

A new distributional model coupling environmental and biotic factors

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ABSTRACT (252 words)

Species distribution models (SDM) are the spatial surrogate of the suitability of a species in the biophysical aspect, since they are based on predicting their presence using climatic and environmental indicators. SDMs are satisfactory at regional scales, where biological interactions such as predation and competition do not influence distribution. However, at the local scale, they are incomplete for characterizing the ecology of a species since the algorithms do not include information about biotic variables. In this paper, we present a mathematical model that couples biophysical and biotic interactions in a spatially explicit way. We used a distributional database of 12 species of sigmodontine rodents from Argentine Patagonia as a study case. We performed numerical simulations of the dynamics of each rodent from a stochastic and spatially explicit population model. The biophysical suitability of each species was modeled using Maxent, which generated an indicator of its patch colonization capacity. The vegetation cover of each patch was characterized with remote sensing indices, associating the coverage with the pressure of aerial predation. The effect of interspecific competition was modeled from the assembly rules proposed by Fox. The initial occupation conditions for each species were proposed as known sites of occurrence, and the temporal evolution of these systems was compared with that obtained from using random initial occupation conditions. The results obtained allow expanding the description of the ecosystems studied and show a great capacity for prediction, so it is expected that this new modeling tool can be used to predict possible future ecological scenarios.

RESUMEN (269 palabras)

Los modelos de distribución de especies (SDM por sus siglas en inglés) representan espacialmente la idoneidad de una especie en el aspecto biofísico, ya que se basan en predecir la presencia utilizando indicadores climáticos y ambientales. Los SDM son satisfactorios a escalas regionales, donde las interacciones biológicas como la depredación y la competencia no influyen en la distribución. Sin embargo, a escala local, son incompletos para caracterizar la ecología de una especie, ya que los algoritmos no incluyen información sobre variables bióticas. En este trabajo presentamos un modelo matemático que acopla interacciones biofísicas y bióticas de manera espacialmente explícita. Hemos utilizado como caso de estudio una base de datos distribucionales de 12 especies de roedores sigmodontinos en la Patagonia Argentina. Realizamos simulaciones numéricas de la dinámica de cada roedor a partir de un modelo poblacional estocástico y espacialmente explícito. La idoneidad biofísica de cada especie se modeló utilizando Maxent, con lo que generamos un indicador de su capacidad de colonización de parches. Se caracterizó la cobertura de vegetación de cada parche con índices de

46 sensores remotos, asociando la cobertura con la presión de depredación aérea. El efecto de la
47 competencia interespecífica se modeló a partir de las reglas de ensamble planteadas por Fox. Se
48 propuso como condición de ocupación inicial para cada especie los sitios de presencia conocidos y
49 se comparó la evolución temporal de estos sistemas con la obtenida a partir de utilizar condiciones
50 de ocupación inicial al azar. Los resultados obtenidos permiten ampliar la descripción de los
51 ecosistemas estudiados y muestran una gran capacidad de predicción, por lo que se espera que pueda
52 utilizarse esta nueva herramienta modelística para predecir posibles escenarios ecológicos futuros.

53

54 **KEYWORDS:** Mathematical model, biotic interactions, Fox's rule, rodents.

55

56 **TOTAL WORDS: 8109 (ONLY TEXT)**

57 **1. Introduction (1040 words)**

58

59

60

“Why do they say you are invincible?”

61

“Because I've never fought.”

62

—attributed to the creator of aikido, Morihei Ueshiba

63

64 The use of mathematical models to describe and analyze ecological systems has
65 experienced significant growth in recent years. They generate predictions, but they are also
66 a tool that allows ordering and systematizing assumptions within a framework, enabling the
67 elucidation of complex biological systems. In recent years, species distribution models
68 (SDMs) have played an increasingly important role in studying the distribution patterns of
69 organisms (Guisan and Thuiller, 2005). The “suitability models” aim at identifying the most
70 influential variables explaining species presence (or presence/absence), and generate
71 potential distribution maps based on different environmental characteristics and scenarios
72 (Felicísimo et al., 2005), representing a species environmental realized niche (Soberón,
73 2007). Predictive spatial modeling based on the analysis of environmental parameters and
74 the presence of species is widely used in environmental, ecological and conservation studies,
75 among others (Yanga et al., 2013; Matyukhina et al., 2014; Yuan et al., 2015).

76 The distribution of a species results from the dynamic interaction of biotic and abiotic
77 factors, although most research has focused on the latter. However, biotic relationships
78 influence the distribution of species greatly, albeit at different scales (Jablonski, 2008).
79 Competition, for example, can lead to species occupying only a fraction of their potential
80 range (Anderson et al., 2002; Pearson and Dawson, 2003; Mateo et al., 2011). This is an
81 important factor that is mostly absent in species distribution studies (Davis et al., 1998;

82 Fitzpatrick et al., 2007), as with other interactions such as facilitation, pollination, herbivory
83 or predation (Sánchez Cordero and Martínez-Meyer, 2000; Hebblewhite et al., 2005; Mateo
84 et al., 2011). At the local level, the ecological processes that determine to a greater extent the
85 diversity of species in communities are habitat selection and ecological interactions
86 (competition and predation), as well as local extinction processes due to stochastic events.
87 The presence and intensity of these processes give rise to different types of communities
88 (Ricklefs and Schluter, 1993; Moreno et al., 2007). Mechanisms that facilitate species
89 coexistence are differences in morphology, diet, and foraging behavior (Kotler, 1989; Scott
90 and Dunstone, 2000).

91 Although incorporating all biotic relationships into models would probably be
92 challenging, the almost universal lack of knowledge about their dynamics at individual
93 species' levels means they are ignored when generating SDMs. Known extrapolation
94 algorithms generally do not receive information on biotic variables (Soberón and Peterson,
95 2005), and intra- and interspecific competition have been modeled only for some simple
96 systems (Bascompte and Solé, 1998). This is undoubtedly a field that will develop in the
97 immediate future, since sufficient maturity has been reached in the techniques to tackle more
98 complex tasks, such as these (Mateo et al., 2011).

99 In this context, mathematical simulations can provide additional support. The effects
100 of biotic interactions are invisible on a regional scale and only begin to manifest themselves
101 from 1:10,000 downwards (between 0.1 and 100 ha) (our observations). Similar problems of
102 scale appear when interpreting species assemblages. Interspecific competition spatially
103 segregates species, particularly when they belong to the same trophic guild (Brown et al.,
104 2002), establishing rules of coexistence or exclusion that are manifested only at micro or
105 local scale.

106 A common methodology for modeling populations with heterogeneous distributions
107 is metapopulation modeling (Levins and Culver, 1971). In metapopulation models, local
108 populations (or subpopulations) of a given species reside in areas that have a certain spatial
109 structure. Each subpopulation is made up of a set of interacting and reproducing individuals,
110 which present a relatively independent dynamic and have finite probabilities of becoming
111 extinct and of colonizing new territories. Each subpopulation is considered to inhabit an area
112 or "patch," so a metapopulation can be characterized as a network of patches occupied by

113 groups of individuals with characteristic migration rates between patches. Metapopulations
114 occupy an arrangement of patches of variable habitat suitability. At this level of description,
115 these patches are the only spatial resource, and can be colonized or vacated according to
116 specified rules. Patches can also be destroyed and become unsuitable for colonization,
117 representing spatial heterogeneity and landscape fragmentation, as in Bascompte and Solé
118 (1998) and Abramson et al. (2017).

119 In Laguna et al. (2015), a mathematical model of a simple food web with two
120 herbivores and one predator was analyzed. Competing herbivores were represented by sheep
121 and guanacos, while the puma (*Puma concolor*) represented the predator. The proposed
122 model combined the concepts of metapopulations and patch dynamics, and included an
123 explicit hierarchical competition between species, affecting their prospect of colonizing an
124 empty patch by having to compete with other species. Based on that work, in the present
125 study we consider the assemblage of sigmodontine rodents that inhabit Patagonia,
126 incorporating additional information about the environmental suitability for each species
127 (based on our Maxent SDMs; Ruiz Barlett et al., 2019), known presence sites, hierarchical
128 competition between species, and a proxy for aerial predation.

129 Fox's assembly rule (1987) states that the incorporation of a new species into a
130 community depends on the type of configuration of its previous occupants. When a level of
131 organization without trophic redundancy is completed (for example a herbivore, an omnivore
132 and a granivore), a redundant species can only enter when the first level is complete. The
133 communities that conform to the rule of assembly are the "favorable states". In other words,
134 if there are three species in the same site, it is unlikely that two of them belong to the same
135 trophic guild (e.g., both herbivores), as these are the "unfavorable states". Kelt et al. (1995)
136 established that the species of rodents studied in this work follow Fox's rule.

137 In Ruiz Barlett et al. (2019) we generated potential distribution models for
138 sigmodontine rodent species that inhabit the Andean-Patagonian forest region and adjacent
139 areas, and we analyzed the main climatic variables influencing them. Based on these
140 analyses, the objective of the present work was to mathematically model the effect of biotic
141 factors (namely, interspecific competition and predation) on the specific composition of
142 rodent assemblages. For this, stochastic numerical simulations of rodent species dynamics
143 were modeled using a spatially explicit metapopulation methodology as described below. We

144 hypothesized that species competition for food resources and aerial predation influence the
145 distribution and composition of Patagonian sigmodontine assemblages. The presence and/or
146 absence of each biotic factor is expected to have significant effects on the possibility of
147 colonizing a new patch and on the spatial arrangement of rodent populations, and these
148 effects are visible with the proposed simulation model.

149

150 **2. Materials and methods (1908 words)**

151

152 ***2.1. Area and species studied***

153

154 Since we are interested in the influence of biotic factors on the distribution of
155 rodents at a local scale, we selected a study area within the geographical distribution of the
156 rodent species of interest, comprising the Andean and transition (forest-steppe ecotone) zones
157 of northwestern Patagonia in Argentina, including Nahuel Huapi National Park and its
158 surroundings (from 38° to 42° South and 68° to 72° West, ~200,000 km²). The climate of
159 this region is temperate-cold (Paruelo et al., 1999) with a steep precipitation gradient from
160 west to east, and a moderate temperature gradient. Annual precipitation ranges from ~4000
161 mm in the Valdivian rainforest to ~230 mm in the Patagonian steppe (Prohaska, 1976), and
162 elevation ranges from 3000 to 500 m. These extremes occur within less than 150 km from
163 west to east, producing some of the sharpest abiotic and biotic transitions on earth
164 (Quintanilla Pérez, 1983; Veblen and Lorenz, 1988).

