last two were represented by six individuals and were not considered in the study. Each rodent species was considered analogous to a "habitat type" characterized by its preference for flooded areas, diet, and individual size (i.e., patch size). *Akodon azarae* and *O. flavescens* are small rodents (19 and 19.5 g, respectively) and mostly herbivores, whereas *O. rufus* and *S. aquaticus* are larger in size (80 and 93 g, respectively) and feed on insects, crustaceous, and other invertebrates. Regarding the tolerance to water, *S. aquaticus* and *A. azarae* represent the extremes: the former is a good swimmer and was only captured in flooded areas; the latter is a bad swimmer and prefers drier areas. *Oligoryzomys flavescens* is also a good swimmer and it is found as well in areas with crops. *Akodon azarae* and *O. rufus* prefer drier areas but the first one had a wider distribution and it is also found in cultivated areas (Cueto and Piantanida 1995; Gómez Villafañe et al. 2012).

From the four species of sigmodontines, 25 species of ectoparasites were collected and identified as *Hoplopleura scapteromydis* Ronderos, *Hoplopleura fonsecai* Werneck, *Hoplopleura aitkeni* Johnson, and *Hoplopleura travassosi* Werneck (Insecta, Phthiraptera); *Polygenis atopus* (Jordan and Rothschild), *Polygenis axius axius* (Jordan and Rothschild), *Polygenis bohlsi* (Wagner), *Polygenis massoiai*

Table 1 Number of captured rodents, number of traps, and number of rodent species and ectoparasites recorded at each site and at all six sites all together (T6). At site BB, we only captured one *O. rufus* individual that was not parasitized and was not considered in the analysis (marked with a parenthesis)

Rodents/Sites	PC	PLV	PLN	LB	BB	PB	T6	Maximum number of ectoparasite species
Scapteromys aquaticus	11	64	9	44	39	38	205	15
Oxymycterus rufus	30	81	18	18	(1)	0	148	15
Oligoryzomys flavescens	10	62	15	7	0	10	98	15
Akodon azarae	16	22	6	9	6	0	59	10
Total number of rodents, N	67	229	48	78	45	48	510	25
Number of rodent species	4	4	4	4	2	2	4	
Total number of traps	159	570	608	479	547	430	2793	
Capturability (%)	42.14	40.18	7.89	16.28	8.23	11.16	18.26	

Del Ponte, *Polygenis pradoi* (Wagner), *Polygenis puelche* Del Ponte, *Polygenis platensis* (Jordan and Rothschild), *Polygenis rimatus* (Jordan), *Polygenis tripus* (Jordan), *Polygenis frustratus* Johnson, and *Polygenis* sp. (Insecta, Siphonaptera); *Laelaps manguinhosi* Fonseca, *Laelaps paulistanensis* Fonseca, *Androlaelaps fahrenholzi* (Berlese), *Androlaelaps* cf. *rotundus* (Fonseca), *Mysolaelaps microspinosus* Fonseca, and *Gigantolaelaps wolffsohni* Oudemans (Acari, Mesostigmata, Laelapidae); *Ixodes loricatus* Neumann (Acari, Ixodida, Ixodidae); *Ornithonyssus bacoti* (Hirst) (Acari, Mesostigmata, Macronyssidae), and *Eutrombicula* sp. (Oudemans) (Acari, Trombidiformes, Trombiculidae).

Site elevation as an indicator of the environmental gradient and captured rodents

Site elevation, $E_{(k)}$, was positively correlated with ectoparasite species richness, $S_{(k)}$ ($r = 0.926$; $t_{(5\ df)} = 4.904$; $p = 0.008$), and with the number of rodent species, $R_{(k)}$ ($r = 0.966$; $t_{(5\ df)} = 7.514$; $p = 0.002$). The topographic levels for each site on the coastal wetland of the Río de la Plata, as well as the mean river level (0.75 m), high tide (1.52 m), and the mean level of river floods (2.48 m), are shown in Fig. 2.

The total number of captured rodents varied among sites: $F_{(5, 15\ df)} = 52.966$ ($p < 0.0003$), but not between rodent species: $F_{(3, 15\ df)} = 6.054$ ($p = 0.059$). The largest number of rodents was captured at PLV ($p < 0.01$, Duncan test). At sites PLV, PC, PLN, and LB, the four host species were captured: $R_{(PLV)} = (R_{(PC)} = (R_{(PLN)} = (R_{(LB)} = 4)))$. *Scapteromys aquaticus* was dominant but represents less than 60% of the total of rodents captured. At PB and BB, we captured two rodent species ($R_{(PB)} = (R_{(BB)} = 2)$), and *S. aquaticus* was dominant (89.7% at PB, and 73.2% at BB). The capturability in each site was PLV = 43.21%, PC = 42.14%, LB = 16.28%, PB = 10%, BB = 8.41%, and PLN = 6.91%. The highest capturability values were recorded at PC and PLV in the Selva Marginal (Table 1). *Akodon azarae* showed the lowest ectoparasite species richness ($p = 0.0144$, Duncan test).

The capturability, presence of rodent species, and the relative dominance of *S. aquaticus* allow us to group the sites in the following way: at one end PC and PLV (capturability > 40%, all four rodent species present, and relative abundance of *S. aquaticus* < 30%), at the other end PB and BB (capturability < 20%, two rodent species present, and relative abundance of *S. aquaticus* > 80%), and in and intermediate position LB and PLN (capturability < 20%, presence of all four rodent species and relative abundance of *S. aquaticus* between 20 and 60%).

Ectoparasites: host range, incidence, prevalence, and species richness at each site

Ectoparasite species richness varied among sites, $F_{(5, 15\ df)} = 9.735$ ($p < 0.0003$), and rodent species, $F_{(3, 15\ df)} = 3.363$ ($p < 0.047$). Considering the six sites together, five species of ectoparasites (20% of the total) collected from the four rodent species were considered "generalists"; four (16% of the total) were collected from three rodents, and six (24% of the total) from two rodents, and all of them were considered "moderately generalists." Ten (40% of the total) were recorded on a single rodent species and were considered "specialists." Regarding the presence of ectoparasites at the different sites, four species (16% of the total) had the highest incidence: they were captured at all six sites. Eight species (32% of the total) were recorded at five sites, one species (4% of the total) was recorded at four sites, four species (16% of the total) were recorded at three and two sites, and eight species (32% of the total) showed the lowest incidence and were captured at a single site (Table 2).

