



Research article

Fleas of mammals and patterns of distributional congruence in northwestern Argentina: A preliminary biogeographic analysis

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ABSTRACT

In few groups of parasites have the patterns of distribution been studied using quantitative methods, even though, the study of these organisms indirectly provides information on the biogeographic history of their hosts, and in turn, the history of the hosts allows elucidation of speciation events of the parasites. Our objective was to quantitatively identify distributional congruence patterns of native fleas in northwestern Argentina. We analyzed 159 georeferenced distributional records of 47 species and six subspecies of fleas in northwestern Argentina using NDM/VNDM software. We found eight consensus areas, defined by 17 species and two subspecies, included in six patterns of distributional congruence (PDCs) with endemic and non-endemic fleas. The PDCs with the greatest values of endemism (E) were mainly associated with Monte and Yungas Forests areas. All patterns indicated strong tendency of the Yungas Forests as a possible endemism area. Our results indicate that distributional congruence centers are generally located in Yungas Forests areas and highlight the importance of these areas in conservation and historical biology. This new information will allow delimitation of areas in the region at a more detailed resolution in the future.

1. Introduction

An area of endemism (AEs) is defined by the congruence of the areas of distribution of two or more species (Espinosa et al., 2001). These areas of endemism are considered as hypotheses of primary biogeographic homology, that is, conjectures about a common biogeographic history among taxa (Morrone, 2001). Sandoval and Ferro (2014) also recognize another area category: patterns of distributional congruence (PDCs), defined only or mostly by sympatric species, not endemic to the study region, and this category provides the first-step testable hypotheses of AEs for future analyses of neighboring regions, or analyses at more inclusive scales (Szumik et al., 2012).

Only in a few groups of parasites have distribution patterns been studied using quantitative methods (Morrone and Gutiérrez, 2005; Liria and Navarro, 2007; Luque and Poulin, 2007; Oliveira et al., 2017). The study of parasites indirectly provides information about the

biogeographic history of their hosts, and in turn, the history of hosts allows elucidation of speciation events in parasites (Escalante et al., 2011).

Fleas are obligatory hematophagous parasites of higher vertebrates; the majority of fleas parasitize mammals, whereas their association with birds is less frequent (Medvedev and Krasnov, 2006). Primary association of fleas with small mammals is observed in all parts of the world (Krasnov, 2008). Fleas have evolutionary adaptations and ecological interactions with other organisms and it is estimated there are 2575 species in the world, therefore, fleas can be an excellent study group for geographic distribution analyses (Krasnov et al., 2005; Hastriter and Whiting, 2009; Bossard, 2014). Krasnov (2008) proposed that geographical distribution of a flea species should be a result of interaction between its responses to the geographical distribution of host/s and to the off-host environment. The degree of flea endemism varies among regions of the world, and in the Neotropical region the main hosts for endemic flea species are rodents of the subfamily Sigmodontinae

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(Cricetidae) and the family Caviidae (Krasnov, 2008). As mammals are becoming more threatened throughout the world, their associated fleas are disappearing at an alarming rate before they are even described, with habitat loss the greatest threat to the species (Kwak and Hastriter, 2020). The natural habitats of the world continue to disappear being replaced by agriculture land, housing, roads, pipelines, and other features of industrial development (Pardini et al., 2017). Since the areas with high endemism have been indicated as promising areas for conservation (Myers et al., 2000), the search and discovery of these areas could be of great value for the conservation of hosts and their parasites.

Fleas are also important from the epidemiological point of view, because they are capable of transmitting pathogenic organisms to wild

and domestic animals and even to humans (Bonvicino et al., 2015). The analysis of the biogeographic patterns of the vector flea species will allow proposing biogeographic hypotheses that can be interpreted to explain the spatio-temporal integration of the endemic species and, in the future, deduce biogeographic factors and history of the different diseases in which fleas participate (Murray et al., 2018).

In Argentina, 130 species, 24 subspecies, and 37 genera belonging to 11 families (Ceratophyllidae, Ischnopsyllidae, Leptopsyllidae, Ctenophthalmidae, Hystrichopsyllidae, Stephanocircidae, Malacopsyllidae, Pulicidae, Tungidae, Rhopalopsyllidae, and Pygiopsyllidae) were recorded, of which 47 species are endemic (Beaucournu et al., 2004; Beaucournu and Gallardo, 2005; Lareschi et al., 2016; López-Berrizbeitia and Díaz,

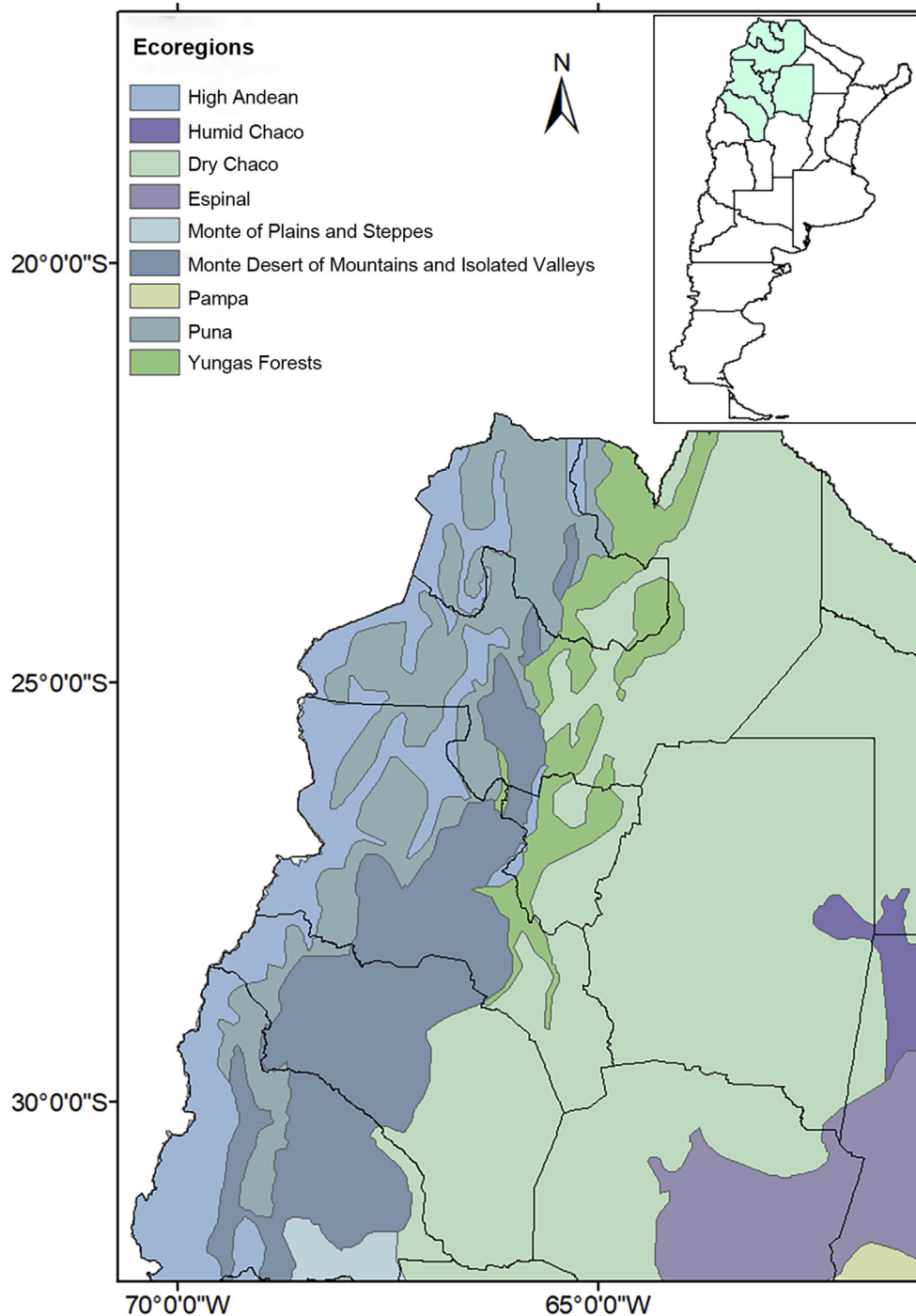


Figure 1. Geographic location of northwestern Argentina, limits, provinces, and ecoregions.