165

166 The following twelve rodent (Rodentia, Cricetidae, Sigmodontinae) species were
167 included in our analyses: *Abrothrix hirta*, *A. olivacea*, *Geoxus valdivianus*, *Notiomys*
168 *edwardsii*, and *Paynomys macronyx* (Abrothrichini); *Oligoryzomys longicaudatus*
169 (Oryzomyini); *Eligmodontia morgani*, *Loxodontomys micropus* and *Phyllotis xanthopygus*
170 (Phyllotini); *Euneomys chinchilloides* and *Irenomys tarsalis* (Euneomyini); and *Reithrodon*
171 *auritus* (Reithrodontini) (Pardiñas et al., 2015; Patton et al., 2015). These species are a subset
172 of those previously studied in Ruiz Barlett et al. (2019), and were chosen because they are
173 those from which we have information about known sites of presence in the study area.

174

2.2 Mathematical model with biotic interactions

Numerical simulations of the dynamics of each rodent species were carried out with a stochastic and spatially explicit metapopulation model, similar to the one proposed by Laguna et al. (2015). In this approach, the different subpopulations from the twelve species inhabit a grid that represents the study area. Each subpopulation of each species can colonize a neighboring patch with a probability that depends on: 1) suitability, 2) the interspecific competition provided by Fox's rule, and 3) the intraspecific competition that underlies the metapopulation approach. Besides, each species also has a probability of vacating a patch due to: 4) aerial predation, and 5) different biotic factors, modeled as a local extinction within that patch. To specify these processes for each species, the model takes into account the following conditions at each cell:

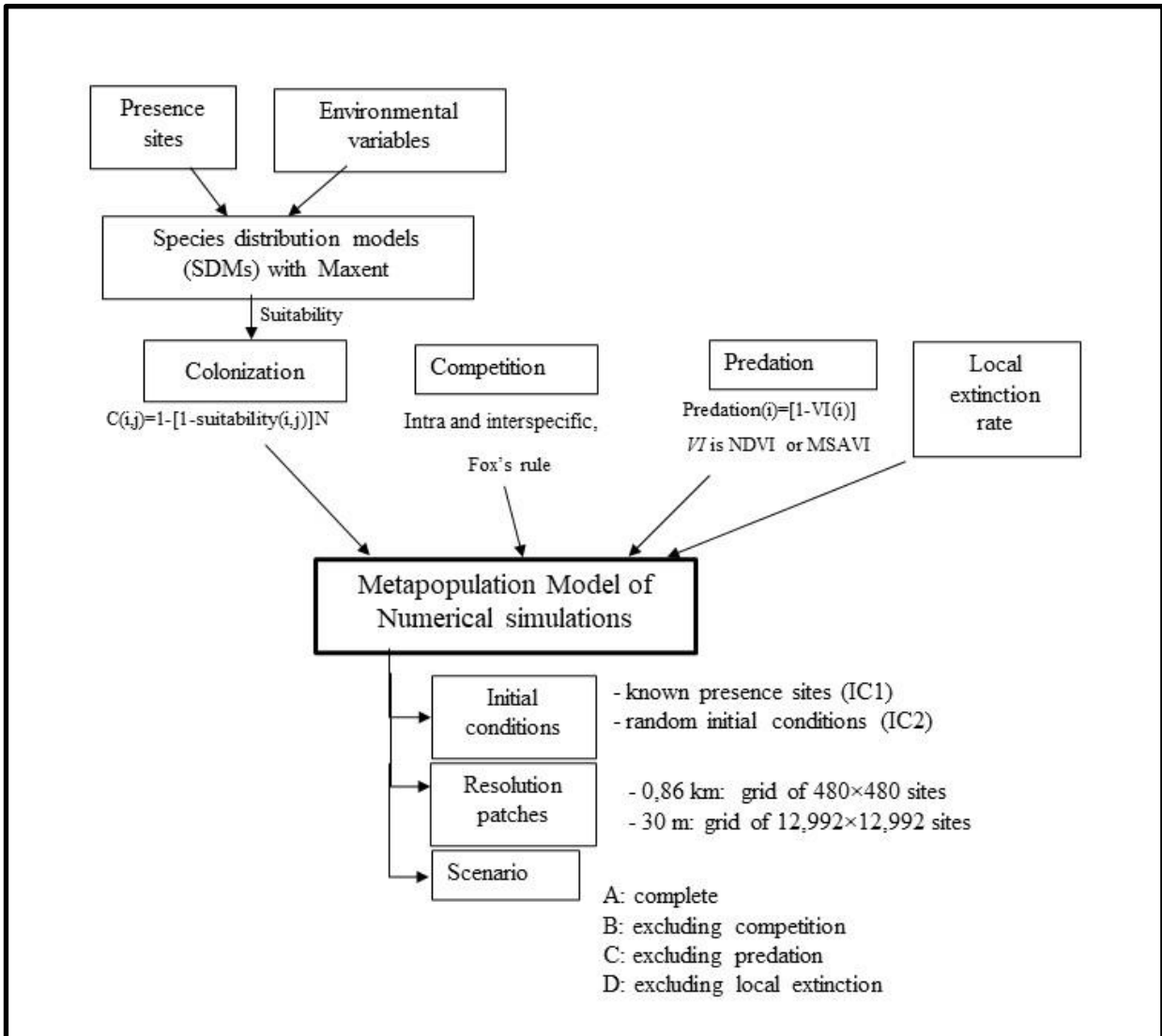
1. **Potential suitability.** For each species, this is the value obtained from the Maxent SDMs, as generated in Ruiz Barlett et al. (2019) from specific sites of presence and environmental variables. It weighs the probability of colonization of an available patch by a given species.
2. **Fox's rule.** As discussed above, this is used to model the effects of competitive interactions between different rodent species. Together with the definition of a hierarchy within each guild, the rule determines a competitive hierarchy that influences the order of arrival of each species to the local assembly into a given patch.
3. **Intraspecific competition.** Metapopulation models prevent the occupation of a patch by a subpopulation of a species that is already occupying the site.
4. The **vegetation cover** at each site is used as a proxy of the probability of predation, given that a higher ground cover provides more protection from aerial predators and consequently decreases the predation risk. In other words, in areas with little or no vegetation, rodents are more likely to be preyed upon. In this work we use two different vegetation indices: NDVI and MSAVI.
5. The **local extinction rate** emulates death from natural causes or complete migration from a patch. Given that the mean lifespan of all the rodent species considered is similar (Jones et al., 2009; Pacifici et al., 2013), we used the same local extinction

206 value (equivalent to a life expectancy of between 1 and 2 years) for all of them
 207 and in all patches.

208 6.

209 **2.3 Model implementation**

210



211

212 **Figure 1.** Schematic representation of the methodology used.

213

214 We consider a square grid of patches that can be either vacant or occupied by one or
 215 more of the species. Time advances discretely and, at each time step, the state of occupation
 216 of a patch is dictated by a stochastic process depending on the ecological processes described

217 above: colonization, predation, and local extinction (Fig. 1). They were implemented as
218 follows:

219

220 *Colonization*

221

222 A first element to consider is the **colonization capacity** of a species. The ability to
223 colonize a patch depends on how it is suited by the species' ecological requirements. We
224 used the environmental suitability information obtained from the SDMs, previously
225 calculated for each species (Ruiz Barlett et al., 2019), as a measure of this. Then, the
226 colonization capacity of site i by species j is the suitability, adequately normalized between
227 0 and 1 to be used as a probability. Furthermore, the colonization of a patch by a given species
228 will depend on the number of neighboring patches occupied by that species (the greater the
229 number of neighboring patches occupied, the greater the probability of becoming occupied).
230 Mathematically, the probability of colonization of patch i by species j is calculated as follows:

231

$$C(i, j) = 1 - [1 - suitability(i, j)]^N$$

232

where N is the number of neighboring patches that are occupied at the time.

233

234 Another ingredient to consider in the colonization process is **competitive**
235 **interactions** between species. They were established by Fox's rule, which groups species
236 into trophic guilds, as analyzed in Kelt et al. (1995). According to Fox's rule, species from
237 different trophic guilds do not have interspecific competition to occupy a patch, while those
238 within the same guild have a hierarchy that must be considered. To complement Kelt's
239 classification, we assumed that the superior competitor is the one with the largest body size,
240 since larger body mass leads to relatively higher fitness (Predavec, 2000). The hierarchical
241 order was determined according to body weight for each species obtained from Secretaría de
242 Ambiente y Desarrollo Sustentable de la Nación y Sociedad Argentina para el Estudio de los
243 Mamíferos (2019). In order to implement this rule, species were classified into four trophic
244 guilds, identifying their hierarchical position in the food web, and ordered by descending
245 hierarchy as follows:

246

Descending hierarchy (i)	Herbivores (h _i)	Granivores (g _i)	Animalivores (a _i)	Omnivores (o _i)
1	<i>Reithrodon auritus</i>	<i>Oligoryzomys longicaudatus</i>	<i>Paynomys macronyx</i>	<i>Abrothrix hirta</i>
2	<i>Euneomys chinchilloides</i>	<i>Eligmodontia morgani</i>	<i>Geoxus valdivianus</i>	<i>Abrothrix olivacea</i>
3	<i>Loxodontomys micropus</i>		<i>Notiomys edwardsii</i>	
4	<i>Phyllotis xanthopygus</i>			
5	<i>Irenomys tarsalis</i>			

247

248

249 Then, the colonization proceeds as follows: 1) the superior competitor of a randomly chosen
 250 trophic guild is the one that has priority to colonize any patch that is not already occupied by
 251 the same species (intraspecific competition), and will do so with probability $C(i, j)$
 252 (suitability); 2) an inferior competitor will only be able to colonize a patch which is not
 253 already occupied by the same species, nor by a superior competitor of the same guild
 254 (interspecific hierarquical competition), and again, the probability of this happening is
 255 $C(i, j)$; and 3) even if the cell is suitable for a species, if it is already occupied by another
 256 species from the same guild and not all other guilds are present on the cell, that species is
 257 forbidden from accessing the patch (Fox's rule).