In addition to differences in host range and incidence, ectoparasites showed differences in their prevalence. Prevalence of the 25 ectoparasite species identified considering all rodent species and sites together is shown in Fig. 3. Values greater than 40% were recorded in two generalist mites: *L. manguinhosi* (53.24%) and *A. fahrenholzi* (46.30%), and in

Fig. 2 Topographic levels for each sampling site at the coastal wetland of the Río de la Plata, Buenos Aires Province, Argentina. Average elevation of sampling sites compared to level 0 at the La Plata Port, mean river level, mean daily high tide level, and mean river floods due to the "sudestadas" (with an average frequency of six per year)
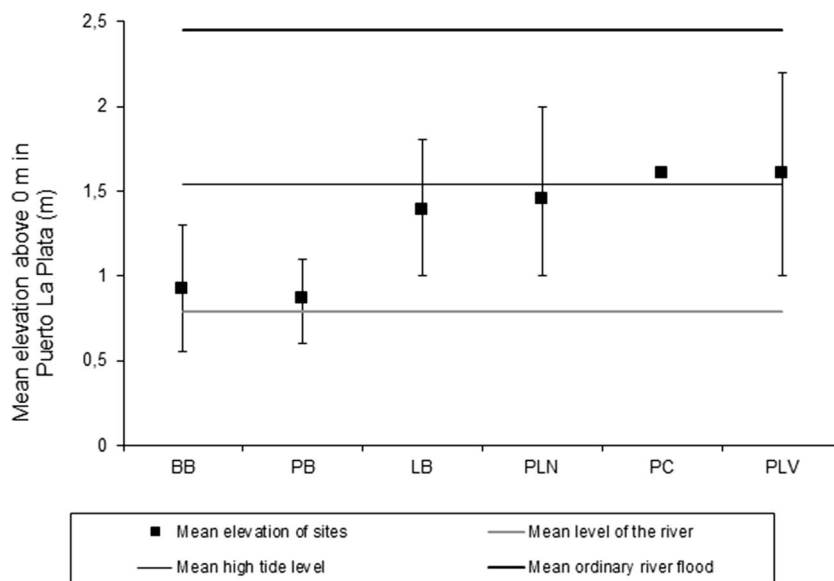
four specific ectoparasites, the mites *M. microspinosus* (79.05%) and the lice *H. travassosi* (75.17%), *H. scapteromydis* (55.85%), and *H. aitkeni* (40.85%). There were ten ectoparasite species with prevalence lower than 5%: nine fleas (four of which were recorded on a single rodent species) and the louse *H. fonsecai* (Fig. 3). For each ectoparasite species, we also considered the percentage of rodents in which it was recorded relative to the total number of rodents captured at all six sites. Twelve ectoparasite species showed values lower than 5%, which means that almost half of the ectoparasite species richness was recorded in only 24 or less rodents. Taking into account the total number of rodents captured in the six sites, S (T6), the species richness of ectoparasites, was greater than the value for any site when considered separately (Table 2).

At sites with lower ectoparasite richness, species composition almost always represented a subsample of the richness at PLV, as well as at all sites together. The highest species richness recorded at the kth site was at PLV ($S_{(PLV)} = 20$) and represented 80% of the total richness at all six sites, and PLV was the site where the highest number of rodents was captured. In the remaining sites, the species richness, and the percentage of this represents of the species richness considering the six sites altogether (S6), was $S_{(PC)} = 16$ (64%), $S_{(PLN)} = 16$ (64%), $S_{(LB)} = 14$ (56%), $S_{(BB)} = 11$ (44%), and $S_{(PB)} = 9$ (36%). The lower ectoparasite species richness at sites BB and PB is in accordance with the fact that only two host species were captured at those sites. As with rodents, ectoparasites allowed grouping sites in a similar way: the highest richness was recorded at PLV ($S_{(PLV)} = 20$) and the lowest at BB and PB ($S_{(BB)} = 11$ and $S_{(PB)} = 9$), whereas PC, PLN, and LB showed intermediate values (Tables 1 and 2).

Ectoparasite species richness per host species

The direct estimation of $\alpha_{(k)}$

In each one of the six sites, the mean ectoparasite species richness per rodent species, $\alpha_{(k)}$, estimated directly from field data are shown in Table 2. As before, this coefficient allowed grouping sites in a similar way: the greatest value was recorded at PLV ($\alpha_{(PLV)} = 11.25$) and the lowest at BB and PB ($\alpha_{(BB)} = 5.5$ and $\alpha_{(PB)} = 5.5$), whereas PC, PLN, and LB showed intermediate values. Considering all six sites together (T6) for a greater number of rodents to be used in the estimation, the average ectoparasite species richness per rodent species was $\alpha_{(T6)} = 13.50$ (SD = 2.38).

The indirect estimation of $\alpha_{(k)}$

Concerning host density, the logarithmic model that relates the ectoparasite species richness on the rth host species at the kth site, $\alpha_{(r, k)}$, as a function of the number of individuals per rodent species is shown in Figs. 4, 5, 6, and 7. In general, for the same number of captured individuals of each rodent species, $\alpha_{(r, k)}$ was higher in sites with higher elevation. The regression equation that relates the ordinate (i.e., richness of ectoparasites when only one rodent was captured, $c_{(k)}$) with the elevation of the sites was not significant ($t_{(15\ df)} = 0.812$, $p = 0.431$) and the average value, independent of the site, was $c = 2.53$ (SD = 0.90). The regression equation that relates the slope of the logarithmic model, $m_{(k)}$, with the elevation of the site, $E_{(k)}$, was $m_{(k)} = -0.0234 + 1.2604 \cdot E_{(k)}$ ($F_{(1,\ 19\ df)} = 11.218$, $p = 0.004$). However, the intersection ($A_2 = -0.0234$) did not differ significantly from 0 ($t_{(19\ df)} = -0.044$,