2019). A large number of these fleas are distributed in northwestern Argentina (NWA), where 55 species and nine subspecies are mainly parasites of sigmodontine rodents (Lareschi et al., 2016; López-Berrizbeitia and Díaz, 2019). Of this total, four species are cosmopolitan, while the rest are native and seven of them are endemic. Most of the eco-regions in NWA are in an accelerated process of degradation, as for example the dry Chaco (Torrella et al., 2007, 2011) and Yungas Forests (Brown et al., 2001). The change from natural vegetation to cultivated areas is a constant threat to mammal hosts in this type of habitat (Ewers and Didham, 2006; Peters et al., 2006). On the other hand, NWA is interesting from the epidemiological perspective because bordering plague endemic areas (Bolivia and Peru) and there are other diseases transmitted by bacterial pathogens recorded in fleas (Schneider et al., 2014; Berger, 2018).

This paper represents the first quantitative analysis of distributional records of parasites of the order Siphonaptera from northwestern Argentina, recognizing patterns of distribution congruence and species that characterize them. In addition, we correlate these distributional patterns with traditional biogeographic divisions of the area as well as with other biogeographic studies of the main hosts of fleas, carried out in the same region (Sandoval and Ferro, 2014; Sandoval et al., 2015).

2. Material and methods

2.1. Study area

Northwestern Argentina (NWA) comprises six provinces: Catamarca, Jujuy, La Rioja, Salta, Santiago del Estero, and Tucumán (Carlevari, 1994; Bolsi et al., 1997a, b) (Figure 1). The region is complex because it harbors a great variety of landscapes (Santillan de Andres and Ricci, 1998), which is reflected in its diversity of flora and fauna (Burkart et al., 1999). The region is characterized by a climatic heterogeneity as a product of latitudinal and altitudinal gradients as well as geomorphological variations. Predominantly, there are two types of climates; warm and humid (subtropical) and cold and dry (arid) associated with the availability of moisture-laden air masses along different altitudinal limits (Godoy-Burki et al., 2014). Biogeographically, NWA is part of the Neotropical Region, one of the greatest phytogeographical regions on earth, and occupies an important portion of the Argentine territory, sharing the Amazonian, Chacoan, and Andean Patagonian Dominions (Cabrera, 1976). According to Burkart et al. (1999), the ecoregions found in NWA are: Yungas Forests (Amazonian Dominion), High Andean and Puna (Andean- Patagonian Dominion), Dry Chaco, Monte Desert of Mountains and Isolated Valleys, and a small portion of Humid Chaco (Chaco Dominion). The Yungas Forests are distributed discontinuously in the Salta, Jujuy, Tucumán, and Catamarca provinces, integrating into the sub-Andean mountains. Their altitudinal range varies between 400 and 3000 m (Burkart et al., 1999). The climate is warm and humid (Cabrera, 1976). This ecoregion is divided into three districts by elevational gradient: transitional Forest, lower Montane Forest, and upper Montane Forest (Cabrera, 1976). The Transitional Forest is a microphyllous semideciduous forest that occurs as a strip on the foothills (350–500 m). The lower Montane Forest occurs on the lower eastern slopes (500–1500 m) and is the rainiest district of the Yungas. The upper Montane Forest appears as a ribbon on the upper slopes of these mountain (1500 m up to 3500 m). In this latter district, two different habitats are found: deciduous forest dominated by Andean alder (*Alnus acuminata*) (1500–2700 m); and bunchgrasses meadows (*Festuca eriostoma*, *Poa lilloi*, and *Stipa saltensis*) above, up to 3500 m, which gives way to the spiny and sparse grasses (*Festuca orthophylla*) of the uppermost vegetation formation: the high Andean steppe deserts of the Puna ecoregion (Cabrera, 1976; Ferro, 2013).

The High Andean extend through the high mountains in the west of Argentina (Cabrera, 1976), it reaches 4400 m in the Jujuy and Salta provinces (Cabrera, 1976; Burkart et al., 1999). The climate is cold and dry, with snow or hail precipitations in any season of the year (Cabrera,

1976); and the vegetation is mainly characterized by a grassland or shrub-steppe (Burkart et al., 1999). The Puna presents elevations above 3000 m. The climate is cold and dry, with a greatly varied temperature range, between 30 °C and below -20 °C (Burkart et al., 1999; Matteucci, 2018). The dominant vegetation type is the shrub-steppe (Cabrera, 1976). The Dry Chaco presents a warm climate, with scarce precipitations (Cabrera, 1976); the characteristic vegetation is xerophytic woodland, but there are also mountain forests, dry savannas and grasslands (Burkart et al., 1999). The Humid Chaco is restricted, in the NWA, to only a small part of the east of the Santiago del Estero province; the climate is subtropical warm; and the vegetation is more diverse than in the Dry Chaco, the forests are mainly represented by willow-leaf red quebracho (*Schinopsis balansae*), guayacán (*Caesalpinia paraguayensis*), white quebracho (*Aspidosperma quebracho blanco*), among others; and lower, trees often appear bordering estuaries and ravines, they include white carob tree (*Prosopis alba*), churqui (*Acacia caven*), spiny hackberry (*Celtis ehrenbergiana*), and grasslands (Burkart et al., 1999). Finally, Monte Desert of Mountains and Isolated Valleys (hereafter referred to as Monte) has a dry subtropical climate. All the ecoregion receives little rainfall, between 80 and 200 mm (Burkart et al., 1999). The vegetation is characterized by a high, very open shrub-steppe, dominated by the jarilla (*Larrea divaricata*), brea (*Parkinsonia aculeata*), and retamo (*Bulnesia broom*), among others (Burkart et al., 1999).

The map of NWA, including provinces and ecoregions (Figure 1), was designed with the ArcGis 10.1 program (ESRI, 2011).

2.2. Data

The taxonomy used herein follows that outlined in Whiting et al. (2008). The main source of data corresponds to the specimens examined during the doctoral thesis of López-Berrizbeitia (2018), from systematic collections and collected specimens (see Appendix I); but we also augmented the information by including published localities of occurrence from the literature for some species (Johnson, 1957; Smit, 1987; Lareschi et al., 2016). A total of 165 records was obtained, 159 georeferenced and six not mapped because the original localities were imprecise or not located. All localities were located and corroborated using maps or satellite images (the Google Earth Pro Version 2016).

Georeferenced records belong to 47 (Appendix II) of the 55 known flea species distributed in NWA. The following species were not included in the analysis: *Pulex irritans* Linné, 1758, *Tunga penetrans* (Linné, 1758), *Ctenocephalides felis* (Bouché, 1835), *Leptopsylla segnis* (Schönherr, 1811), *Nosopsyllus fasciatus* (Bose d'Antic, 1800), and *Xenopsylla cheopis* (Rothschild, 1903); because they are not native species and, *Hectopsylla broscus* Jordan and Rothschild, 1906 and *Hectopsylla psittaci* Frauenfeld, 1860 because no localities were found.