258

259 *Predation*

260

261 For predation, an aerial predator (for example, an owl) was simulated by prey
 262 exposure obtained indirectly from vegetation indices (NDVI and MSAVI) of the study area.
 263 Vegetation cover, such as rosehip (*Rosa eglanteria*), shrubs and colihue cane (*Chusquea*
 264 *culeou*) provides protection from predators, while areas without or with scarce vegetation are
 265 more exposed to aerial predation. In the model, the values of vegetation indices were

266 normalized to lie in the interval [0,1] so that the probability of predation is defined at each
267 site i as:

$$268 \quad \text{Predation}(i) = [1 - VI(i)]^\alpha$$

269 where VI is NDVI or MSAVI, and $\alpha = 0.25$. This functional form gives a probability of
270 predation that decays monotonically with the vegetation cover. The value of the coefficient
271 α was chosen phenomenologically, since it gives a range of almost linear decay at low values
272 of VI , while turning down rapidly only when the protection provided by the cover approaches
273 1. The precise form of the function is not particularly important, but a departure from
274 linearity, as provided by the exponent α , ensures that the VI does not underestimate predation
275 in forest areas, which would be unrealistic.

276 Vegetation index (NDVI) with a resolution of 0.86 km was taken from Ruiz Barlett et al.
277 (2019). Besides, vegetation indices with a resolution of 30 meters were generated using
278 Landsat 8 images, with dates from 2018-01-13 to 2018-02-07, obtained from
279 www.earthexplorer.usgs.gov. Images were processed and NDVI and MSAVI indices were
280 generated using SNAP (SNAP, 2014) and QGIS software (QGIS Development Team, 2011).

281 *Local extinction*

282

283 At each step of time, each subpopulation has a probability e of becoming extinct
284 (the same for all species and all patches). This probability of **local extinction** accounts for
285 both death due to natural causes and the possibility of migration, and in both cases the effect
286 is the same: the vacating of a patch by a given species.

287

288 *2.4 Model dynamics*

289

290 We studied the dynamics of this model through computer simulations performed on
291 a system enclosed by impenetrable barriers. To perform a typical realization, we defined the
292 parameters of the model and set an initial condition of patch occupation. We consider two
293 different initial conditions (IC):

294 IC₁: At time zero, the only patches occupied on the grid are those containing the
295 known sites of presence of each species in the selected study area (see in Ruiz Barlett et al.,
296 2019).

297 IC₂: At time zero, each species randomly occupies any cell on the grid in a given
298 proportion. We tested values between 0.01% and 20% of patches occupied by each species.

299 From these initial conditions, the dynamics rules produce a temporal evolution of
300 the occupation of cells in the system, through colonization, predation and local extinction.
301 After a transient period of time, a steady state is achieved where there are fluctuations but no
302 substantial changes in the occupation of patches for a considerable number of steps, as shown
303 below. The temporal evolution of the fraction of patches occupied for each species during
304 the whole process is recorded. Also, when the steady state is reached, we perform
305 measurements of the number of visits that each species makes in each patch. The value
306 obtained corresponds to the fraction of time that the species occupied the patch in the steady
307 state. We present these results as color maps and name them *distribution maps*. The patches
308 that were visited the most, represented with warm colors, are visited half the time (that is,
309 about 500 times in a simulation that lasts 1000 steps). The cells with cold colors (blue, light
310 blue) indicate that, although environmentally favorable areas, they are less visited by the
311 species.

312

313 ***2.5 Scenarios analyzed***

314

315 Numerical simulations were performed in grids of two different sizes. We call
316 Model 1 the one corresponding to a system with patches of 0.86 km forming a grid of
317 480×480 sites (with a total of 230,400 patches). Besides, Model 2 corresponds to a system
318 with patches of 30 m in a grid of 12,992×12,992 sites (with a total of 168,766,080 patches).
319 The reason for adding Model 2 has to do with the fact that effects of biotic interactions are
320 manifested only at micro or local scales.

321 We use Model 1 to analyze how and to what extent each ecological process
322 influences the behavior of the species, and how much the steady state of the system depends
323 on the two different initial conditions, IC₁ and IC₂. In this case we use as a proxy for aerial
324 predation only the vegetation index NDVI.

325 The following scenarios were generated:

326 -Scenario A, or “complete,” including all the ecological processes discussed above:
327 colonization (including suitability, Fox’s rule, and hierarchy), predation (VI: NDVI) and
328 local extinction;

329 -Scenario B, including predation and local extinction, but excluding competition;

330 -Scenario C, including competition and local extinction, but excluding predation
331 (i.e., without NDVI);

332 -Scenario D, with competition and predation, but excluding extinction.

333 Besides, with Model 2 we study only the complete scenario (scenario A) with
334 random initial conditions (IC2). In this case, two vegetation indices with a resolution of 30
335 m were used: NDVI and MSAVI. The potential distribution maps generated with Maxent,
336 with pixels with a resolution of 0.86 km, were converted to 30 m patches.

337 To analyze the relevance of the scale in the biotic interactions we compare the
338 distribution maps obtained with the two patch resolutions (Models 1 and 2).

339

340 **3. Results**

341

342 To determine the influence of biotic factors in the distribution of rodents through the
343 proposed model, we first analyzed scenarios with different initial conditions and then the
344 behavior of species for the different scenarios detailed in the previous section using the
345 Models 1 and 2.

346

347 ***3.1 Initial conditions***

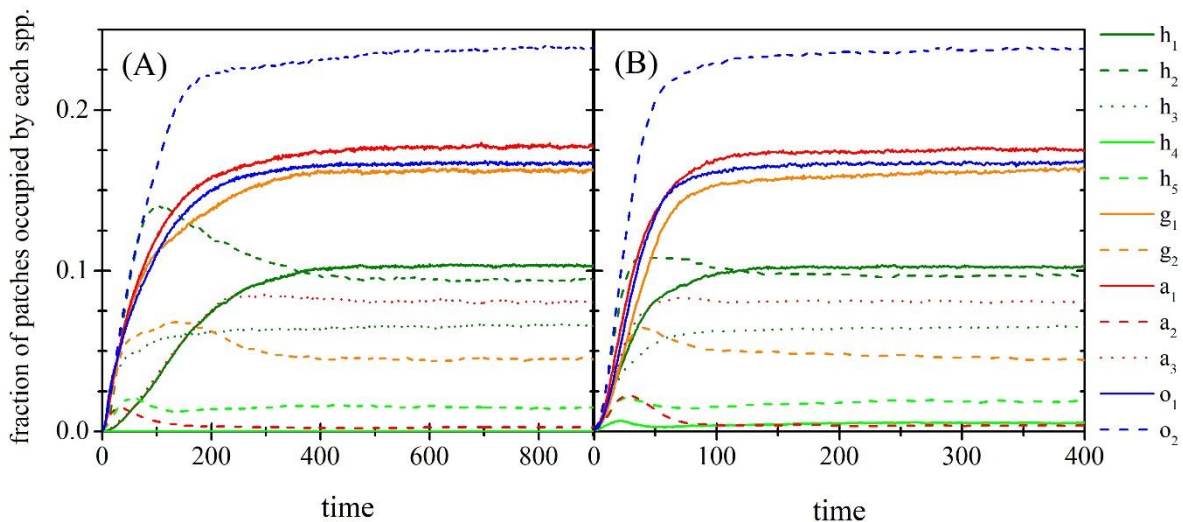
348

349 To analyze how much the steady state of the system depends on the initial occupancy
350 of the species, we use Model 1 to perform numerical simulations under different initial
351 conditions. As we said, with IC2 we tested fractions of patches initially occupied in the range
352 [0.1% - 20%], and compared with the behavior observed with IC1. In Fig. 2 we show a
353 comparison for the cases with IC1 and IC2=0.1%, as they have a similar number of initially
354 occupied patches. In both cases, the fraction of occupied patches is initially very small (about
355 10^{-3}), and for this reason the curves seem to start from zero. The fraction of occupied patches

356 in the steady state is almost identical, the difference between ICs is the shorter time necessary
 357 to reach the steady state in the model with a random distribution starting point (IC2), than for
 358 the model with known sites of presence (IC1). As expected, the larger the fraction of initially
 359 occupied sites, the faster the system reaches the stationary state: a system with IC2=20%
 360 reaches the steady state 50 times faster than a system with IC1 (not shown here). However,
 361 the fraction of patches occupied at the steady state is the same for all the IC studied, and this
 362 result suggests a remarkable robustness of the results. It is worth noting that, while IC2 is
 363 computationally more efficient, IC1 is ecologically better justified. In the following section
 364 we show the simulations generated with IC2=0.1%, in order to maintain the proportion of
 365 initially occupied sites in similar proportion to IC1.

366
 367

PLACE FIGURE 2 HERE



368

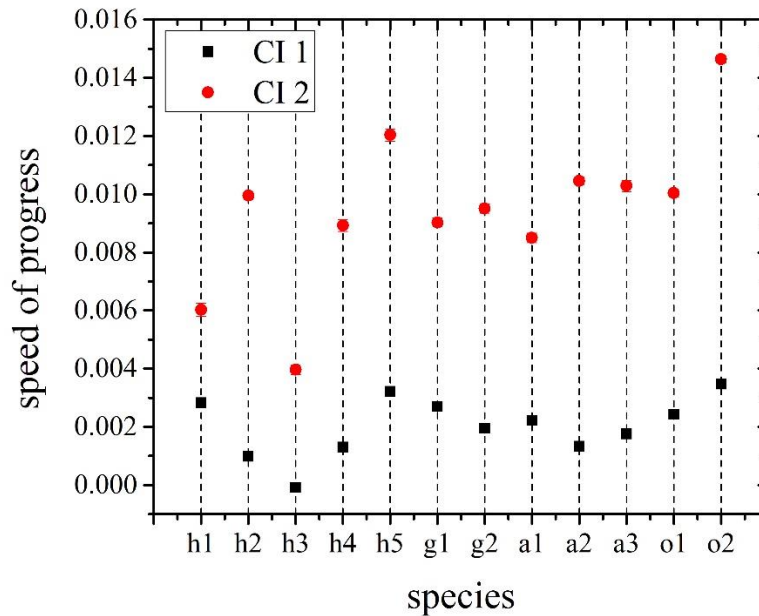
369 **Figure 2.** Evolution of systems with two different initial conditions, showing the fraction of patches
 370 occupied as a function of time. Left: known sites of presence for each species (IC1). Right: random
 371 distribution sites (IC2=0.1%). Species are h₁: *Reithrodon auritus*, h₂: *Euneomys chinchilloides*, h₃:
 372 *Loxodontomys micropus*, h₄: *Phyllotis xanthopygus*, h₅: *Irenomys tarsalis*, g₁: *Oligoryzomys*
 373 *longicaudatus*, g₂: *Eligmodontia morgani*, a₁: *Paynomys macronyx*, a₂: *Geoxus valdivianus*, a₃:
 374 *Notiomys edwardsii*, o₁: *Abrothrix hirta*, o₂: *Abrothrix olivacea*.
 375

376 We analyze the expansion of the species in the very first moments of evolution,
 377 when the progress is linear with time. This regime allowed us to calculate the speeds at which
 378 species colonize the patches for the two ICs studied (see Fig. 3). When comparing the speeds
 379 in both cases, we found that the case with random initial conditions (IC2) was faster (Fig. 3),

380 the fastest species being *A. olivacea* (o₂) and *P. xanthopygus* (h₅), and the lowest one *L.*
 381 *micropus* (h₃) in both, IC1 and IC2 cases. A similar pattern was found in the model with
 382 known sites of presence as starting point (IC1), but the order of species following the first
 383 two was a little different. But perhaps the most interesting result was observed for IC2, where
 384 within each guild the superior competitors presented the lowest rate of expansion with respect
 385 to the species of the same guild.