Table 2 Ectoparasite species recorded on each rodent species at each site and at the six sites all together (T6). Sites were ordered from highest to lowest ectoparasite species richness, and ectoparasite species were ordered from highest to lowest incidence. The letters in each box/cell indicate the presence of the ectoparasite on a rodent species: *SA*, *S. aquaticus*; *OR*, *O. rufus*; *AA*, *A. azarae*; and *OF*, *O. flavescens*. In the last four rows we show the average number of host species on which each ectoparasite was recorded, $b_{(k)}$; the average number of ectoparasite species on each host species, $\alpha_{(k)}$; in parenthesis and separated by a dash the richness values $\alpha_{(k, Max)}$ and $\alpha_{(k, min)}$; and the number of host species, $R_{(k)}$ (SD represents the standard deviations). The values shown in parenthesis below the species richness recorded at the kth site, $S_{(k)}$, represent the percentage that this value represents in relation to the ectoparasite species richness considering all sites together (next to last column). *SI*, species incidence

Ectoparasites/ sites	PC	PLV	PLN	LB	BB	PB	T6	Si
O. bacoti	SA-OR-OF	SA-OR-AA-OF	SA-OR	SA-OR	SA	SA	SA-OR-AA-OF	6
A. fahrenholzi	SA-OR-AA	SA-OR-AA-OF	SA-OR-AA-OF	SA-OR-AA-OF	SA	SA	SA-OR-AA-OF	6
L. manguinhosi	SA-OR-OF	SA-OR-OF	SA-OR-OF	SA-OF	SA	SA-OF	SA-OR-OF	6
Eutrombicula sp.	SA-OR	SA-OR-AA-OF	SA-OR-AA	SA-OR-AA	SA	SA-OF	SA-OR-AA-OF	6
A. cf. *rotundus*	AA	SA-OR-AA-OF	OR-AA	AA	AA		SA-OR-AA-OF	5
I. loricatus	SA-AA-OF	SA-OR-AA-OF	SA-OR-AA	SA-OR-AA	AA		SA-OR-AA-OF	5
L. paulistanensis	OR-OF	SA-AA-OF	OF	OF		OF	SA-AA-OF	5
G. wolffshoni	OF	SA-OF	OF	OF		OF	SA- OF	5
M. microspinosus	OF	OF	OF	OF		OF	OF	5
H. scapteromydis		SA	SA	SA	SA	SA	SA	5
H. aitkeni	AA	AA	AA	AA	AA		AA	5
H. travassosi	OF	OF	OF	OF		OF	OF	5
P. atopus	SA-OF		SA-OF	SA-OR-OF	SA		SA-OR-OF	4
P. axius			OR	SA-OR	SA		SA-OR	3
P. massoiai	OR	SA-OR	SA-OR				SA-OR	3
P. bohlsi		SA-OF			SA		SA-OF	2
P. rimatus		OR					OR	1
Polygenis sp.			AA				AA	1
H. fonsecai	OR						OR	1
P. axius axius		SA-AA-OF					SA-AA-OF	1
P. pradoi		OR					OR	1
P. puelche		OR					OR	1
P. platensis		SA					SA	1
P. tripus		OR-AA					OR-AA	1
P. frustratus	OR-OF						OR-OF	1
$S_{(k)}$	15 (60%)	20 (80%)	16 (64%)	14 (56%)	11 (44%)	9 (36%)	$S = 25$	
$\alpha_{(k)}$	6.75 [9–4] SD = 2.217	11.25 [13–9] SD = 1.708	7.25 [8–6] SD = 0.96	6.5 [8–5] SD = 1.29	5.5 [8–3] SD = 3.536	5.5 [6–5] SD = 0.707	$\alpha = 13.50$	
$b_{(k)}$	1.80 SD = 0.862	2.25 SD = 1.25	1.81 SD = 0.98	1.857 SD = 1.027	1.00 SD = 0	1.222 SD = 0.441	$b_{(4)} = 2.16$	
$R_{(k)}$	4	4	4	4	2	2	$R = 4$	
$S_{(k)} = R_{(k)} \alpha_{(k)}/b_{(k)}$	15.12	19.71	13.01	14.23	7.44	7.28	25	

$p = 0.965$). So, the indirect estimations of $\alpha_{(k)}$ which are presented in Table 4 were done with the following expression: $\alpha_{(k)} = 2.53 + [1.2604 \cdot E_{(k)}] \cdot \text{Ln} [n_{(k)}]$.

Mean number of ectoparasite species recorded on each rodent species, $b_{(k)}$

The direct estimation of $b_{(k)}$

Values of $b_{(k)}$ directly estimated for the six sites as well as for all sites considered together are shown in Table 2. The greatest value was found at site PLV ($b_{(PLV)} = 2.25$) where each ectoparasite "parasitized" on average more than two rodent species of the four present and the site showed the highest elevation. The lowest values were recorded at sites with lower

elevation, $E_{(PB)} = 0.87$ m and $E_{(BB)} = 0.92$ m, where each ectoparasite "used" in average almost one rodent species ($b_{(BB)} = 1$, $b_{(PB)} = 1.22$) of the two available, showing in PB they acted as specialists. The remaining sites showed intermediate elevation values as well as coefficient b (Table 2).

The indirect estimation of $b_{(k)}$

For the indirect estimation of $b_{(k)}$, in sites PB and BB, where $R_{(k)} = 2$, the average proportion of ectoparasites collected from one or two rodent species were, respectively, $j_{(1)} = 0.89$, and $j_{(2)} = 0.11$ and $b_{(k)} = 1.11$. In the sites LB, PLN, PLV, PC, and T6 where $R_{(k)} = 4$, the average proportion of ectoparasites collected only from $r = 1$ or more rodent species was not significant when regressed on the mean number of individuals per rodent species: for $j_{(1)}$ ($t_{(4\ df)} = -2.57$, $p = 0.083$), for $j_{(2)}$ ($t_{(4}$