2.3. Distributional analysis

To identify AEs (defined only or mostly by sympatric endemic species) and PDCs (defined only or mostly by sympatric, but not endemic species) of flea species in NWA, we used the methodology proposed by Szumik et al. (2002) and Szumik and Goloboff (2004). This method considers patterns of species distribution in order to identify, among all the possible combinations of quadrats in which the study area is divided, those that delimit an area of endemism, by means of a score of endemism (E) given by the number of endemic species for each combination of quadrats. To determine how many species appear as endemic, endemism itself is determined for each species (Szumik and Goloboff, 2004) and the score of endemism or E represents the sum of individual endemism values for all species considered as endemic for a given set of quadrats (see Appendix III).

We analyzed our matrix of georeferenced data using grid cells of three different sizes, 0.50°, 0.75°, and 1° per side. Grid origin was defined and located at 70° long W and 21° lat S. We carried out the endemism analysis through a heuristic search and default NDM parameters:

searching groups of cells by adding or eliminating one cell at a time, and saving groups defined by two or more endemic species and with scores higher than or equal to 2.0. We analyzed our matrix considering filling values for assumed and observed presence.

Finally, we obtained consensus areas using the strict consensus rule with 50% similarity in species. The method is implemented in the NDM program v. 2.5 (Goloboff, 2005) and the results obtained can be viewed with the VNDM v. 2.5 (Goloboff, 2005). The distributional patterns were evaluated in the context of traditional biogeographic divisions by plotting the distribution of the defining species upon the terrestrial ecoregions as defined by Burkart et al. (1999).

3. Results

A total of 159 georeferenced records of 47 flea species and six subspecies (19 genera and seven families) was analyzed. The mammal hosts of these flea species belong to the orders Didelphimorphia (Didelphidae), Cingulata (Dasypodidae), Carnivora (Canidae), Chiroptera (Molossidae, Phyllostomidae, and Vespertilionidae), Rodentia (Cricetidae, Chinchillidae, Caviidae, Ctenomyidae, Octodontidae, and Muridae). The family that hosts most flea species is Cricetidae (Rodentia), represented by the subfamily Sigmodontinae and particularly by the genera *Akodon*, *Eligmodontia*, *Phyllotis*, and *Oligoryzomys*. Species of the rodent families Ctenomyidae and Caviidae were associated with several flea species. Chiroptera was parasitized by the families of fleas Ischnopsyllidae and Tungidae, and by an accidental record of the family Stephanocircidae.

We identify patterns of distributional congruence (PDCs) shared by several native, endemic, and non-endemic species from the study area. The analysis resulted in a total of eight consensus areas characterized by 17 species and two subspecies (Table 1). Only three species are endemic (*Cleopsylla barquezi* López-Berrizbeitia, Hastriter and Díaz, 2016, *Plo-copsylla chicoanaensis* López-Berrizbeitia, Sanchez, Barquez and Díaz, 2018, and *Tetrapsyllus spegazzinii* López-Berrizbeitia, Hastriter, Barquez and Díaz 2019) from the study region. It is important to mention that these three flea species parasitize the same cricetid rodents (*Akodon spegazzinii* Thomas, 1897 and *Phyllotis osilae* J. A. Allen, 1901) distributed in elevation areas such as Puna or the last stratus of Yungas Forests.

The first analysis, searching for sets with cell size 0.50°, did not result in any set. The second analysis, employing the 0.75° grid identified only two sets. The set 0 (score = 2.184103) characterized by two genera and three species and the set 1 (score = 2.834559) by four genera and four species, two endemic (*C. barquezi* and *P. chicoanaensis*) from the study area. The consensus analysis necessarily produced the same result in this case, these areas are discontinuous and associated with the northern and southern Yungas Forests and High Andean, and Puna (Table 1).

A new search using the 1.0° grid identified eight sets. The set 0 (score = 3.300000) was characterized by four genera and five species, the set 1 (score = 4.366667) by five genera and seven species (two endemic, *C. barquezi* and *P. chicoanaensis*), the set 2 (score = 2.154412) by two genera and three species, the set 3 (score = 3.300000) by three genera and three species (two endemic, *T. spegazzinii* and *C. barquezi*), the set 4 (score = 3.300000) by four genera and five species, the set 5 (score = 3.323052) by five genera and six species, the set 6 (score = 2.870301) by three genera and four species and the set 7 (score = 3.306373) by five genera and five species (two endemic *C. barquezi* and *P. chicoanaensis*), the consensus analysis produced six consensus areas (Table 1).

The PDCs with the greatest values of endemism (E) are mainly associated with Monte and Yungas Forests and were found in the 1° grid size (Table 1, area 4, score = 4.61667; area 7, score = 3.57305; area 8, score = 3.55637). Twelve species are present in this area and only two are endemic (*C. barquezi* and *P. chicoanaensis*); additional details regarding the supporting species of these areas are listed in Table 1.

3.1. Patterns of distributional congruence

1. Northern and Southern Yungas Forests (Figure 2A-B). Two consensus areas were equivalent to this pattern (area 1, Figure 2A; area 5, Figure 2B). This was obtained analyzing grid sizes 0.75° and 1° and corresponds to a discontinuous area. Four species [*Adoratopsylla intermedia intermedia* (Wagner, 1901), *Polygenis puelche* Del Ponte, 1963, *P. acodontis* (Jordan and Rothschild, 1923), *P. tripus* (Jordan, 1933)] characterize this PDC. Some of these fleas parasitize the typical hosts of Yungas Forests ecoregion such as the marsupials, *Marmosa (Micoureus) budini* Thomas, 1920, *Thylamys cinderella* (Thomas, 1902), and *Thylamys sponsorius* (Thomas, 1921), and rodents such as *Oligoryzomys brendae* Massoia, 1998 and *Necromys lactens* (Thomas, 1918) (the last species is more frequent in mountain grasslands).
2. Puna, High Andean, and Southern Yungas Forests (Figure 3). One consensus area was equivalent to this pattern (area 2, Figure 3). This PDC was obtained analyzing grid size 0.75° and corresponds to a discontinuous area. Four species [*Polygenis pradoi* (Wagner, 1937), *P. chicoanaensis*, *Hectopsylla gracilis* Mahner, 1982, and *C. barquezi*] characterize this PDC, and two are endemic. Some hosts of these fleas usually inhabit high elevation areas, as do those rodents of the tribe Phyllotini, of which we can mention *Eligmodontia hirtipes* (Thomas, 1902) and *Eligmodontia puerulus* (Philippi, 1896) typical species of the Puna and High Andean.
3. Monte and Southern Yungas Forests (Figure 4A-B). Two consensus areas were equivalent to this pattern (area 6, Figure 4A; area 8,

Table 1. Summary of information on the consensus areas: species composition with their respective score, number of cells for each area, maximum scores, and grid size of each consensus areas.