386

PLACE FIGURE 3 HERE



387

388 **Figure 3.** Speed of progress of the species during the first 15 time steps: comparison of the two IC.
 389 Dispersion bars are included.

390

391 **3.2 Model 1: scenarios**

392

393 In order to separate the contribution of each ecological process to the behavior of
 394 the system, we perform numerical simulations with the different scenarios described in the
 395 previous section. In Fig. 4 we show the evolution of the fraction of patches occupied by each
 396 species for scenarios A, B, C and D. Scenario A and B are similar, although some species
 397 have different occupations. The absence of predation (scenario C) greatly modifies the
 398 fraction of occupied patches, which is higher for all species (between 0,8 - 1 for several

399 species). As a consequence, the system needs more time to reach steady state (see Fig. 4, C).
400 Besides, scenario D, without local extinction, is very similar to scenario A (Fig. 4, D).

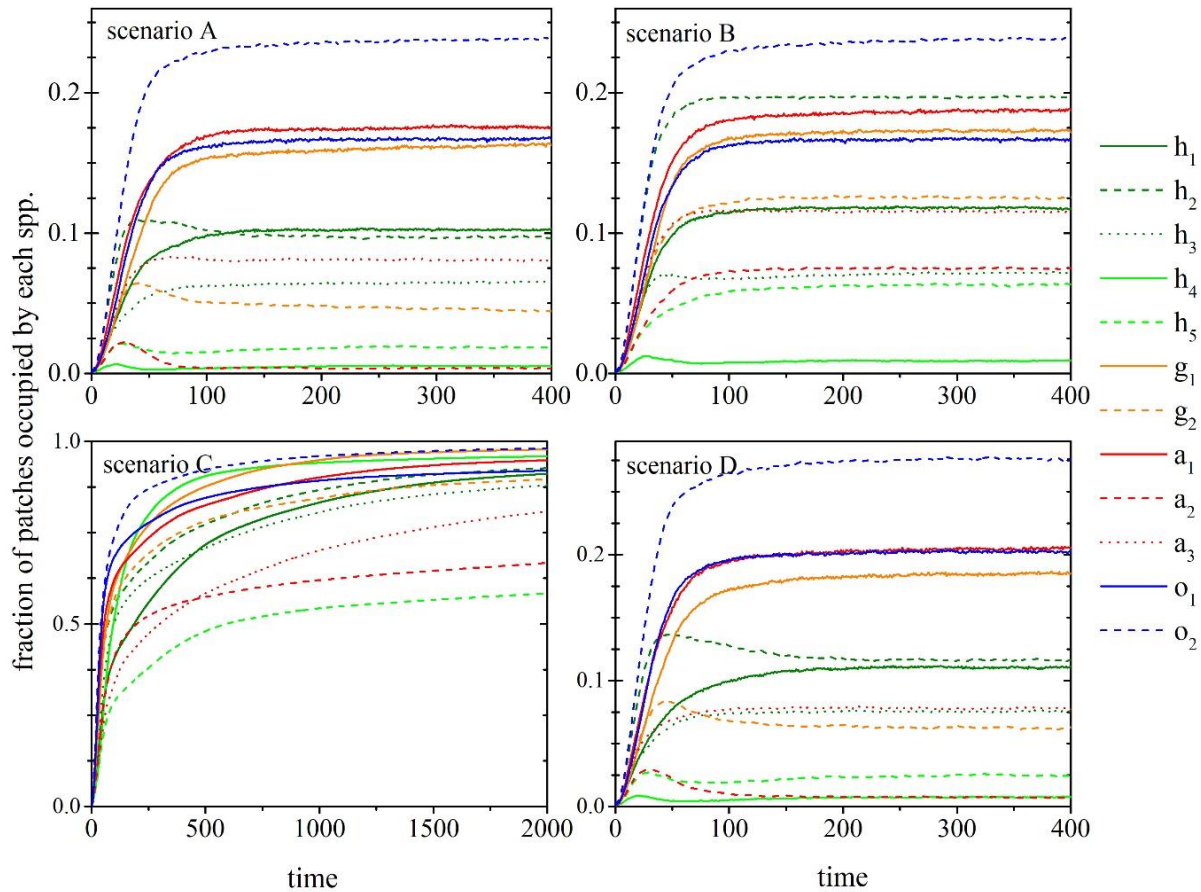
401 The species with the largest occupation area in all scenarios is *A. olivacea* (o₂),
402 meaning that competition and predation have little impact on its colonization. Species with
403 more restricted occupation areas are *Geoxus valdivianus* (a₂), *Irenomys tarsalis* (h₅) and
404 *Phyllotis xanthopygus* (h₄).

405 The species ordering varies slightly between scenarios, especially from the second
406 species onwards: the first is always *A. olivacea* (o₂) but the second and third are *Paynomys*
407 *macronyx* (a₁), *A. hirta* (o₁) and *O. longicaudatus* (g₁) in scenario A, whereas in scenario B,
408 *A. olivacea* is followed by *Euneomys chinchilloides* (h₂) and *P. macronyx* (a₁). A close group
409 of species in scenario C is observed, with *A. olivacea* (o₂), *O. longicaudatus* (g₁) and *P*
410 *xanthopygus* (h₄) followed by almost all the other species with high patch occupancy. The
411 order of species in scenario D is the same as in scenario A, except for a slight change in some
412 species like *E. chinchilloides* (h₂) or *O. longicaudatus* (g₁). Competition and predation were
413 the most important variables shaping the rodent community at this scale, and the influence
414 of local extinction was small when compared to the other studied variables.

415

416

PLACE FIGURE 4 HERE



417

418 **Figure 4.** Evolution curves of species occupations for the different scenarios. Scenario A: complete
 419 scenario. Scenario B: without Fox' rule. Scenario C: without predation (NDVI). Scenario D: without
 420 local extinction. Note the different scales in each case. Species are h_1 : *Reithrodon auritus*, h_2 :
 421 *Euneomys chinchilloides*, h_3 : *Loxodontomys micropus*, h_4 : *Phyllotis xanthopygus*, h_5 : *Irenomys*
 422 *tarsalis*, g_1 : *Oligoryzomys longicaudatus*, g_2 : *Eligmodontia morgani*, a_1 : *Paynomys macronyx*, a_2 :
 423 *Geoxus valdivianus*, a_3 : *Notiomys edwardsii*, o_1 : *Abrothrix hirta*, o_2 : *Abrothrix olivacea*.
 424

425 In scenarios A and B, where extinction has little weight and predation has more
 426 weight, rodent species quickly spread across a lower number of patches compared to scenario
 427 C (without predation), leading to rapid segregation. However, without predation and at the
 428 same time-span, the species are not entirely spatially segregated, as is the case in scenarios
 429 A and B, which take longer to stabilize (temporally speaking) and occupy many more
 430 patches. For example, among the herbivores that inhabit the steppe (*R. auritus* and *E.*
 431 *chinchilloides*), strong spatial segregation is observed following Fox's rule. The model
 432 suggests that *E. chinchilloides* is not common in areas where *R. auritus* is present, even
 433 though the area is suitable for both species according to Maxent's potential distribution maps
 434 (see Supplementary Material 1). The fraction of patches occupied for *E. chinchilloides* at the

435 beginning of the simulation increases rapidly, and decreases as the occupied patches of *R.*
436 *auritus* (h1) increase (Figure 4, A). In scenarios without predation and without Fox's rule
437 (Figure 4, B and C), the increase in occupied patches is monotonic, without decreasing, which
438 could indicate the significant impact that predation and competition have on these species.
439 In scenario A for *I. tarsalis* (h5) and *G. valdivianus* (a2), patch colonization is limited within
440 their environment to areas where *L. micropus* (h3) and *P. macronyx* (a1) did not colonize.
441 Both *I. tarsalis* (h5) and *G. valdivianus* (a2) in scenarios B and C saw an increase in the
442 occupied patches of both species. *E. morgani*, in the model presents a fraction of 0.05 of
443 occupied patches in the complete scenario, which increases to 0.12 without Fox's rule,
444 whereas in the model without predation it reaches 0.8.

445

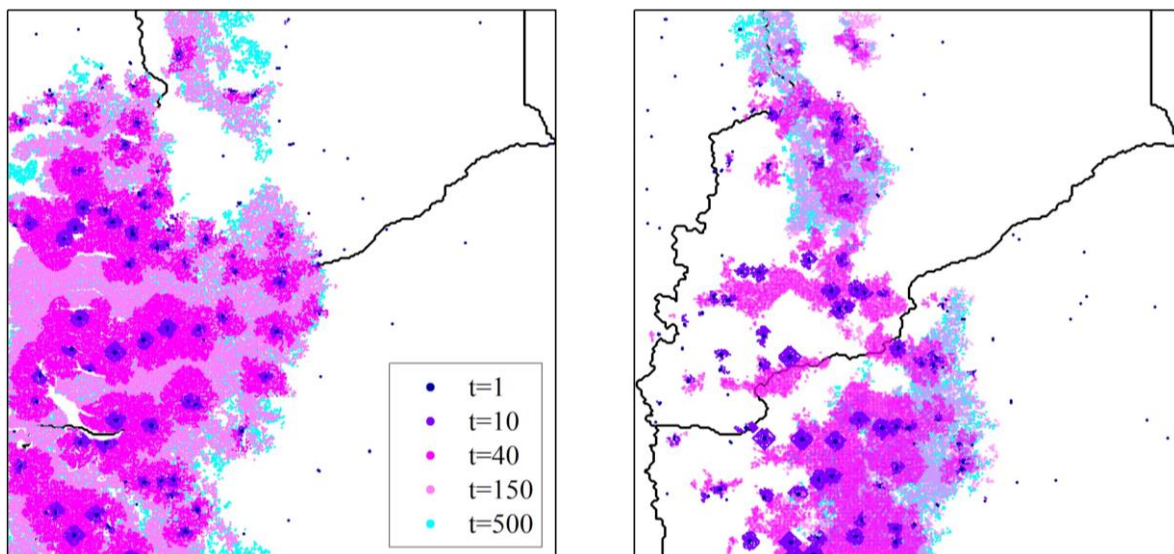
446 To illustrate the dynamical behavior of the metapopulations, we show in Fig. 5
447 snapshots at different simulation times of the occupancy of two species (*O. longicaudatus*
448 and *E. morgani*). Starting from IC1 (the known presence sites), species colonize new patches
449 as time evolves ($t = 1, 10, 40, 150$ and 500), until reaching a final steady state where no
450 further changes are observed (1000 steps in these examples). Complementary information
451 can be obtained from the distribution maps generated for the different scenarios.