Fig. 3 Prevalence of each ectoparasite species considering all host species and sites together
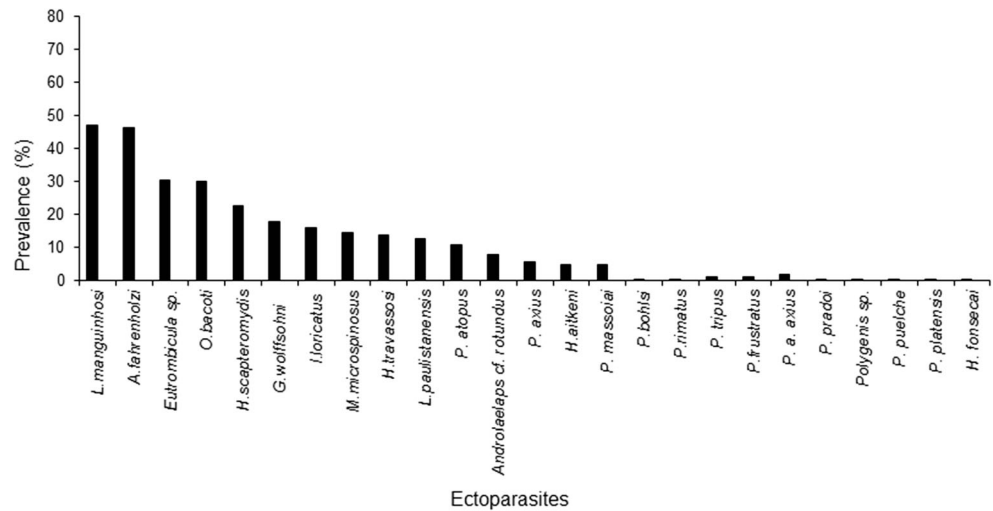
$_{df)} = -0.29$, $p = 0.79$), for $j_{(3)}$ ($t_{(4\ df)} = -1.39$, $p = 0.26$), and for $j_{(4)}$ ($t_{(4\ df)} = 1.84$, $p = 0.16$). So, the average proportions were considered independent from rodent density: $j_{(1)} = 0.40$, $j_{(2)} = 0.24$, $j_{(3)} = 0.16$, and $j_{(4)} = 0.20$ and coefficient b was $b_{(T6)} = 2.16$ (SD = 1.179).

Model validation

The model with which we calculated the ectoparasite richness for the kth site, $S_{(k,\ cal)}$, was $S_{(k,\ cal)} = R_{(k)} \cdot [2.53 + (1.2604 \cdot E_{(k)}) \cdot \mathrm{Ln}\ (n_{(k)})/[\sum_{r=1,..,4}\ (j_{(r)} \cdot r)]$, where the terms between square brackets in the numerator represent $\alpha_{(k)}$, and those in the denominator, represent $b_{(k)}$.

In order to perform a rigorous validation, the calculated values and the field-observed values have to be completely independent. Thus, we used information of three different studies: (1) from localities of Ramallo and San Nicolás in the Buenos Aires Province, presented as a single site (Nava et al. 2003), coded R-SN; (2) from Otamendi in Campana county, Buenos Aires Province (Colombo et al. 2013), and coded by us: OT; (3) a compilation of information from sigmodontine and murine rodents from different localities of the Buenos Aires Province (Castro et al. 1987), which we subdivided in two assemblies—A11, from rodents captured in sites located in the "rolling pampa," "pampa arenosa," and "pampa interserrana" regions of the Buenos Aires Province sensu Gandini (2011), which are far from wetlands and not affected by the environmental gradient characterized in our study; and A5, from rodents captured mainly on sites of the wetland of the Paraná River delta. Concerning A11, despite the localities were in different geographic regions of the Buenos Aires Province, the habitat outside urban areas was

Fig. 4 The logarithmic model that relates the ectoparasite species richness on *Scapteromys aquaticus* at the kth site
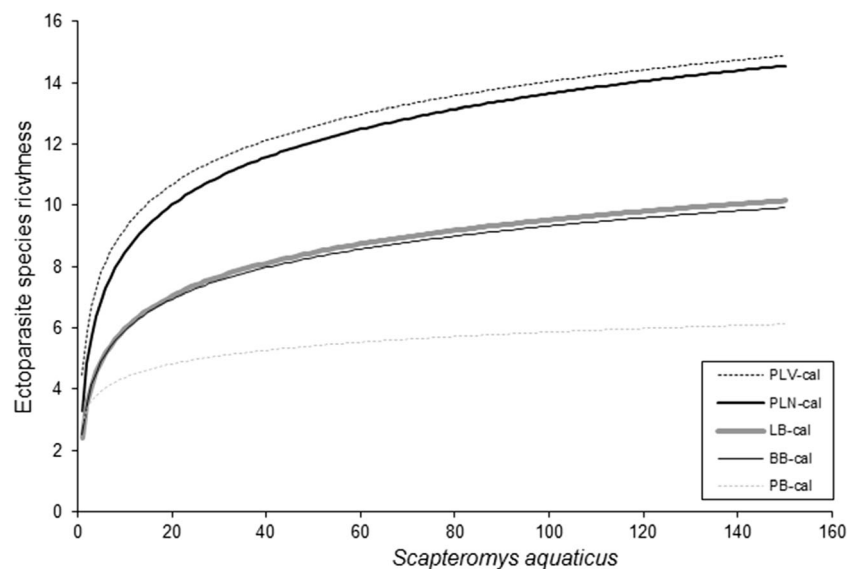
Fig. 5 The logarithmic model that relates the ectoparasite species richness on *Oxymycterus rufus* at the *k*th site
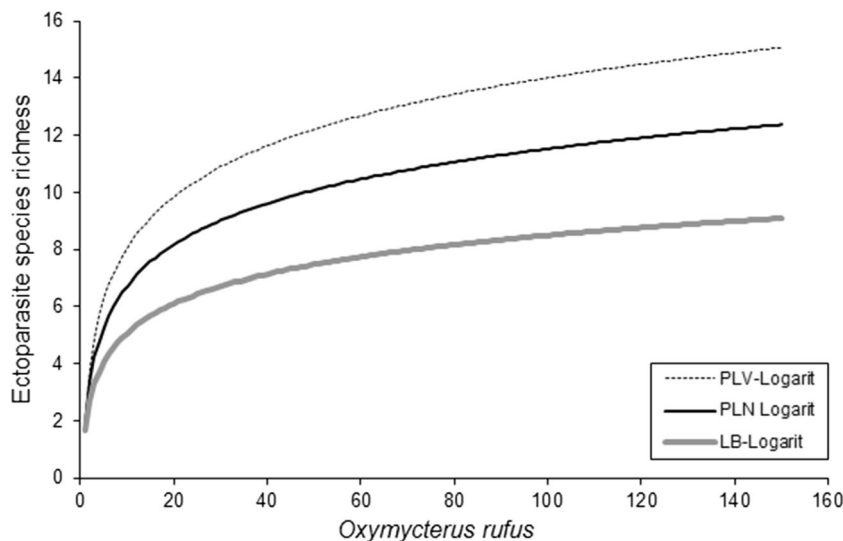
homogenized by agriculture and livestock. Details are presented at Supplementary 2.