Consensus areas	Species (score)	Number of cells	Maximum score	Grid size
1	<i>P. puelche</i> (0.750), <i>P. acodontis</i> (0.608), <i>A. i. intermedia</i> (0.825)	8	2.43410	0.75°
2	<i>P. pradoi</i> (0.750), <i>P. chicoanaensis</i> (0.875), <i>H. gracilis</i> (0.463), <i>C. barquezi</i> (0.746)	4	3.08456	0.75°
3	<i>T. cavicola</i> (0.666), <i>A. i. intermedia</i> (0.633), <i>H. gracilis</i> (0.535; 0.647), <i>P. acodontis</i> (0.764–0.798), <i>P. puelche</i> (0.700–0.714), <i>H. pulex</i> (0.588–0.714)	16	3.37030	1°
4	<i>T. cavicola</i> (0.650), <i>C. barquezi</i> (0.722), <i>H. gracilis</i> (0.544), <i>P. chicoanaensis</i> (0.550), <i>P. pradoi</i> (0.611), <i>T. palpalis</i> (0.722), <i>P. acodontis</i> (0.566)	9	4.61667	1°
5	<i>P. puelche</i> (0.716), <i>A. i. intermedia</i> (0.750), <i>P. tripus</i> (0.687)	8	2.40441	1°
6	<i>T. spegazzinii</i> (0.700), <i>C. barquezi</i> (0.693), <i>P. tripus</i> (0.606)	5	2.25000	1°
7	<i>N. c. hemisus</i> (0.311), <i>H. gracilis</i> (0.584), <i>T. palpalis</i> (0.642), <i>P. acodontis</i> (0.701), <i>P. platensis</i> (0.616), <i>T. bleptus</i> (0.465)	14	3.57305	1°
8	<i>M. grossiventris</i> (0.509), <i>C. barquezi</i> (0.833), <i>P. chicoanaensis</i> (0.588), <i>P. pradoi</i> (0.666), <i>P. agenoris</i> (0.708)	6	3.55637	1°

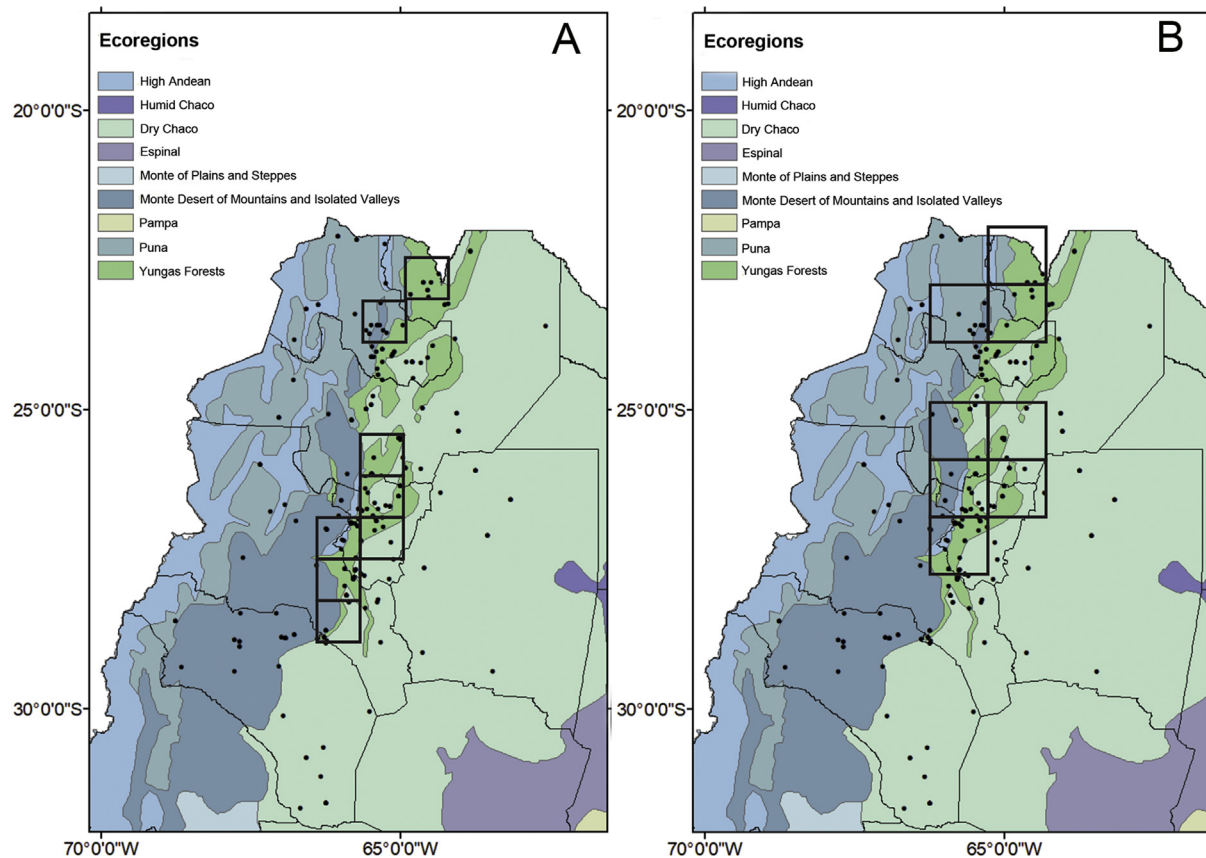


Figure 2. Northern and southern Yungas Forests PDC. A) Consensus area 1, with a grid of cells of $0.75^\circ \times 0.75^\circ$. B) Consensus area 5, with a grid of cells of $1^\circ \times 1^\circ$.

- Figure 4B). This was obtained analyzing grid size 1° . Seven species [*T. spegazzinii*, *C. barquezi*, *Malacopsylla grossiventris* (Weyenbergh, 1879), *Plocopsylla chicoanaensis*, *P. pradoi*, *P. tripus*, *Phthiropsylla agenoris* (Rothschild, 1904)] characterize this PDC, and three are endemic. These endemic species were found on widely distributed rodents such as *Akodon caenosus* Thomas, 1918, even if, in Argentina, most of the records, come from the Yungas Forests, and also on rodents distributed along the Andean slopes of northwestern Argentina, as *A. spegazzinii* and *Akodon simulator* Thomas, 1916 (Pardiñas et al., 2015).
- Monte and Yungas Forests (Figure 5). One consensus area was equivalent to this pattern (area 4, Figure 5); this is the area with the greatest endemicity value (score = 4.61667) (Table 1). This was obtained analyzing grid size 1° . Seven species [*Tiamastus cavicola* (Weyenbergh, 1881), *C. barquezi*, *H. gracilis*, *P. acodontis*, *P. chicoanaensis*, *P. pradoi*, and *Tiamastus palpalis* (Rothschild, 1911)] characterize this PDC, and two are endemic (*C. barquezi* and *P. chicoanaensis*). Some of these fleas were recorded parasitizing cricetid rodents, and among them some species with few records such as *Andalgalomys otrogii* Williams and Mares, 1978, but also some caviomorph rodents of the genera *Microcavia* and *Galea* among them. In northwestern Argentina, *Microcavia maenas* (Thomas, 1898) occurs in Catamarca, La Rioja, Salta, and Tucumán provinces, mainly in Dry Chaco, Monte, and Puna (Teta et al., 2017), and *Galea leucoblephara* Burmeister, 1861 occurs in the lowlands of Argentina (Dunnun, 2015), although in the northwest it was mainly recorded in Yungas Forests and Dry Chaco (López-Berrizbeitia, 2018).
 - South-eastern Dry Chaco, Monte, Yungas Forests, and Puna (Figure 6). One consensus area was equivalent to this pattern (area 7, Figure 6). This was obtained analyzing grid size 1° . Six species [*Neotyphloceras crassispina hemisus* Jordan, 1936, *H. gracilis*, *T. palpalis*, *P. acodontis*, *Polygenis platensis* (Jordan and Rothschild,

1908), *Tetrapsyllus bleptus* (Jordan and Rothschild, 1923)] characterize this PDC. All the flea species that characterize this pattern were mainly recorded parasitizing cricetid rodents. Particularly, *Neotyphloceras crassispina hemisus* a flea which infests a wide range of rodents, including rare or uncommon taxa with few records such as *Eligmodontia bolsonensis* Mares, Braun, Coyner, and van den Bussche, 2008 or *Phyllotis alisosiensis* Ferro, Martínez, and Barquez, 2010.