452

453

PLACE FIGURE 5 HERE

454



455 **Figure 5.** Snapshots of the evolution of the simulations. Left: *Oligoryzomys longicaudatus* (g_1).
456 Right: *Eligmodontia morgani* (g_2). The simulation time of each snapshot is indicated in the figure.

457 In Figure 6 we show the distribution maps of scenarios A (complete) and B (without
458 Fox's Rule) together with the SDMs generated with Maxent, for three species (maps of the
459 remaining species are presented in Supplementary Material 1). In the distribution maps, the
460 area occupied by species with the complete model (scenario A) is reduced with respect to the
461 ideal area (>50%) of the Maxent SDM maps for species *E. chinchilloides* (h₂), *P.*
462 *xanthopygus* (h₄), *I. tarsalis* (h₅), *E. morgani* (g₂) and *G. valdivianus* (a₂). This might be due
463 to aerial predation and competition for resources. In contrast, in *A. hirta* (o₁), *A. olivacea* (o₂),
464 *O. longicaudatus* (g₁), *R. auritus* (h₁), *L. micropus* (h₃) and *P. macronyx* (a₁) the occupied
465 area was greater than the Maxent ideal area of each species.

466 When comparing the fraction of occupied patches in the steady state, with and
467 without Fox rule, the species that do not present changes in occupancy are the two omnivores,
468 *O. longicaudatus* (g₁), *P. macronyx* (a₁), *R. auritus* (h₁). The species that increase the fraction
469 of occupied patches without Fox's rule are *E. chinchilloides* (h₂), *I. tarsalis* (h₅), *E. morgani*
470 (g₂) and *G. valdivianus* (a₁), showing to be sensitive to competitors. Between species from
471 the same guild, as in *O. longicaudatus* (g₁) and *E. morgani* (g₂), a change in distribution maps
472 is observed with and without Fox's rule, between scenario A and B (see Fig. 6).

473 *P. xanthopygus* (h₄) is the species with the largest predation pressure observed in
474 the model. This species displays a very low occupancy in Scenario A, close to 0 (Fig. 4, A).
475 The map presents two areas of reduced distribution compared to the potential distribution
476 map of Maxent (Supplementary material 1, h₄); the same thing happens in the case without
477 Fox's rule. In the absence of predation, this species increases its occupancy abruptly over
478 time, being one of the species with the highest fraction of patches occupied in the simulation
479 (Fig. 4, C).

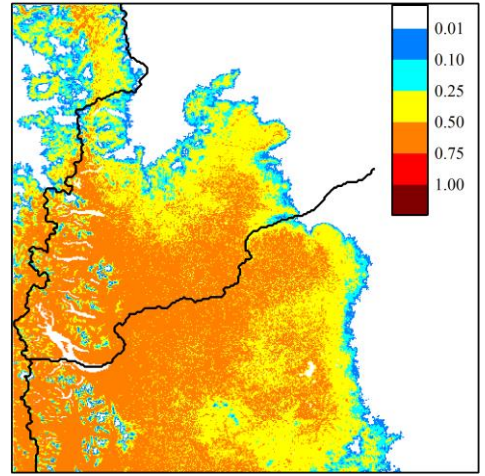
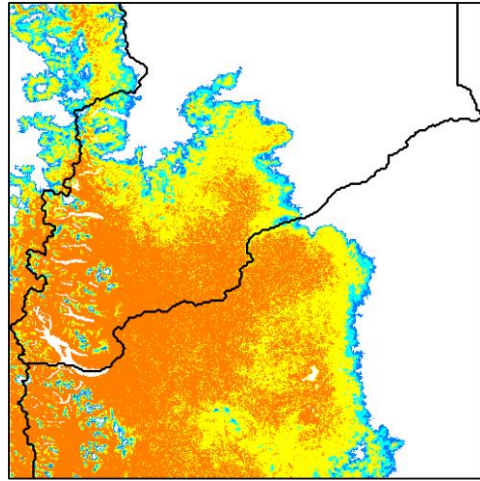
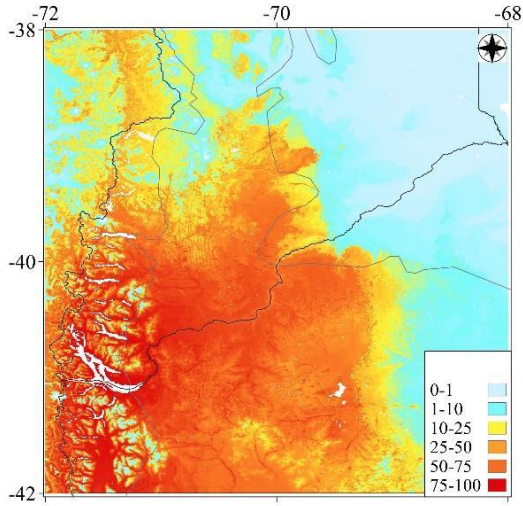
480 **PLACE FIGURE 6 HERE**

481

482

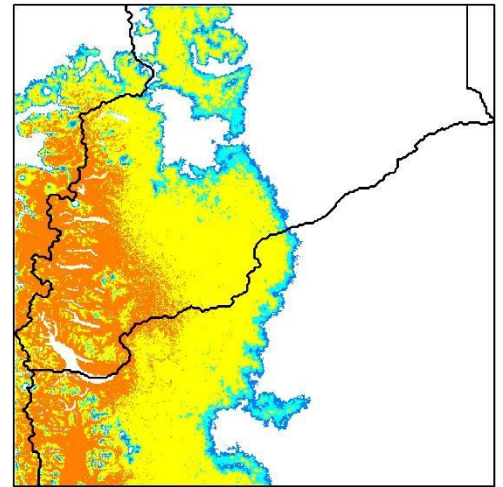
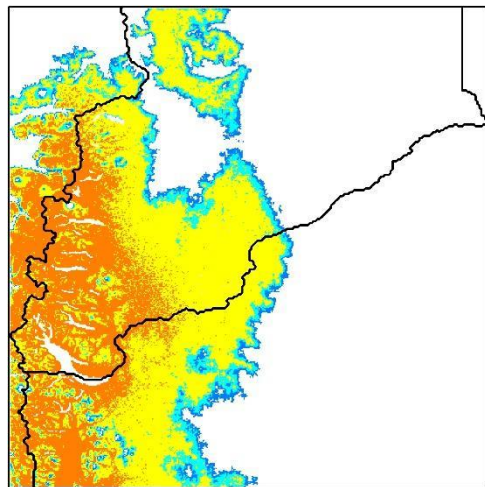
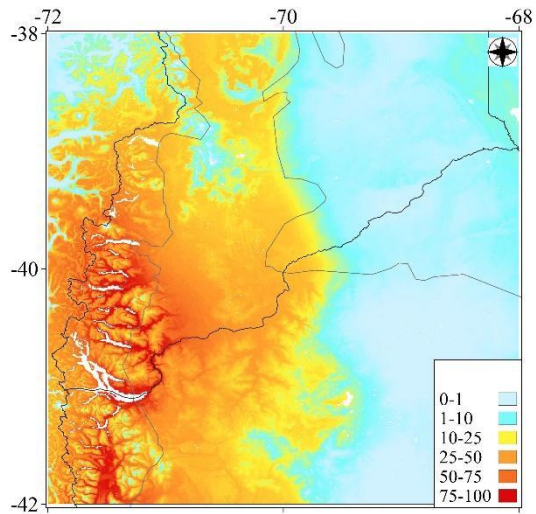