The R-SN site
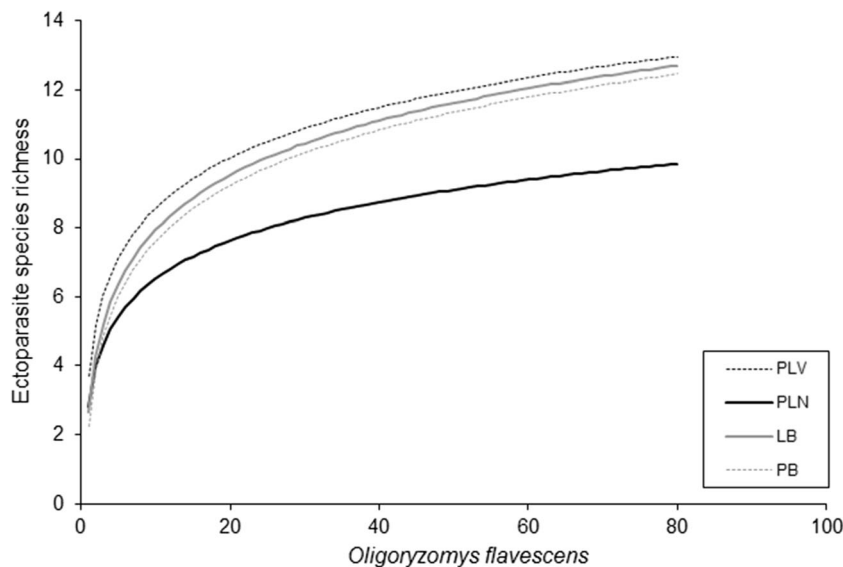
The number of rodent species, $R_{(R-SN)}$, was four: *S. aquaticus*, *O. flavescens*, *A. azarae*, and *H. brasiliensis*, and the registered ectoparasite species richness was $S_{(R-SN)} = 10$ (Table 3). Coefficients α and b directly estimated from field data were $\alpha_{(R-SN)} = 5.0$ (SD = 0.816) and $b_{(R-SN)} = 2.0$ (SD = 1.155).

The coefficient $\alpha_{(R-SN)}$ indirectly estimated with our model considering two elevations: 1.16 m (the average of the sites PB, BB, PLN, and LB) and 1.42 m (the average of the sites LB, PLN), and a mean number of individuals per rodent species, $n_{(R-SN)} = 13.75$, were, respectively, $\alpha_{(R-SN, 1.42)} = 7.221$ and $\alpha_{(R-SN, 1.16)} = 6.256$. Concerning coefficient b, the proportion of hosts "parasitized" by each ectoparasite in the site R-SN was positively correlated ($r = 0.949$, $t_{(4\ df)} = 5.20$, $p = 0.014$) with the proportion in the six sites considered together, T6, and did not differ from T6 ($\chi^2_{(3\ df)} = 2.512$, $p > 0.45$). Coefficient b estimated indirectly was the same as that for all six sites considered together: $b_{(R-SN)} = 2.16$ (SD = 1.179).

The ectoparasite species richness calculated with our model for the two mentioned elevations were $S_{(R-SN, cal)} = 13.37$ ($E_{(R-SN)} = 1.42$ m) and $S_{(R-SN, cal)} = 11.77$ ($E_{(R-SN)} = 1.16$ m). The average of both values of ectoparasite richness was $S_{(R-SN, cal)} = 12.57$ (SD = 1.133) and did not differ significantly from the observed value $S_{(R-SN, obs)} = 10$ ($t_{(1\ df)} = 3.21$, $p = 0.096$, one-tail test). The mean α value for sites PLN and LB if all ectoparasite species (except lice) were considered equals $\alpha_{(R-SN, 1.42)} = 6.376$, and for PB, BB, PLN, and LB equals $\alpha_{(R-SN, 1.16)} = 5.440$ (Table 2). Using these new values of α, the ectoparasite species richness was $S_{(R-SN, cal)} = 10.91$ similar to the observed value: $S_{(R-SN)} = 10$.

Fig. 6 The logarithmic model that relates the ectoparasite species richness on *Oligoryzomys flavescens* at the *k*th site

Fig. 7 The logarithmic model that relates the ectoparasite species richness on *Akodon azarae* at the *k*th site
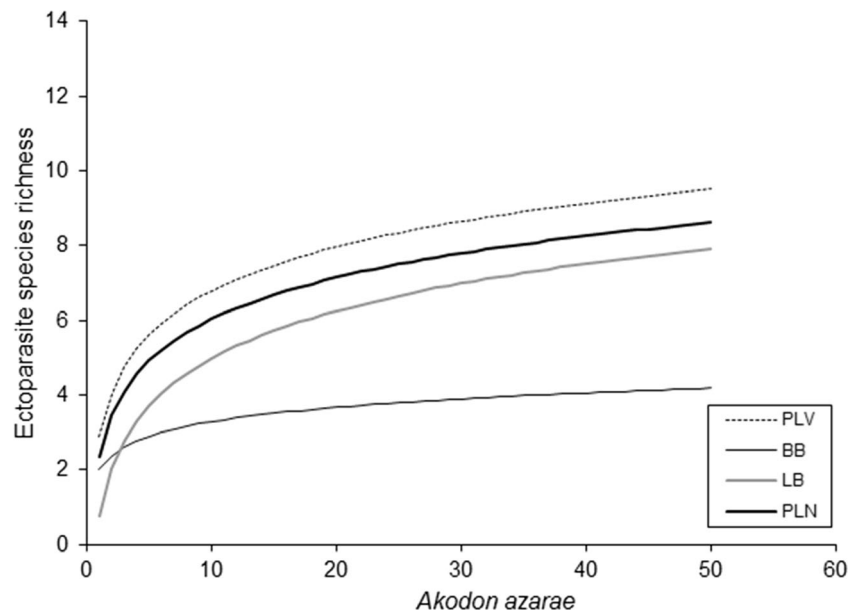
The OT site

