The widespread distribution and niche breadth of *Rhadinopsylla* fleas: via dispersal routes of small rodents

Megan Truman
Lake Forest College
Lake Forest, Illinois 60045

Introduction:

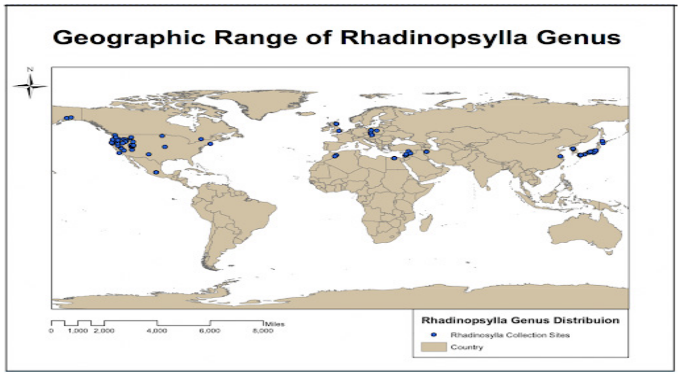
In biogeography, mechanisms of physical and environmental barriers shape the distribution of species. According to Darwin, these barriers also play an important role in the geographical ranges of organisms (Darwin 1873). The geographic range of a species reflects the species ecological niche (Brown and Lomolino 1998). An ecological niche is defined as the resources required for a species to persist in an environment. Two factors influence the breadth of an ecological niche: abiotic and biotic conditions. Abiotic factors include the physical space a species occupies, the temperature, and seasonality, whereas biotic factors include food requirements and the interactions between species (Hutchinson 1959). A species' niche breadth relies heavily on its specialization because its ecological niche is shaped by interactions with other species. The specialization of a species is its adaptation to a specific resource, function, or environment (Dictionary.com 2021). Species specialization influences the distribution of a species as it shapes the niche breadth of these organisms. A negative correlation has been discovered between the degree of specialization and the geographic range of a species (Krasnov et al. 2005). This correlation aligns with the niche breadth hypothesis which states that species able to tolerate a broad range of environmental conditions tend to have more suitable habitats to occupy, and therefore, have wider geographic ranges than species that tolerate only a narrow range of conditions (Brown 1984). This specialized relationship is frequently demonstrated through parasite-host interactions. This relationship determines species distributions as the parasite and host often coevolve (*Parasitic Relationships* 2021). The interaction of parasites living on hosts and adapting to their environment is due to the parasite's dependency on the host for food. As a result, the distribution of hosts determines the geographic range of many species of parasites (Shenbrot et al. 2007). Consequently, the niche breadth of the parasites is also determined by the geographic ranges of hosts. As discussed above, specialization shapes niche breadth. In parasite-host relationships, host-specificity is a determinant in the livable distribution of the parasite. Host-specificity falls into three categories: host-specific, host-opportunistic, and opportunistic . Host-specific parasites are highly specific and thus they will often have identical tolerances and geographical ranges as a single host species as their livability depends on having access to that specific host. Host-opportunistic parasites can have several different host species and thus are often distributed across the geographic ranges of several hosts. Finally, opportunistic parasites can exploit many hosts and therefore achieve a geographically scattered abundance (Shenbrot et al. 2007). The parasite-host relationship of fleas and small rodents offers the ideal model of this relationship, although these interactions occur in many other organisms as well. Due to the importance of host-specificity in the geographic ranges of organisms, we will be studying the parasite-host relationship of *Rhadinopsylla* subspecies and their small rodent hosts. Specifically, the *Rhadinopsylla* subspecies of *R. rectofrontia*, *R. heiseri*, and *R. syriaca*. These subspecies of *Rhadinopsylla* are categorized as "nest fleas"; nest fleas typically remain under host shelter for their entire lifetime (Medvedev et al. 2020). *Rhadinopsylla* subspecies reside in the Holarctic region, which includes North America and Europe. This genus of fleas offers a model for testing the distribution of fleas as they disperse via parasitized rodents like ground squirrels, gerbils, voles, and mice across the Holarctic region (Medvedev et al. 2020). Although host-specificity varies among the *Rhadinopsylla* subspecies, most can feed on many small mammal hosts (Medvedev et al. 2020). The level of host-specificity within *R. rectofrontia*, *R. heiseri*, and *R. syriaca* will vary amongst each subspecies, but it also reveals the niche breadth and therefore, the geographic range of these fleas. The parasite-host relationship between *Rhadinopsylla* subspecies and small rodents provides us with a better understanding of their distribution and geographic range. These interactions allow us to form two hypotheses for the pattern and mode of distribution for fleas. First, we hypothesize that *Rhadinopsylla rectofrontia*, *R. heiseri*, and *R. syriaca* have similar fundamental niches and geographic ranges despite their global distribution. Second, we hypothesize that these subspecies formed similar fundamental niches and distribution via dispersal of their small rodent hosts.