- Western Dry Chaco, Monte, Yungas Forests, Puna, and High Andean (Figure 7). One consensus area was equivalent to this pattern (area 3, Figure 7). This was obtained analyzing grid size 1° . Six species [*T. cavicola*, *A. i. intermedia*, *H. gracilis*, *P. acodontis*, *P. puelche*, and *Hectopsylla pulex* (Haller, 1880)] characterize this PDC. These flea species were recorded on cricetids and caviomorph rodents; except *H. pulex*, a parasite of bats, such as *Tadarida brasiliensis* (I. Geoffroy St.-Hilaire, 1824) and *Eumops perotis* (Schinz, 1821), collected in Yungas Forests and Dry Chaco.

4. Discussion

Endemic species are those restricted to a specific geographical area, which means they only occur there, and nowhere else (Cowling, 2001). These species represent the result of complex evolutionary and ecological processes that merit high conservation priority (Young et al., 2002). Our objective was to present a first estimate on possible areas of endemism characterized by fleas in one of the most complex regions of Argentina. The absence of strict patterns of endemism may be due to a low number of genera and species in the analysis. Our knowledge of the distribution of species is still incomplete as evidenced by the irregular distribution of sampling localities. Indeed, a recent study has not only produced novel distribution records in the region, but also led to the discovery of new species (López-Berrizbeitia and Díaz, 2019). Thus, many species, even

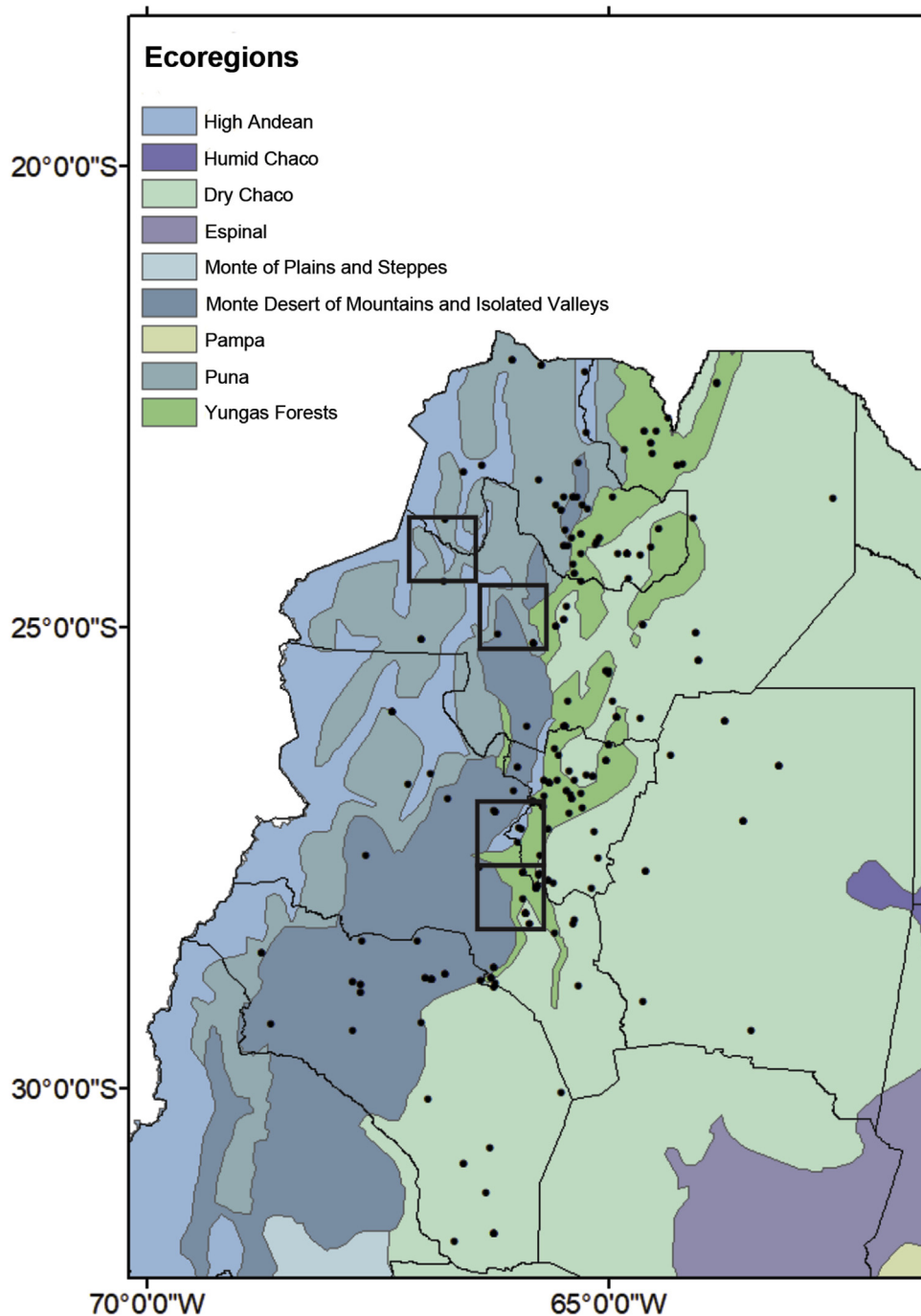


Figure 3. Puna, High Andean and Southern Argentinean Yungas Forests PDC, Consensus area 2, with a grid of cells of $0.75^\circ \times 0.75^\circ$.

still those undescribed, may be present, especially at the almost unexplored areas of higher elevations.

Morrone and Gutiérrez (2005) proposed that although the comparison of biogeographical patterns exhibited by coevolving taxa is not usually addressed, based on their relationship, similar distributional patterns of host and parasite taxa should be expected. In the case of mammals, main hosts of fleas have more defined biogeographic patterns, because there is more information about their geographical distribution compared to that of parasites (Sandoval and Ferro, 2014; Sandoval et al., 2015). Traub (1980) considered that geographical distribution of some flea species is probably related to the plate tectonics and subsequent dispersal and redistribution of the host taxa.

Our database recovered eight consensus areas and we recognized six patterns of distributional congruence for the order Siphonaptera in NWA. Two of these are extensive: South-eastern Dry Chaco, Monte, Yungas Forests, and Puna (area 5, Figure 6) and Western Dry Chaco, Monte, Yungas Forests, Puna, and High Andean (area 6, Figure 7). Among the species that represent the resulting sets, 15 flea species are distributed in Yungas Forests, of which only two (*P. tripus* and *P. puelche*) are exclusive of this ecoregion. All patterns show strong tendency of the Yungas Forests as a possible endemism area. Sandoval and Ferro (2014) identified the entire latitudinal extension of the Yungas Forest as a discrete biogeographical unit in the NWA geographical context, likewise Sandoval et al. (2015) supported that the Southern sector of the Yungas Forests is a