The number of rodent species, $R_{(OT)}$, was six: *S. aquaticus*, *O. flavescens*, *O. nigripes*, *O. rufus*, *A. azarae*, and *H. brasiliensis*, and the registered ectoparasite species richness was $S_{(OT)} = 9$ (Table 3). Coefficients α and b directly estimated from field data were $\alpha_{(OT)} = 7.67$ (SD = 1.75) and $b_{(OT)} = 5.22$ (SD = 0.97). Coefficients α and b calculated indirectly were $\alpha_{(OT)} = 10.58$ and $b_{(OT)} = 4.0$, and the ectoparasite

species richness calculated with our model exceeded by almost 60% the observed value: $S_{(OT, \, cal)} = 15.87$.

Interestingly, sites PLV and PC had the same elevation that the one considered for OT, and in each one of those sites the species richness of ticks and mesostigmatic mites was 9 (Table 2). The mean proportion that ticks and mesostigmatic mites represent with respect to the total ectoparasite richness in PLV and PC was 0.556 (SD = 0.123). Assuming this proportion does not vary in OT, the calculated $\alpha(OT)$ value for only ticks

Table 3 Rodents and ectoparasites recorded in sites R-SN and OT, Buenos Aires Province, Argentina. Presence of an ectoparasite species is denoted by 1. Coefficients $b_{(k)}$, $\alpha_{(k)}$, $R_{(k)}$, and $S_{(k)}$ as in Fig. 2. Rodents: *SA*, *Scapteromys aquaticus*; *AA*, *Akodon azarae*; *OF*, *Oligoryzomys flavescens*; *HB*, *Holochilus brasiliensis*; *ON*, *Oligoryzomys nigripes*; *OR*, *Oxymycterus rufus*. Ectoparasites: *LM*, *Laelaps manguinhosi*; *LP*, *Laelaps paulistanensis*; *AF*, *Androlaelaps fahrenholzi*; *AR*, *Androlaelaps* cf. *rotundus*; *MM*, *Mysolaelaps microspinosus*; *GW*, *Gigantolaelaps wolffsohni*; *IL*, *Ixodes loricatus*; *CW*, *Craneopsylla wolffhuegeli*; *PA*, *Polygenis atopus*; *PR*, *Polygenis rimatus*; *GSP*, *Gigantolaelaps* sp.; *AT*, *Amblyomma triste*; *MSP*, *Mysolaelaps* sp.; *OB*, *Ornithonyssus bacoti*

Site R-SN						Site OT							
Rodents Ectoparasites	SA	AA	OF	HB	Hosts per ectoparasite species	SA	AA	OF	ON	OR	HB	Hosts per ectoparasite species
LM	1	1	1	1	4	1	1	1	1	1	1	6
LP			1		1		1	1	1	1		4
AF	1	1		1	3	1	1	1	1	1	1	6
AR		1			1	1	1	1	1	1	1	6
MM			1		1							
GW	1		1	1	3							
IL		1			1	1	1	1	1		1	6
CW	1		1	1	3							
PA	1			1	2							
PR			1		1							
GSP							1	1	1	1		4
AT						1	1	1	1	1	1	6
MSP							1	1	1	1		4
OB						1	1	1	1	1		5
					$b = 2.00$							$b = 5.22$
$\alpha = 5.0$	5	4	6	5		6	9	9	9	8	5	$\alpha = 7.67$
$S_{(R-SN)} = 10$						$S_{(OT)} = 9$						

and mesostigmatic mites would be $0.556 \cdot \alpha(OT) = 5.887$ which now gives a value of ticks and mesostigmatic mites richness: $S(OT, cal) = [\alpha(OT) \cdot 0.556] \cdot 6/4 = 8.33$, which is closer to the observed value $S(OT, obs) = 9$.

The assembly A5

The number of rodent species, $R_{(A5)}$, was five: *S. aquaticus*, *O. flavescens*, *H. brasiliensis*, *O. rufus*, and *D. kempi*, and the ectoparasite species richness was $S_{(A5)} = 22$ (Table 4, columns I to V). Coefficients α and b directly estimated from field data were $\alpha_{(A5)} = 8.60$ (SD = 4.39) and $b_{(A5)} = 1.909$ (SD = 1.019).

Coefficient α calculated considering an elevation equal to 1.16 m and a mean number of individuals per rodent species varying from 20 to 100 were $\alpha_{(A5)} = 8.23$ ($n = 20$), $\alpha_{(A5)} = 9.55$ ($n = 40$), $\alpha_{(A5)} = 10.32$ ($n = 60$), $\alpha_{(A5)} = 10.87$ ($n = 80$), and $\alpha_{(A5)} = 11.29$ ($n = 100$). Concerning coefficient b, the proportion of hosts "parasitized" by each ectoparasite in A5 did not differ from the proportion in the six sites considered together, T6 ($\chi^2_{(3\ df)} = 0.556$, $p > 0.5$), and its value was $b_{(A5)} = 2.26$. The corresponding ectoparasite species richness calculated with our model were $S_{(A5,\ cal)} = 18.21$ ($n = 20$), $S_{(A5,\ cal)} = 21.13$ ($n = 40$), $S_{(A5,\ cal)} = 22.84$ ($n = 60$), $S_{(A5,\ cal)} = 24.05$ ($n = 80$), and $S_{(A5,\ cal)} = 24.99$ ($n = 100$), and the observed value, $S_{(A5)} = 22$, did not differ from the average calculated value, $S_{(A5,\ cal)} = 22.24$ (SD = 2.67) ($t_{(3\ df)} = 0.203$ $p = 0.242$, one-tail test).

The assembly A11

The number of rodent species, $R_{(A11)}$, was 11: *A. azarae*, *A. dolores*, *C. laucha*, *C. musculinus*, *N. lasiurus*, *E. typus*, *R. auritus*, *M. musculus*, and *R. rattus*, and the ectoparasite species richness excluding our data was $S_{(A11)} = 41$ (Table 4, columns VI to XVI). Coefficients α and b directly estimated from field data were $\alpha_{(A11)} = 7.54$ (SD = 5.47) and $b_{(A11)} = 2.0$ (SD = 1.414).