483 o2: *Abrothrix olivacea*



484

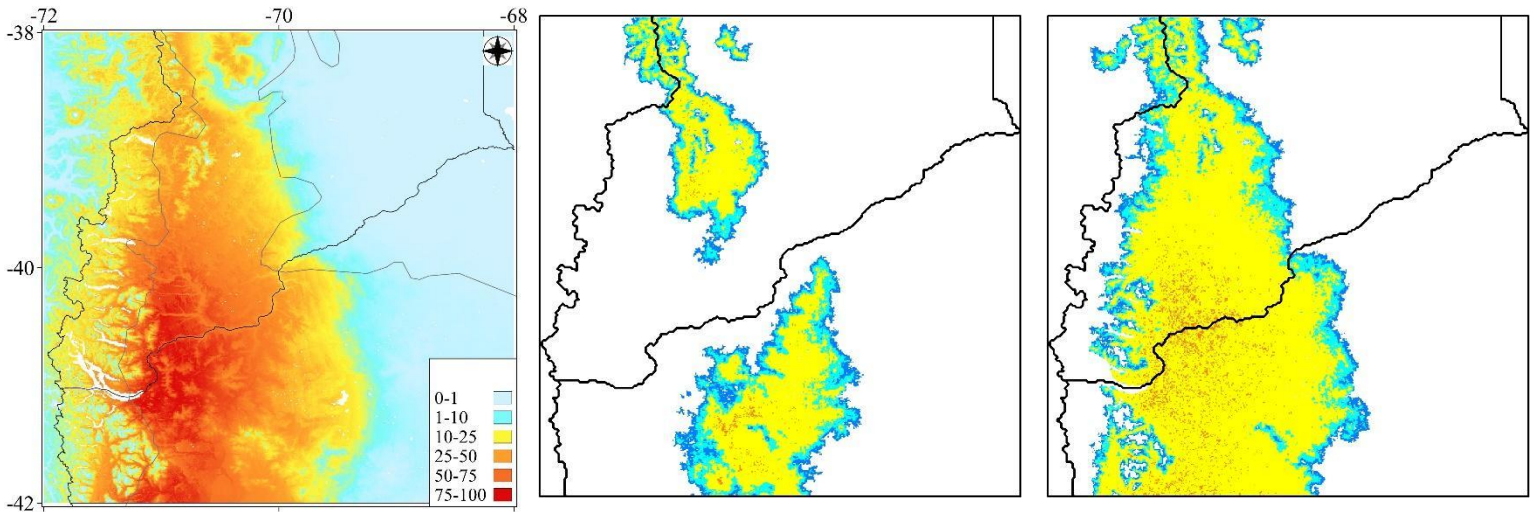
485 g1: *Oligoryzomys longicaudatus*



486

487

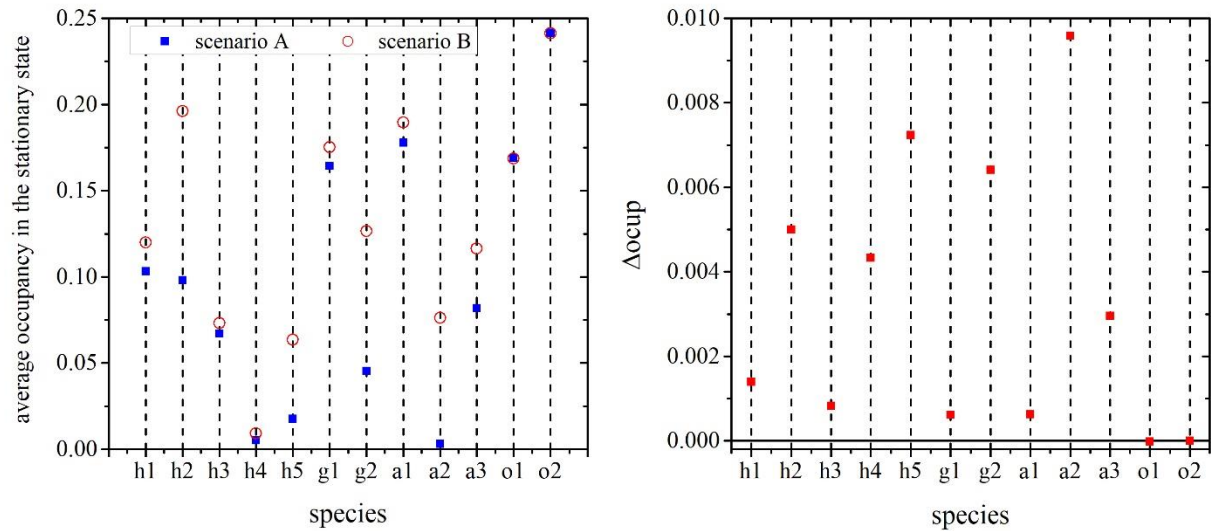
488



490
 491 **Figure 6. Left:** SDMs generated with Maxent. **Center:** Distribution maps with Model 1 in Scenario
 492 A. **Right:** Distribution maps with Model 1 in Scenario B. Maps for the other species are presented in
 493 Supplementary Material 1.
 494

495
 496 To quantify the difference between distribution maps of Scenarios A and B we
 497 calculate the mean occupations in the steady state (averaging the last 100 steps) in both cases
 498 (Fig. 7, left panel). Again, *A. olivacea* (o_2) was the species that occupied the highest average
 499 number of patches in the steady state, with and without Fox's rule.

500 Besides, the relative difference in occupations for each species, given by $\Delta_{occup} =$
 501 $\frac{occupation(scenario\ B) - occupation(scenario\ A)}{occupation(scenario\ B)}$ was calculated to get a measure of each species'
 502 gain from not competing (Fig. 7, right panel). When comparing the fraction of occupied
 503 patches in the steady state, with and without Fox's rule, the species that did not present
 504 changes in occupancy were the two omnivores, and the superiors of each trophic guild, *O.*
 505 *longicaudatus* (g_1), *P. macronyx* (a_1), and *R. auritus* (h_1). The species that increased the
 506 fraction of occupied patches without Fox's rule were *E. chinchilloides* (h_2), *I. tarsalis* (h_5),
 507 *E. morgani* (g_2) and *G. valdivianus* (a_2), showing to be sensitive to competitors. Among the
 508 animalivore species, *P. macronyx* (a_1) occupied more patches than *G. valdivianus* (a_2).



50

510 **Figure 7.** The final states of the average occupancy in the steady state, with and without Fox's rule
 511 (right) and difference in occupations (left).

512

513 **3.3 Model 2: resolution 30 meters**

514

515 Since the biotic factors of competition and predation are visible at a local -patch-
 516 scale, we carried out numerical simulations with the Model 2, using recently available images
 517 with a resolution of 30 meters. In Figure 8 we show the distribution maps for three species
 518 and two different vegetation indices (NDVI and MSAVI) for the calculation of aerial
 519 predation. The maps of the other species are presented in Supplementary Material 2.

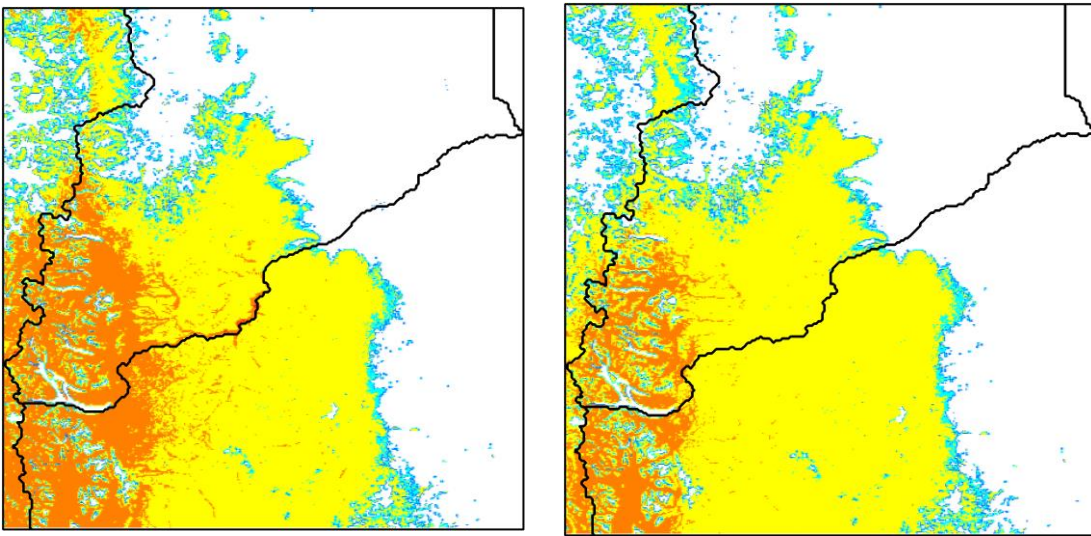
520 The reason behind the inclusion of the MSAVI index is that it is more suited for
 521 areas with sparse vegetation than NDVI. However, in general, the distribution maps obtained
 522 with MSAVI present the same distribution patterns than the ones obtained with NDVI, but
 523 smaller areas of high occupancy for some species, as *E. chinchilloides* (h₂), *L. micropus* (h₃)
 524 or *O. longicaudatus* (g₁).

525 Compared maps at both resolutions (Figs. 6 and 8, and their respective
 526 Supplementary materials) showed similar results, albeit with small patches of occupancy
 527 appearing at the 30 m resolution model that were not visible in Model 1, as is the case in *P.*
 528 *xanthopygus* (h₄), *E. morgani* (g₂), *G. valdivianus* (a₂), *I. tarsalis* (h₅) and *A. hirta* (o₁). In the

529 species with the largest area of occupancy, *A. olivacea* (o_2), the area with the highest
530 occupancy is smaller in Model 2 (Fig. 8) than in Model 1 (Fig. 6). An opposite behavior is
531 observed for *R. auritus* (h_1), where the main area of occupancy is smaller in Model 2,
532 although several dispersed patches are observed. In *E. chinchilloides* (h_2), on the other hand,
533 the main area of occupancy is greater and, again, dispersed patches are observed (see Supl.
534 Mat. 2).