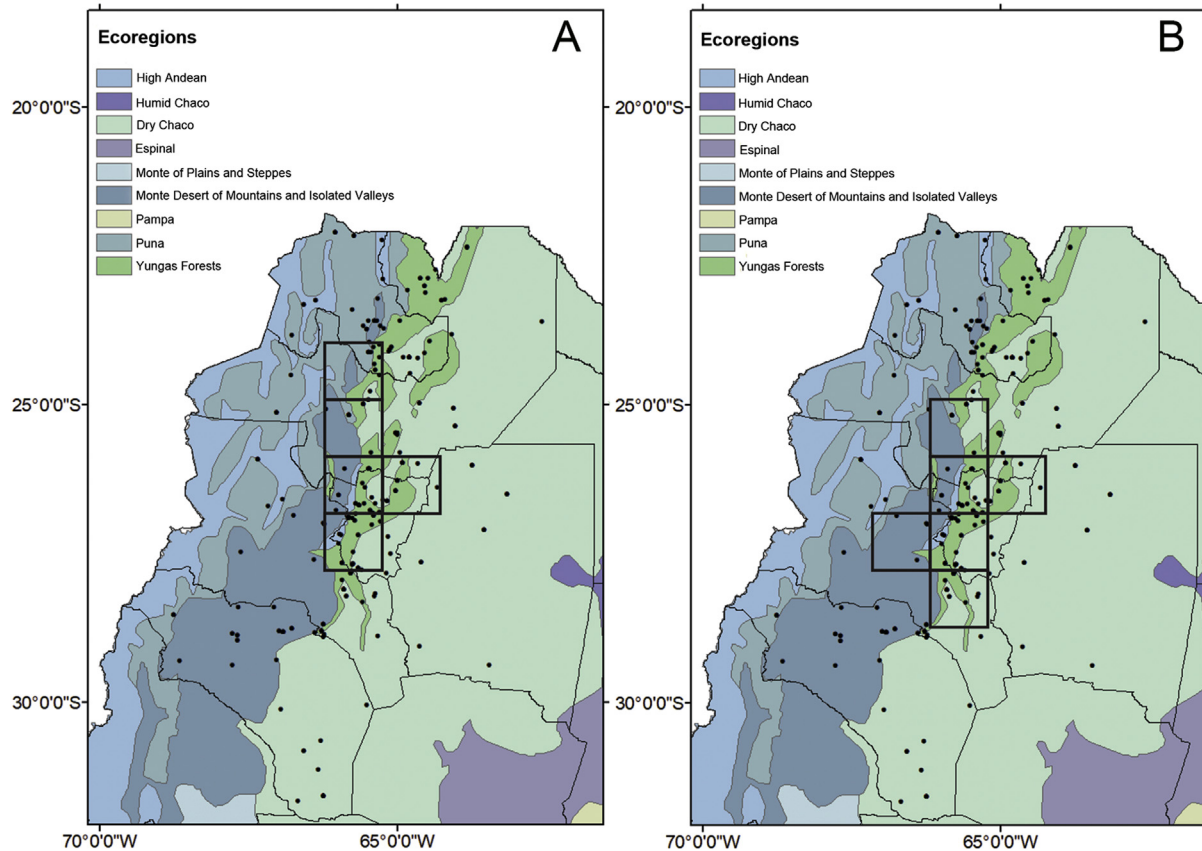


Figure 4. Monte and Southern Argentinean Yungas Forests PDC. A) Consensus area 6, with a grid of cells of $1^\circ \times 1^\circ$. B) Consensus area 8, with a grid of cells of $1^\circ \times 1^\circ$.

distinctive faunal AE, at least in the case of endemic small mammals. Sandoval et al. (2015) suggested that the main habitat types for endemic small mammal species are not the western or eastern arid or semi-arid biomes, but rather the eastern humid Andean slopes and the results of our study partially agrees with that, because the endemic species of flea are mainly distributed in areas of Yungas Forests but the Monte Desert of Mountains and Isolated Valleys would also be harboring endemic species.

In the NWA, López-Berrizbeitia and Díaz (2019) observed that the greatest diversity of fleas in the Yungas Forests is the reflection of one of the areas with the highest biodiversity in the Neotropical region; therefore, in this study, species richness patterns for fleas and patterns of congruence distributional were generally consistent. Congruence between species richness and endemism patterns has been found in other groups, for example, birds (Lei et al., 2007), plants (López-Pujol et al., 2011), rodents (do Prado et al., 2014), aphids (Gao et al., 2018), and lepidopterans (Zhuang et al., 2018). This congruence confirms the hypotheses that AoEs could have acted as centers of speciation in the past (Terborgh, 1992; Ochoa and Flores Vilella, 2006; Gao et al., 2018). This is frequently related to areas characterized by diverse habitats and stable climates, which maintain long-term speciation and persistence (Gao et al., 2018). In this study, the center of species richness and the uncovered PDCs are located along the southern Yungas Forests.

Consensus areas that obtained the highest endemism scores included species from different ecoregions, such as *N. c. hemisus* and *T. bleptus* present in almost all habitats in NWA, from the high peaks of the Andes, through the mountainous sectors of the Yungas Forests to the vast plains of Dry Chaco. *Tetrapsyllus bleptus* was even recorded in a transitional zone between Yungas Forests and the High Andean parasitizing *A. spegazzinii*, *P. osilae* and *P. xanthopygus*. Only two species were not recorded in Yungas Forests, *T. palpalis* and *M. grossiventris*, the first being present in Dry Chaco and Monte, while the second in Dry Chaco and Puna; undoubtedly these species are following their hosts, which are rodents of

the genera *Ctenomys* and *Eligmodontia* for *T. palpalis* and mainly armadillos of the genera *Euphractus* and *Tolypeutes* for *M. grossiventris*.

The pattern of distributional congruence 4 (Monte and Yungas Forests) was also found by Sandoval et al. (2015), but as an area of endemism in strict sense, named *South-eastern Andean Slopes merged with Southwestern Andean Biomes I (SE-SW)* with *Eligmodontia moreni* (Thomas, 1896) as an endemic species, whose association with the flea species *H. gracilis* and *T. palpalis*, recorded in the equivalent pattern to that found by us.

Sandoval et al. (2015) identified the High Andean and Puna as discrete biogeographic units in the geographic context of NWA and proposed these areas as part of larger AEs extending southward in Argentina and northward into Bolivia. In our study, Puna and High Andean are part of a pattern, but in combination with the southern Yungas Forests, with the districts of lower and upper Montane Forests.

The use of different grid sizes allows the exploration of distributional patterns in different scales and corroborates the results of previous studies (Aagesen et al., 2012). According to Szumik et al. (2002), very small grid cells will make all distributions entirely discontinuous, and then only very small areas of endemism, or none at all, will be recognized. In contrast, very large grid cells are likely to recognize very large areas of endemism, with many species appearing as endemic in each area. Our results, using a little diverse database over a complex area, are in concordance with the above expectations. The pattern Puna, High Andean, and Southern Yungas Forests was only recovered using the 0.75° grid in the NDM searches, with only four species supporting the obtained areas. The smallest cell size used identified Andean PDC (Figure 3). This result was obtained because these areas exhibit a higher number of more exclusive flea species in a small area, mainly due to the elevational gradient, as *A. i. intermedia*, *H. gracilis* or *P. chicoanaensis*. In contrast, detection of areas of endemism through an environmental gradient that varies along the latitude or longitude, as occurs in the pattern 5 and 6,