Methods:

This study included 216 samples from the *Rhadinopsylla* genus, collected in the field by outside sources within the last fifty years. This genus contains 18 different subspecies, but we compared the three subspecies of *R. heiseri*, *R. syriaca*, and *R. rectofrontia*. We chose these subspecies because they had large sample sizes and their samples had relatively few replicated coordinates. The *R. heiseri* subspecies contained 30 samples, and of those samples, there were 19 independent locations due to 7 samples with replicates. *R. heiseri* samples were collected from locations in Utah and California, U.S.A. The *R. syriaca* subspecies contained 18 samples, and of those, there were 6 independent locations due to 3 samples with replicated coordinates. The *R. syriaca* samples were collected from locations in Lebanon and Syria. The *R. rectofrontia* subspecies contained 19 samples, and of those samples, there were 10 independent locations due to 5 samples with replicated coordinates. *R. rectofrontia* samples were collected from locations in Japan. The coordinates that samples were collected from were used to graph the geographic range, and test the possible niche breadth, of the genus and each subspecies. These variables were used to test whether the *Rhadinopsylla* subspecies' range of distribution, mode of distribution, and niche breadths are similar. These tests were achieved via the use of MaxEnt software and the ArcGIS mapping system. MaxEnt software was used to map the geographic range and predict the niche breadth of R. heiseri, R. syriaca, and R. rectofrontia. The samples of the Rhadinopsylla genus and subspecies were run through MaxEnt to predict their global niche breadth. This process consisted of a total of four MaxEnt trials and four individual geographical maps. Each MaxEnt trial run was based on the BIO 374 Lab Assignment instructions and used the suggested settings. Along with MaxEnt, the ArcGIS mapping software was used to map the global locations of the entire *Rhadinopsylla* genus as a whole, along with the specific sites of *R. heiseri*, *R. syriaca*, and *R. rectofrontia*. We utilized ArcGIS because it accurately predicts and displays the geographic distributions of the *Rhadinopsylla* genus and subspecies. The coordinates of the *Rhadinopsylla* genus were entered into ArcGIS to produce a map of their precise locations. Then the coordinates of *R. heiseri*, *R. syriaca*, and *R. rectofrontia* were entered into ArcGIS to produce a map of their definite locations.

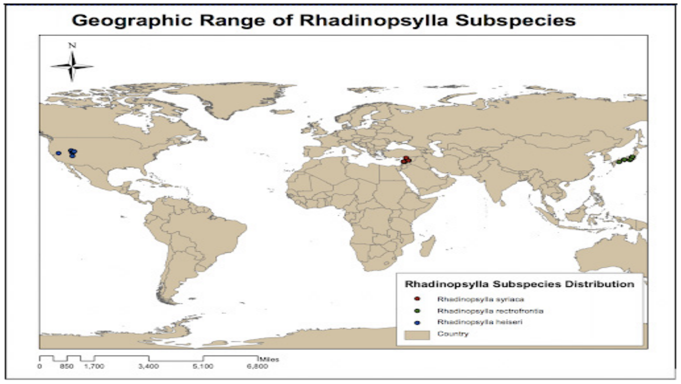
Results:

Figure 1. The Known Distribution of the Entire Rhadinopsylla Genus Via ArcGIS Mapping Software.



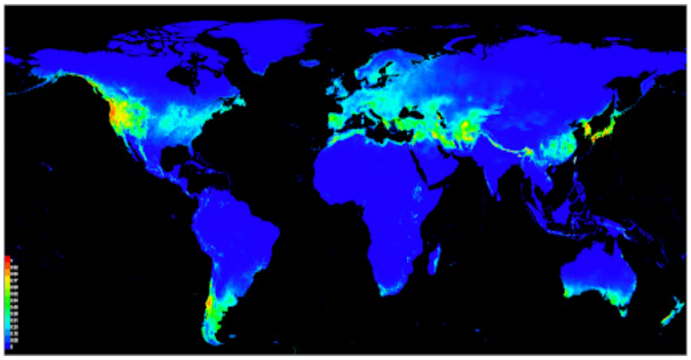
The precise localities of the sites in which the 18 Rhadinopsylla subspecies were collected. These samples made up a total of 216 collection sites, with 164 of those samples mapped due to replicated coordinates.