535 **PLACE FIGURE 8 HERE**

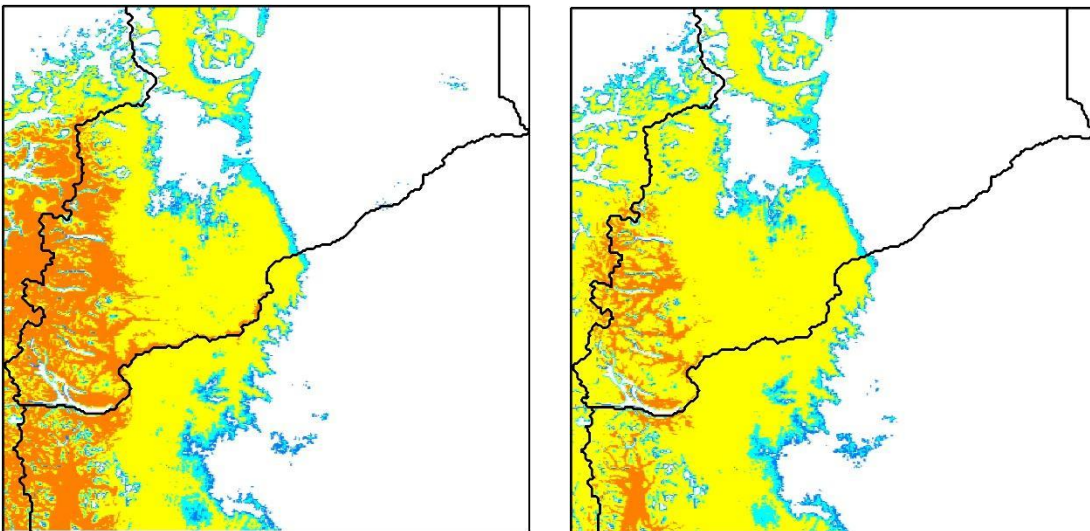
536 o_2 : *Abrothrix olivacea*



544

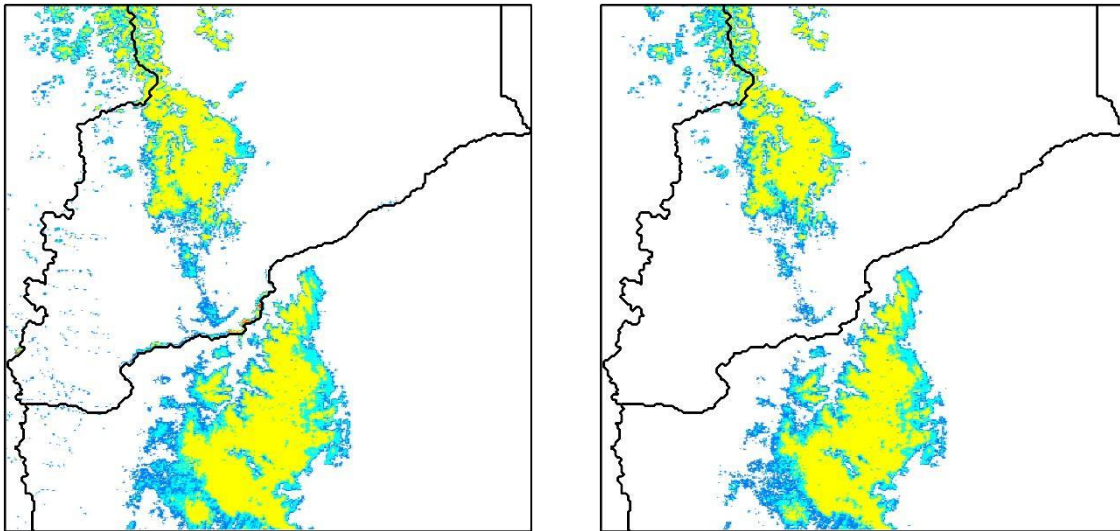
545

546 g_1 : *Oligoryzomys longicaudatus*



556

557 g2: *Eligmodontia morgani*



558

559 **Figure 8** Distribution maps of Model 2. **Left:** NDVI, **Right:** MSAVI. (The maps of the other species
560 are in Supplementary material 2).

561

562 *E. morgani* (g_2) seems to suffer from competitive exclusion by *O. longicaudatus*
563 (g_1), with a distribution reduced to small patches where the competitor is present. *G.*
564 *valdivianus* (a_2) and *I. tarsalis* (h_5), species living in the Patagonian forest, also compete in
565 their trophic groups occupying small patches throughout the area, in coincidence with known
566 sites of presence of each species, a pattern that was not visible in Model 1.

567

568 **3.4 Overlap between the model and real data**

569

570 Distribution maps can be used to quantify the degree of overlap between the
571 patches most visited by a given species in the metapopulation model and the sites where it
572 was actually found. We use the maps generated with Model 2 for the two vegetation indices,
573 NDVI and MSAVI, and $IC2=0.1\%$ to evaluate the proportion of coincidence of sites inside
574 or outside the areas for each species (see Table 1). In both cases, the species that do not
575 overlap are *G. valdivianus* (a_2), *I. tarsalis* (h_5), *E. morgani* (g_2) and *P. xanthopygus* (h_4),
576 whereas the rest of the species have a good match.

577

578

PLACE TABLE 1 HERE

579

Table 1. Table of coincidences with sites of presence of each species, for two implementations of Model 2, with NDVI and MSAVI (c: coincidences).

580

581

Specie	Category	N° sites of presence	NDVI		MSAVI	
			c	%	c	%
<i>Reithrodon auritus</i>	h1	5	2	40	2	40
<i>Euneomys chinchilloides</i>	h2	19	13	68	14	74
<i>Loxodontomys micropus</i>	h3	43	25	58	24	56
<i>Phyllotis xanthopygus</i>	h4	5	0	0	0	0
<i>Irenomys tarsalis</i>	h5	30	1	3	2	7
<i>Oligoryzomys longicaudatus</i>	g1	47	43	91	43	91
<i>Eligmodontia morgani</i>	g2	28	1	4	0	0
<i>Paynomys macronyx</i>	a1	45	41	91	41	91
<i>Geoxus valdivianus</i>	a2	44	1	2	0	0
<i>Notiomys edwardsii</i>	a3	3	2	67	2	67
<i>Abrothrix hirta</i>	o1	57	52	91	53	93
<i>Abrothrix olivaceus</i>	o2	37	34	92	33	89

582

583

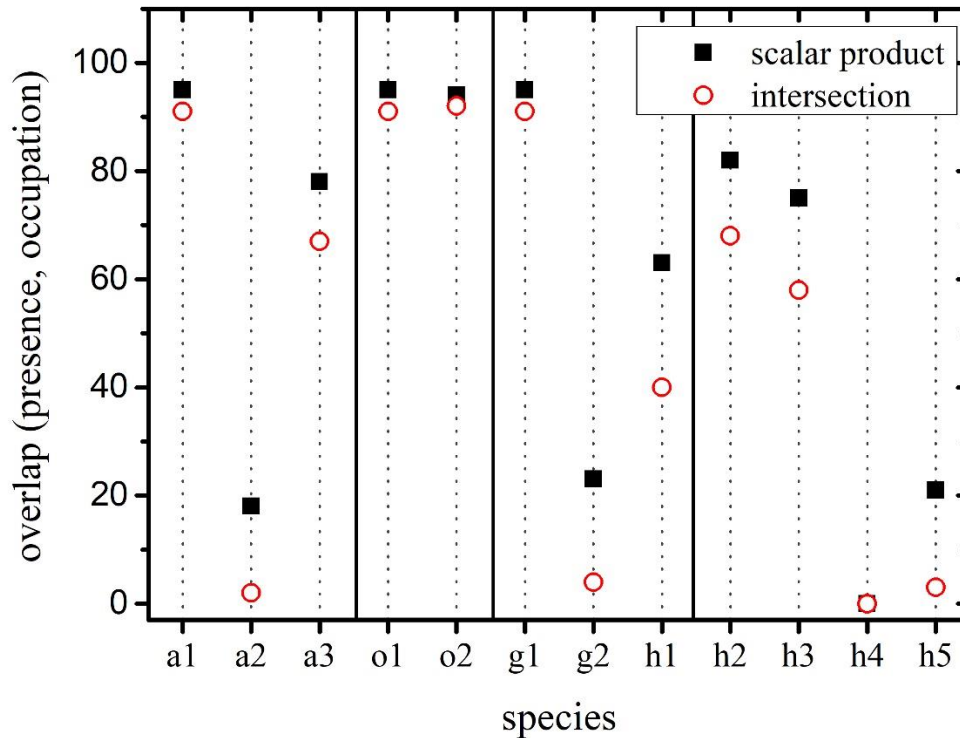
Two other ways to evaluate the degree of overlap between the known data and those obtained with the model are shown in Fig. 9. One metric, named *intersection* in the figure, corresponds to calculating the ratio between the number of patches with occupancy higher than 10% and the number of sites of presence. The other is the *scalar product* between the normalized vectors of presence and occupation. In this last case, no occupation threshold is needed (as the 10% used in the first one). High values of these quantities indicate that the model is good at predicting the sites where the species was actually found. It is worth noting that the species that present low values of these quantities coincide with those in Table 1, while the remaining ones have coincidence values greater than 50%.

592

593

PLACE FIGURE 9 HERE

594



595

596 **Figure 9.** Overlap between presences and occupations, characterized by two metrics: intersection and
 597 scalar product, as defined in the text.

598

599 The results presented in this section show that rodent species are strongly affected by
 600 biotic factors, especially aerial predation and, to a lesser extent, competition and extinction.
 601 Both aerial predation and competition for resources have effects on the evolution of the
 602 species and on the maps of the final stage.

603

604

605 **4 Discussion**

606

607 On a continental or regional scale, climate is the dominant factor in delimiting the
 608 geographic range, while, at more local scales, factors such as topography and land cover type
 609 become increasingly important. At progressively smaller scales, factors including biotic
 610 interactions and microclimate may become most relevant, since climate and topography
 611 become invariant (Pearson and Dawson, 2003). Our models show how interspecific
 612 interactions (i.e., predation, competition) shape a rodent community at a scale of 1=10.000
 613 or below. The distribution models generated through numerical simulations using
 614 environmental variables (from SDMs) and biotic variables are consistent, showing a clear

615 effect of predation and competition in the spatial arrangement of the different species of
616 rodents. Pearson and Dawson (2003) showed that biotic interactions have important impacts
617 on the distribution of species. They define the natural system as a complex network of
618 interactions and feedback between species, so changes in the distribution of a single one may
619 have important repercussions on the distribution of many others. Therefore, modeling
620 strategies based solely on bioclimatic envelopes can, in some cases, lead to distributions on
621 a continental or regional scale that lose predictive power on a local scale. Through the
622 simulation models presented here, we described how populations and their distributions are
623 altered by predation and competition, showing experimentally how species influence each
624 other's distribution, following Fox's (assembly) rule.

625 The coincidence of the final states of both ICs suggests a remarkable robustness in
626 our results. Models evolved from an initial condition consisting of sites of known presence
627 achieve a density similar to those that use randomly distributed sites for initial conditions. In
628 addition, we tested much larger initial densities (20% of the sites initially occupied), and in
629 all the cases the same steady state was reached, showing independence of the initial
630 conditions.

631

632 4.1 Biotic variables

633 The effect of predation is the biotic variable that showed the highest influence with
634 the spatial arrangement or habitat selection of the studied species. We observed that the
635 absence of predation greatly modified the occupation models: all species show a considerable
636 increase in the fraction of occupied patches, without reaching a balance. The models showed
637 areas (or patches) that rodent species could occupy if predators were eliminated or non-
638 existent. Indeed, the ecosystem can undergo a drastic change if a key species is eliminated,
639 and in most cases the keystone species is a predator that can control the distribution and
640 population of large numbers of prey species (Mills et al., 1993; Laguna et al., 2015). Such
641 cases of top-down control of the ecosystem have even been the subject of field
642 experimentation (Terborgh et al., 2001). In our study, the vegetation cover provided shelter
643 and reduced predation risk (Bisceglia, 2014; Corbalán, 2004). As such, predation acts as a
644 selective pressure, influencing habitat selection (rodents tend to use covered sites to a greater
645 extent) and foraging activity (Guidobono, 2013). Some rodents inhabiting arid environments,

646 where vegetation cover can be very low or inexistent, live in rocky areas that could also be
647 used as refuges (such as *E. chinchilloides*; Pearson and Christie, 1991; Pardiñas et al., 2003).

648 The factor with the largest influence in the specific composition of rodent
649 assemblages in the study area is interspecific competition. Models generated without Fox's
650 rule (scenario B) show effects in both the evolution curves of some species and the final
651 spatial occupation. This rule reduces the occupied sites, the proportion of patches that some
652 species occupy is greater and in less time in the absence of competition, while it does not
653 modify the occupancy for other species (e.g. *E. morgani* and *O. longicaudatus* respectively).