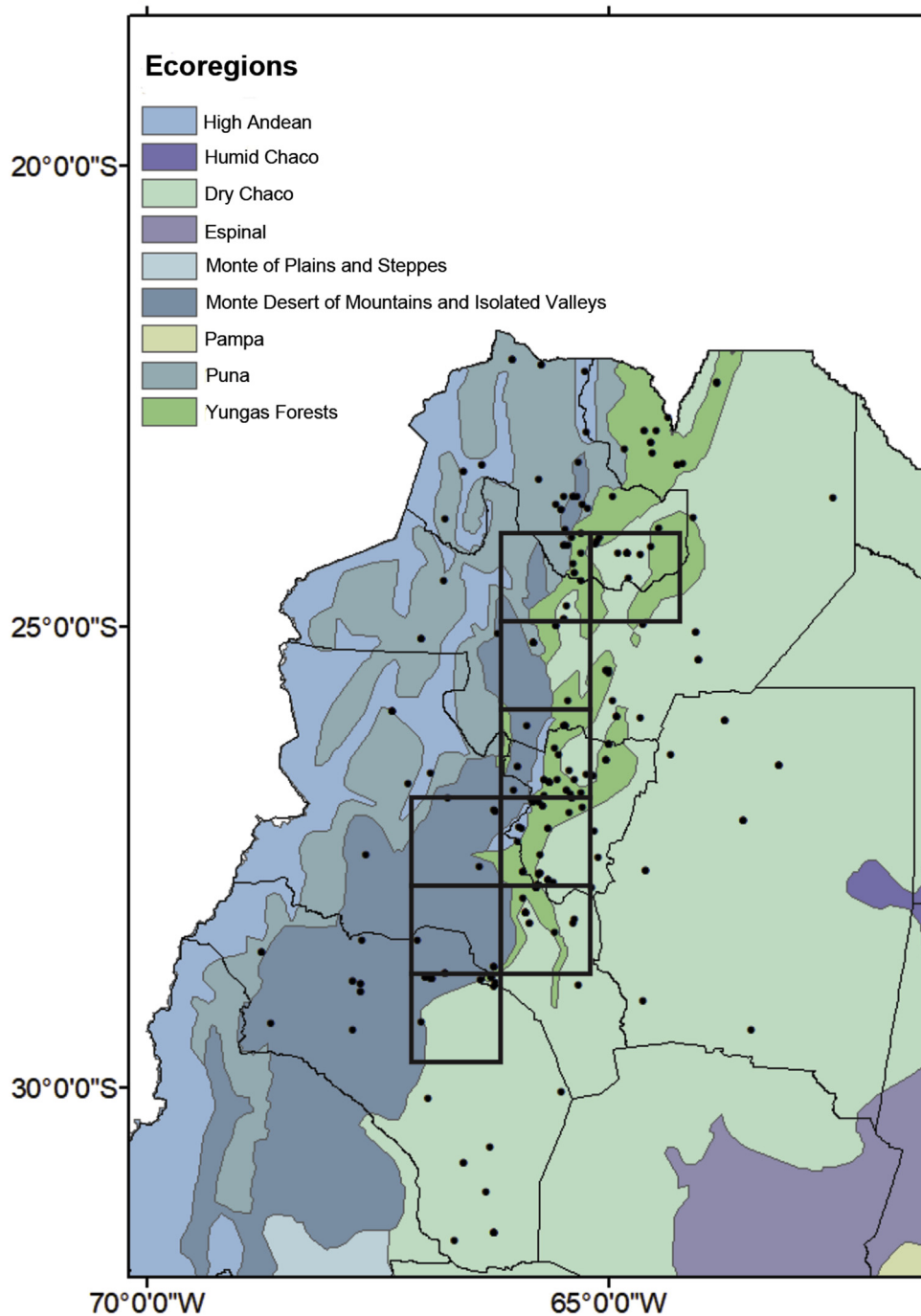


Figure 5. Monte and Yungas Forests PDC, Consensus area 4, with a grid of cells of 1° x 1°.

demands larger grid sizes. Considering our results, the use of small grid cells appears to be more restrictive and rigorous, generating only two PDCs; so, in this study, we consider that the NDM algorithm, using small grids, experienced some difficulties in the recognition of PDCs. In future approaches the use of more records of fleas would allow this hypothesis to be tested. By increasing the size of the cells, the number of sets and consensus areas also increased; however, with the 1.0° grid Western Dry Chaco was not represented by any pattern, because although extensive portions of the region were sampled, the ectoparasite records are still scarce or insufficient (López-Berrizbeitia, 2018). The use of larger grid cells recovered numerous PDCs: our areas comprise elements from different habitats, including species from transitional areas between forest and open habitats. For example, *T. bleptus* or *H. gracilis* that inhabit

environments between the last district of the Yungas Forests and the High Andean in Tucumán province. This is probably a consequence of the past common history among parasites and their hosts that currently inhabit these biomes whose ancestors lived in transitional areas (do Prado et al., 2014).

The consensus area and therefore the PCDs are characterized, mainly, by species that are parasites of several species of rodents; except *H. pulex* (Tungidae), *Hormopsylla fosteri* (Rothschild, 1903), *Myodopsylla isidori* (Weyenbergh, 1881), *Myodopsylla wolffsohni wolffsohni* (Rothschild, 1903), *Sternopsylla distincta speciosa* (Rothschild, 1903) (Ichnopsyllidae) exclusive parasites of bats and *M. grossiventris* and *P. agenoris* (Malacopsyllidae) of armadillos. The degree of association between a particular flea species and a particular host species varies from specific associations

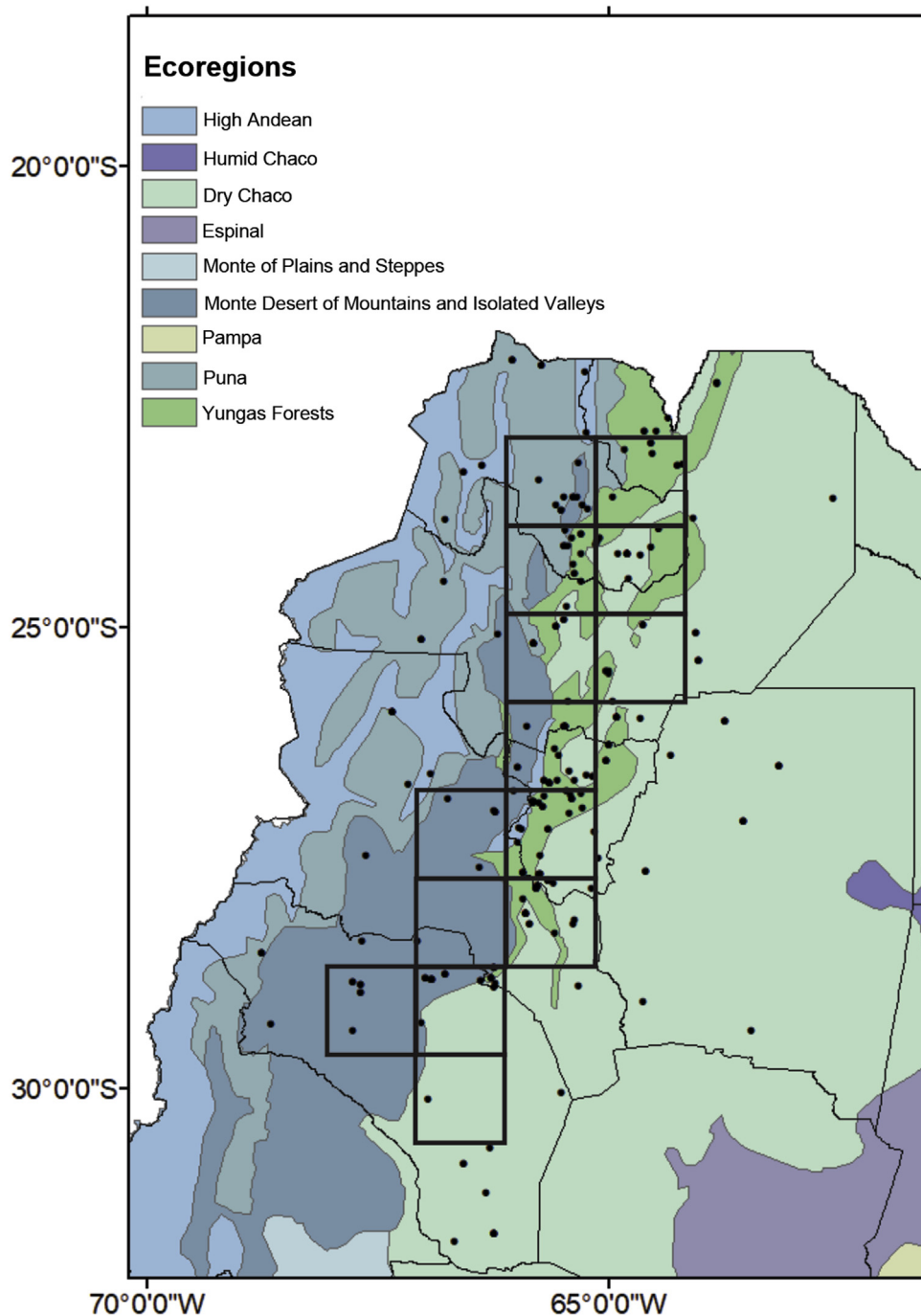


Figure 6. South-eastern Dry Chaco, Monte, Yungas Forests, and Puna PDC, Consensus area 7, with a grid of cells of 1° x 1°.

to more general associations, and most flea species are specific at genus or subfamily level of host (Marshall, 1981). In our study, the most fleas are specific at the order level of host, but some species parasitize more than one order of mammals, as *Craneopsylla minerva* (Rothschild, 1903) (Stephanocircidae) recorded on Rodentia and Didelphimorphia.