Coefficient α indirectly estimated with our model considering an elevation of 1.6 m and the following mean numbers of individuals per rodent species, 20, 40, 60, 80, and 100, were $\alpha_{(A11)} = 8.57$ ($n = 20$), $\alpha_{(A11)} = 9.97$ ($n = 40$), $\alpha_{(A11)} = 10.79$ ($n = 60$), $\alpha_{(A11)} = 11.37$ ($n = 80$), and $\alpha_{(A11)} = 11.82$ ($n = 100$). The proportion of ectoparasites recorded from one, two, and three of more rodent species in assemblies composed of completely different rodent species like A11 did not differ significantly from the six sites considered together, T6. In effect, T6: $j_{(1)} = 0.40$, $j_{(2)} = 0.24$, $j_{(3)} = 0.16$, $j_{(4)} = 0.20$, and A11: $j_{(1)} = 0.585$, $j_{(2)} = 0.244$, $j_{(3)} = 0.122$, $j_{(4)} = 0.049$ ($\chi^2_{(3\ df)} = 4.55$, $p > 0.25$). This indicates that the proportion of specialist ectoparasites, moderately generalists and generalists, remains fairly constant despite considering sigmodontine and murid rodents, and coefficient $b_{(A11)} = 2.86$.

The ectoparasite species richness calculated with our model were $S_{(A11,\ cal)} = 32.97$ ($n = 20$), $S_{(A11,\ cal)} = 38.34$ ($n = 40$), $S_{(A11,\ cal)} = 41.49$ ($n = 60$), $S_{(A11,\ cal)} = 43.72$ ($n = 80$), and $S_{(A11,\ cal)} = 45.45$ ($n = 100$), and the observed ectoparasite species richness did not differ from the average calculated richness, $S_{(A11,\ cal)} = 40.39$ (SD = 4.93) ($t_{(3\ df)} = -0.275$, $p = 0.398$, one-tail test).

Apart from the former, the $S_{(k,\ cal)}$ values of each one of the six sites as well as all sites considered together of the coastal Río de la Plata wetland, T6, are shown in Table 4. Despite not being a true validation, the values did not differ significantly from the observed values ($\chi^2_{(6\ df)} = 0.967$, $p > 0.5$) (Table 2).

Discussion

Herein we presented our model based on the fact that closely related host species, with similarities in their habitat and diet, may have similar or identical parasite faunas (Poulin 2014). Our model satisfactorily predicts the specific richness of ectoparasite associated with different rodent assemblages that differ in the environmental stress and in the local rodent populations. The higher the environmental stress (greater frequency and/or intensity of floods), the lower the ectoparasite species richness is. The possible causes are (1) a direct effect on ectoparasites, particularly those species that spend most of their life cycle off the host that would have higher chances of being eliminated by frequent floods; (2) a direct effect on rodents, with a more intense and negative effect on those species not adapted to water, eliminating or decreasing local populations of these species making it more difficult for ectoparasites to colonize them; (3) a direct effect on the dominant vegetation of each locality. In this case, the different food sources and/or refuges against predators of rodents (e.g., owls) would in turn affect the rodents (Muñoz-Pedreros et al. 2016).

The analysis of the interaction of the components of the model allows us to evaluate the effect of each of them in determining the specific richness of ectoparasites in a given site. If the number of rodent species, R, remains constant, the mean number of parasitized hosts per ectoparasite species, b, in the denominator will also remain constant because of the way we calculate it. So, an increase in the ectoparasite richness will be attributed to an increase in the mean number of ectoparasite species per host, α, due to an increment in rodent population density and/or to an environment with less stress. On the contrary, if the number of rodent species increases ($R > 4$) while rodent population density and the environmental stress do not change (i.e., α, remains constant), b also increases linearly but at a lower rate than R. In effect, following the expression to obtain b for $R > 4$ (with $j(1) = 0.4$, $j(2) = 0.24$, and $j(3) = 0.16$), it gives $b = 1.36 + [0.2 \cdot (4 + R)/2] = 1.76 + 0.1 \cdot R$. This means that even though the coefficient b in the denominator will augment, the much higher increment

Table 4 Rodents and ectoparasites recorded in different counties and sites of Buenos Aires Province, Argentina (Castro et al. 1987). Presence of an ectoparasite species is denoted by 1. Coefficients $b_{(k)}$, $\alpha_{(k)}$, and $S_{(k)}$ as in Fig. 2. Rodents: *SA, Scapteromys aquaticus; OR, Oxymycterus rufus; OF, Oligoryzomys flavescens; HB, Holochilus brasiliensis; DK, Deltamys kempi; AA, Akodon azarae; CL, Calomys laucha; RR, Rattus rattus; CM, Calomys musculinus; MM, Mus musculus; RSP, rattus sp.; RA, Reithrodon auritus; AD, Akodon dolores; NL, Necromys lasiurus; ET, Eligmodontia typus.* Ectoparasites: *Af, Androlaelaps fahrenholzi; Ar, Androlaelaps* cf. *rotundus; Lp, Laelaps paulistanensis; Ob, Ornithonyssus bacoti; Gw, Gigantolaelaps wolffshoni; Esp, Eutrombicula sp.; Lm, Laelaps manguinhosi; Pr, Polygenis rimatus; Cmw, Craneopsylla minerva wolffhuegeli; Mm, Mysolaelaps microspinosus; Pa, Polygenis atopus; Pf, Polygenis frustratus; Ppu, Polygenis puelche; Pby, Polygenis byturus; Pb, Polygenis bohlsi; Psp, Polygenis sp.; Es, Eulaelaps stabularis; Paa, Polygenis axius axius; Xc, Xenopsylla cheopis; Pp, Polygenis platensis; Cmm, Craneopsylla minerva minerva; Nf, Nosopsyllus fasciatus; Nl, Nosopsyllus londinensis; Lma, Laelaps mazzai; Le, Laelaps echidnina; Ho, Hoplopleura oenomydis; Ls, Leptopsylla segnis; Ps, Polyplax spinulosa; Om, Ornithonyssus meprai; Ppy, Polygenis pygaerus; Po, Polygenis occidentalis; E32, Polygenis acodontis; E33, Amblyomma tigrinum; E34, Pulex irritans; Ln, Laelaps nuttali; Lt, Laelaps thori; Cb, Cavilaelaps bresslaui; Hf, Hoplopleura fonsecai; Hs, Hoplopleura scapteromydis; Ha, Hoplopleura aitkeni; Hc, Hoplopleura contigua; Hd, Hoplopleura delticola; Hi, Hoplopleura ingens; Hsi, Hoplopleura similis; hsp, hoplopleura sp.; Har, Hoplopleura argentina; Mycm, Mycoptes musculinus; Myom Myobia musculi*