654

655 4.2 Types of communities

656 Generalist or eurytopic species such as *L. micropus*, *O. longicaudatus* and *P.*
657 *macronyx* can occupy and proliferate in a wide variety of habitats in the forest and in the
658 broad ecotone between the forest and the Patagonian steppe. These species show, in the
659 indicators studied with Maxent, a wide range of tolerance to climatic and environmental
660 variables. They are the species that occupy the largest number of patches. In contrast, habitat
661 specialists such as *E. chinchilloides* have a much narrower niche breadth and, consequently,
662 occupy the few patches of habitat where it can proliferate, usually with little or no presence
663 of competitors (Brown, 1995; Pearson, 1987). They are the ones that occupy the least number
664 of patches.

665 The omnivore species of the genus *Abrothrix* occupied more patches in total in all
666 scenarios. Omnivory can be a form of adaptation to the unpredictability of the environment,
667 since these generalist and opportunistic species vary their diet according to the local and
668 seasonal availability of food resources (Noy-Meir 1979, 1980; Corbalán, 2004). *Abrothrix*
669 *hirta* appears to be a "local specialist" (Fox and Morrow, 1981) in response to the availability
670 of local resources; it is strongly insectivorous in semi-arid regions (Meserve, 1981), but
671 strongly fungivorous in forested regions (Meserve et al., 1988). Regarding *Abrothrix*
672 *olivacea*, in a heavily altered pine plantation Muñoz-Pedreros et al. (1990) found it to be
673 herbivorous. However, in less disturbed habitats, this species has been shown to be quite
674 omnivorous (Meserve, 1981; Pearson and Pearson, 1982; Meserve et al., 1988).

675 This differential use or resource partitioning facilitates the coexistence of species
676 within a community (Kotler and Brown, 1988; Shenbrot et al., 1999). The diverse geographic

677 adaptations exhibited by these species result in distinct efficiencies in resource acquisition
678 from the ecosystem and subsequent biomass conversion. In that sense, a surrogate of their
679 success could be the number of patches occupied in the model, if each patch has the same
680 density of individuals of each species. Following this assumption, generalist and omnivorous
681 species, by avoiding competition for specialized resources, are the most “successful” in terms
682 of the breadth of their geographic range (measured in number of occupied patches in the
683 model).

684

685 *4.3 Different spatial resolutions*

686 Species minimize the energy costs of interspecific competition through niche
687 segregation, especially in the habitat and trophic dimensions. Such segregation determines
688 the spatial arrangement of populations at a given site. The version of our model with 30
689 meters of resolution has brought us closer to a description of this process.

690 The different resolutions of patches allowed differentiating the effect of competition
691 by Fox’s rule and that of aerial predation in the distribution map obtained in the steady state
692 of the model. These factors that operate at a scale of patches, are reflected even better at 30
693 m resolution. It is at this scale (for example, under a patch of shrubs) that intra-guild exclusion
694 among rodents occurs. Moving from under the canopy of perennial shrubs to bare ground
695 within a few meters of the bush edge, rodents undergo striking and important changes with
696 respect to microclimate, substrate, resource availability, and predation risk (Kotler and
697 Brown, 1988). The apparent coexistence at the scale of 1 km conceals this spatial segregation,
698 driven by Fox’s rule, that operates at another scale. As the simulation progresses, with smaller
699 patches and greater detail of vegetation cover, colonization or predation interactions are
700 greater for the total study area and spatial arrangement changes for some species.

701 Habitat selection is a process by which an animal chooses from among alternative
702 available habitat resources (Johnson, 1980; Litvaitis et al., 1994); it is a hierarchical process
703 (Hutto, 1985) that can occur at a variety of spatial scales from the macrohabitat to the
704 microhabitat level (Kotler and Brown, 1988). The importance of the spatial scale in habitat
705 selection studies has been demonstrated by diverse authors and can directly influence results
706 and their interpretation (Morris, 1987; Corbalan, 2006).

707

708 *4.4 Vegetation indices*

709 We used different vegetation indices to evaluate the effect of each one on the models,
710 and across the different habitats found in the study area. To the east is the Patagonian steppe,
711 with low vegetation cover, and to the west the Patagonian forests with abundant coverage.
712 The NDVI, which is arguably the most used index in remote sensing, has the advantage of
713 being calculated in a very simple way, while its disadvantages are the low efficiency to
714 normalize the effect of the soil and its lower sensitivity to the presence of dense vegetation
715 (Gilabert, 1997; Kinderknecht et al., 2017). We also used the *modified soil adjusted*
716 *vegetation index* (MSAVI) because in areas with sparse vegetation, surface reflectance and
717 vegetation indices are influenced by exposed soil (Huete, 1988; Qi et al., 1994; Huete et al.,
718 2002). Probably, for the species that inhabit the steppe (such as *E. morgani*, *E. chinchilloides*)
719 the model with MSAVI could better represent their distributional pattern than the ones with
720 NDVI, improving the resolution in areas of scarce coverage, and allowing a better
721 discrimination of small patches of vegetation. For forest-dwelling species, however, NDVI
722 may be a good option.

723 It is important to note that the results of the model, regarding the effect of predation,
724 may be simplified and biased by the fact that we used an indirect proxy for it, in terms of the
725 role played by vegetation cover, as represented by the vegetation indices. Future versions of
726 these models may consider the influence of terrestrial predators, such as foxes, cats, grisons
727 and marsupials, which may be less influenced by vegetation cover compared to aerial
728 predators. However, habitat suitability in terms of vegetation cover, could be a determining
729 factor for the population growth of the species most vulnerable to aerial predation (Bisceglia
730 2014). This author agrees that patches with greater vegetation cover offer shelter, reducing
731 the risk of predation, and in many cases providing a greater availability of food (Thompson,
732 1982; Jaksic, 1986; Simonetti, 1989). For an assemblage of Chilean small mammals, all
733 species showed a clear preference for closed shrubby environments, and a strong response to
734 simulated predation (Simonetti, 1989).

735

736 *4.5 Model*

737 The novel combination of Maxent and Fox's rule within the same simulation model,
738 also including vegetation indexes, allows us to discriminate the effect of competition and
739 predation on the number of occupied patches. There is an important distinction between how
740 a species would function on its own and how it does in the presence of competitors (Leibold,
741 1995; Crawley, 1997; Pearson and Dawson, 2003). The fact that competition and predation
742 influences the distribution of a species was recognized in experiments (Davis et al., 1998).
743 Predation is a fluctuating biotic interaction, with strong temporary effects and on some
744 members of the ensemble only (Meserve et al., 2003). In this way, the possibility arises that
745 rodent populations are regulated not only by a bottom-up mechanism (of availability of
746 resources), but also by a top-down mechanism (presence of predators) (Bisceglia, 2014;
747 Meserve et al., 2003).

748 Members of the same assemblage can respond differently to the same environmental
749 conditions (Meserve et al., 2003, 2011; Haythornthwaite and Dickman, 2006), coexisting in
750 the same habitats. The simulation model suggests that predation pressure does not necessarily
751 change the spatial distribution of the species, but rather regulates the abundance of
752 individuals and, by maintaining a balance of competing species, mitigates competitive
753 exclusion and allows coexistence. This means that the absence or presence of a species should
754 not necessarily be expected due to predation, since the main impact is on relative abundance,
755 which is invisible on maps and metapopulation models. For this reason, results of the biotic
756 interaction models generated in this study focused on distribution (and not abundance), and
757 must be interpreted within the conceptual framework of spatially explicit ecological niche
758 modeling and metapopulation models. In this context, the role of biotic interactions in the
759 delimitation of species distribution areas may be somewhat blurred, but this is precisely
760 because they are distribution models and not abundance models, where results would be
761 expected most prominent in terms of the role of biotic interactions. It is interesting to note
762 here that one of the reasons why competition seems to have no influence on the range of
763 these species, as has been documented for large vertebrates occupying the habitat matrix and
764 not small patches, may be because in the case of small mammals the process operates at a
765 microscale in heterogeneous environments. Competition does not influence geographical
766 distribution, it only influences local spatial arrangement.

767 The models resulting from this work provide a first approximation from real data
768 (i.e., known presence sites of different species living in the study area), including
769 environmental information from SDMs, and incorporating the influence of biotic
770 interactions. Following a metapopulation methodology where the species initially inhabit the
771 patches where their known site of presence is located, with different rules and probability
772 data, they may or may not colonize a neighboring patch, be predated, or become extirpated.
773 These models allow studying population dynamics combining information on individual
774 species traits and habitats, including physical barriers or anthropic effects, with real field
775 data. We hope this can be a starting point for new models analyzing species populations,
776 allowing us to predict future scenarios in a changing environment, such as the effect of
777 climate change.

778

779 **Conclusions**

780

781 From the results of this work, the following could be tested in other study sites and
782 with other species, with a view to looking for general processes and patterns:

783

- 784 ● The predictive power of climatic indicators decreases at the local scale because they
785 become spatially invariant, becoming irrelevant to explain species dynamics at
786 smaller spatial scales.
- 787 ● At local scales, the composition of species assemblages in heterogeneous patches is
788 driven by interspecific competition, the mechanism of which follows rules of
789 coexistence linked to their trophic guild.
- 790 ● The smaller the scale, the greater the influence of biotic factors and the intervention
791 of chance, that is, stochastic processes that escape the patterns that can be
792 deterministically modeled.
- 793 ● Species belonging to the same trophic guild are segregated in habitat preference,
794 minimizing coexistence in the same habitat patch.
- 795 ● Predation pressure influences the pattern of occupation of patches with different
796 cover or quality of refuge.

- 797 ● A complete distribution model must include the influence of climate in the
798 conformation of the set of regional species (gamma diversity), and the influence of
799 biotic interactions in the conformation of the structure of local assemblages (alpha
800 diversity), which determine the arrangement of microhabitat spatial patches, and
801 spatial disposition as a surrogate of processes driven by the abundance of species.
- 802 ● The most successful species in occupying patches (surrogate of the size of the
803 geographic range) are the omnivorous and habitat generalists, that is, those that best
804 avoid competitive interference for resources.
- 805 ● We find a notable similarity with the strategy of never fighting to never be defeated,
806 as stated in the quote from the Aikido sensei that we used at the beginning of the
807 paper. The energy saved by avoiding fighting can be redistributed into gaining
808 occupied territory. Can we learn from mice?

809
810

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812

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