Flea diversity in an area is not determined only by host species, but by environmental parameters inherent to the habitat, that will determine nest and den conditions (temperature, humidity, and construction material) (Krasnov et al., 1997). All these characteristics will complete basic flea needs like food, habitat, and mating opportunities (Marshall, 1981), favoring flea species and population abundance (Acosta and Fernandez, 2015). Although the detailed knowledge of temperature and humidity preferences of fleas is scarce (Krasnov et al., 2001); in general, successful

development of pre-imaginal fleas takes place at air temperatures greater than 10–15 °C, but lower than 30 °C, and relative humidity greater than 60% (Marshall, 1981; Krasnov, 2008). It has been speculated that prolonged survival of quiescent adults within the cocoon is in part due to a reduction in respiratory water loss because less time is spent with the spiracles open (Silverman and Rust, 1985). Larvae, in contrast, cannot close their spiracles, and thus are extremely sensitive to low humidity (Roberts et al., 1996). In the Yungas Forests, the fleas were recorded, mainly, in the second district, the lower Montane Forest, which is characterized by the highest rainfall, exceeding 3000 mm annually, and less extreme temperatures (Cabrera, 1976), with the predominant soils sometimes rich in organic matter (Burkart et al., 1999). Taking into account the combination of these properties that characterize to the

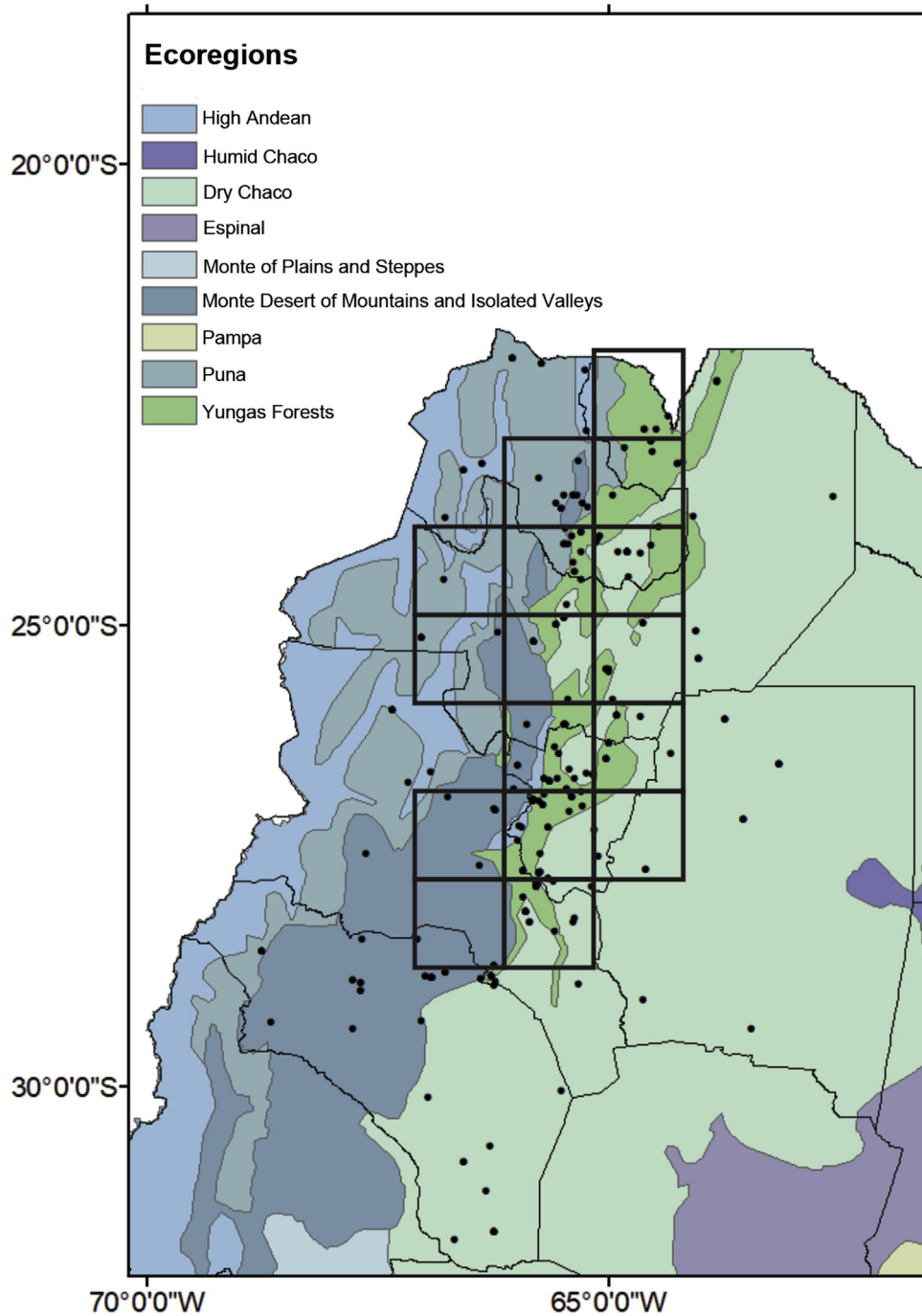


Figure 7. Western Dry Chaco, Monte, Yungas Forests, Puna and High Andean PDC, Consensus area 3, with a grid of cells of 1° x 1°.

ecoregion, we could, definitely, assume that the environment of host shelters and burrows is optimal for the development of eggs and larvae.

Finally, this new information will allow the delimitation of areas in the region at a more detailed resolution, establishing their importance according to their gamma diversity, degree of endemism, and the occurrence of relict taxa within them.

5. Conclusion

We studied the biogeographical patterns of the flea species in northwestern Argentina using the VNDM method for the first time. Our results indicate centers of distributional congruence are generally located in the Yungas Forests and highlight the importance of these areas for

conservation and historical biology. The shared evolutionary history between hosts and their parasites is multidimensional, if this association is the product of a coevolution by descent or by colonization, or if within the story there is more than one process involved (Brooks and McLennan, 1993; Escalante et al., 2011), then we could know more about its diversification process.

It would be interesting to conduct more biogeographical studies involving more than one taxon, since parasites and their hosts represent an adequate system finding shared and exclusive patterns between them, in such a complex and evolutionary area, and to be able to make inferences about a history of coevolution. More research is required to address the underlying mechanisms and evolutionary stories that contribute to current distribution patterns.

Declarations

Author contribution statement

M. Fernanda López-Berzbeitia: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Roxana Acosta-Gutiérrez: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data.

M. Mónica Díaz: Analyzed and interpreted the data; Wrote the paper.

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Competing interest statement

The author declare no conflict of interest.

Additional information

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