| | Assembly A5 | | | | | | Assemby A11 | | | | | | | | | | | |
Rodents Ectoparasites	SA	OR	OF	HB	DK	$b_{(A5)}$	AA	CL	RR	CM	MM	CL	RSP	RA	AD	NL	ET	$b_{(A11)}$
Af	1	1	1	1	1	4	1	1	1	1	1			1		1	1	8
Ar		1	1		1	3	1	1	1	1						1		5
Lp	1	1	1	1		4	1	1		1				1				4
Ob		1				1			1	1	1							3
Gw	1		1	1		3				1								1
Esp							1	1		1								3
Lm			1			1												
Pr		1	1			2	1	1								1		3
Cmw		1	1			2	1							1				2
Mm	1		1			2	1	1								1		3
Pa		1				1												
Pf		1	1	1		3	1											1
Ppu							1	1		1								3
Pby		1				1		1		1								2
Pb								1										1
Psp	1		1			2	1	1								1		3
Es	1		1		1	3	1	1						1		1		4
Paa		1	1			2										1		1
Xc								1	1				1					3
Pp				1		1		1										1
Cmm		1	1			2	1									1		2
Nf									1				1					2
Nl									1									1
Lma								1			1						1	3
Le									1		1							2
Ho									1									1
Ls									1				1					2
Ps									1									1
Om									1									1
Py		1				1												
Po								1										1
Pac										1								1
At	1					1												
Pi											1							1
Pn									1									1
Lt																1		1

Table 4 (continued)

Rodents Ectoparasites	Assembly A5						Assemby A11											
	SA	OR	OF	HB	DK	$b_{(A5)}$	AA	CL	RR	CM	MM	CL	RSP	RA	AD	NL	ET	$b_{(A11)}$
Cb																1		1
Hf		1				1												
Hs	1					1												
Ha							1								1			2
Hc			1			1												
Hd											1							1
Hi										1								1
Hsi								1				1						2
Hsp																1		1
Har														1				1
Mycm											1							1
Myom											1							1
						$b = 1.909$												$b = 2.0$
$\alpha = 8.60$	8	13	13	6	3		13	16	13	11	7	1	3	5	1	11	2	$\alpha = 7.54$
$S_{(A5)} = 22$																		$S_{(A11)} = 41$

in the number of rodent species will explain the increment in the ectoparasite richness. For example, the value of $S(\text{PLV})$ was double the average between the sites with lower ectoparasite richness, $S(\text{PB})$ and $S(\text{BB})$. In this case, the three coefficients of the model also doubled the average values of the sites PB and BB. In effect, $R(\text{PLV})/[R(\text{PB}) + R(\text{BB})]/2 = 2.0$, $\alpha(\text{PLV})/[\alpha(\text{PB}) + \alpha(\text{BB})]/2 = 2.047$, and $b(\text{PLV})/[b(\text{PB}) + b(\text{BB})]/2 = 2.025$. Thus, the increase in ectoparasite richness in PLV was attributed to both an increase in R and mainly an increase in α. Considering the sites with the same number of rodent species and equal coefficient b, but with extreme values of ectoparasite richness, $S(\text{PLV}) = 20$ and $S(\text{R-SN}) = 10$, the coefficient α in PLV was 2.252 times greater than that in R-SN, and the increment in ectoparasite richness in PLV was attributed to the increase in α due to the greater number of rodents and possibly a lower water stress. Despite the different composition of rodent species, richness calculated at R-SN was somewhat higher than the observed richness. Given that the authors collected only laelapid mites and fleas, recorded richness might have been higher if lice were also considered.

Ecological communities are usually represented as ecological networks. Not only the specific richness but also other ecological network structures, like structural patterns which influence ecological dynamics, are affected by environmental variability (Takemoto et al. 2014). We provide evidence that an increase in the average species richness, α, has the same effect on total species richness than if the increase occurred on the number of rodent species, R, or even a similar decrease of the coefficient b. If all rodent species were inhabited by specific ectoparasite species (i.e., $b = 1$), total species richness would equal the product between average richness, α, and the number of rodent species, R, and would indicate modularity in the rodent-ectoparasites relationship (Fortuna et al. 2010). Thus, coefficient b can also be considered an indicator of the structure of the food web assemblage formed by rodent species and ectoparasites, fundamentally if estimated directly. If we build a table locating rodent species present at a site in each column and ectoparasite species in each row, when $b = 1$, the trophic structure will be compartmentalized (i.e., the division of the network into relatively independent sub-networks) (Graham et al. 2009; Ulrich and Almeida-Neto 2012). In effect, when properly ordering the rows and columns of the table, the cells that indicate presence (with a 1 value) will have a "diagonal" architecture (Fortuna et al. 2010). In this case, ectoparasite richness at the site will depend on the number of rodent species (i.e., habitats) and all rodent species will be "unique habitats" since they have different specific ectoparasites.

We consider our model robust and capable of providing reliable estimates of ectoparasite species richness on rodents in terms of three coefficients relatively quick and easy to get in the field. Ectoparasites are an essential part of every ecosystem representing a major factor in global biodiversity (Klimpel et al. 2007), and rodents play an important role as reservoir hosts for vector-borne disease agents (Gil et al. 2010). Thus, our model is a useful tool in topics related to biodiversity and epidemiology. Besides, our model could be adapted to habitats other than temperate wetlands if a suitable estimate of an environmental gradient is found. In addition, it could be possible to adapt the model to other host taxa.

Compliance with ethical standards

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