Figure 2. The Known Distribution of the *Rhadinopsylla* Subspecies, *R. Syriaca*, *R. rectofrontia*, and *R. heiseri* Via ArcGIS Mapping Software.



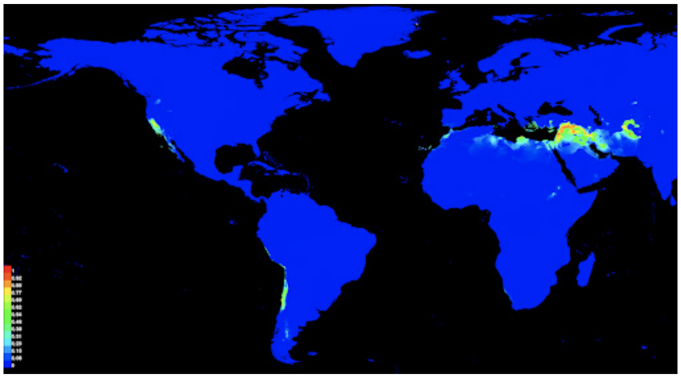
The precise localities of the sites in which the three Rhadinopsylla subspecies were collected. Of the 67 total samples for all three subspecies, 35 of those locations were mapped due to replicates. R. syriaca accounted for 18 total samples and 6 mapped locations within Lebanon and Syria. R. rectofrontia accounted for 19 total samples and 10 mapped locations within Japan. R. heiseri accounted for 30 total samples and 19 mapped locations within Utah & California, U.S.A.

Figure 3. Predicted Niche Breadth of the Entire *Rhadinopsylla* Genus Via MaxEnt.



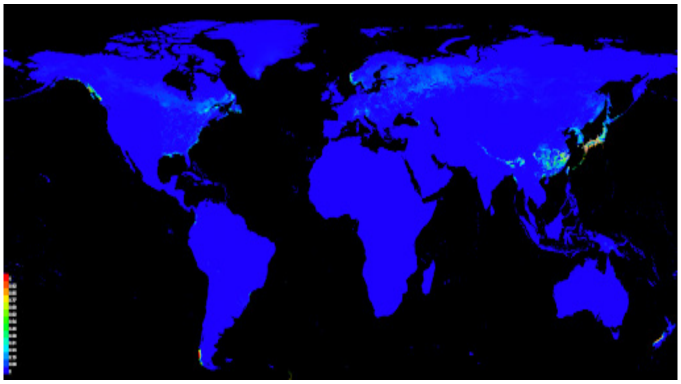
The fundamental niche of the Rhadinopsylla genus. This map displays the areas that contain the proper set of conditions in which these fleas can survive and reproduce. The warmth of color increasingly correlates with the most likely areas in which Rhadinopsylla can occur. These areas include the northwest quadrant of N. America, the Middle East, Japan and East Asia, southern South America, and southern Australia.

Figure 4. Predicted Niche Breadth of *Rhadinopsylla* syriaca Via MaxEnt.



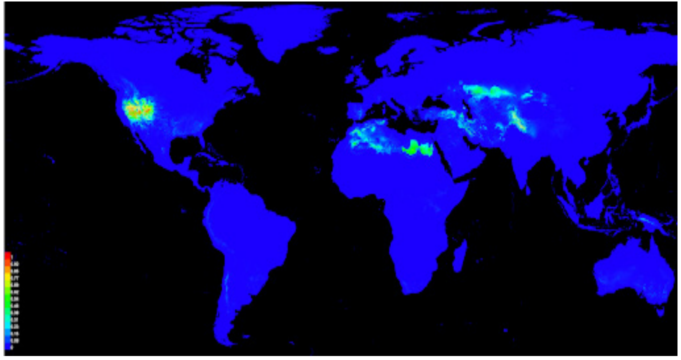
The fundamental niche of the Rhadinopsylla syriaca subspecies. This map displays the areas containing the proper set of conditions in which this subspecies can survive and reproduce. These areas include the Middle East, the western coast N. America, and a small fraction of western S. America.

Figure 5. Predicted Niche Breadth of *Rhadinopsylla rectofrontia* Via MaxEnt.



The fundamental niche of the Rhadinopsylla rectofrontia subspecies. This map displays the areas containing the proper set of conditions in which this subspecies can survive and reproduce. These areas include East Asia, Japan, and a portion of northwestern N. America.

Figure 6. Predicted Niche Breadth of *Rhadinopsylla heiseri* Via MaxEnt.



The fundamental niche of the Rhadinopsylla heiseri subspecies. This map displays the areas containing the proper set of conditions in which this subspecies can survive and reproduce. These areas include western N. America, northern Africa, and western Asia.

The predicted geographic range of the *Rhadinopsylla* genus (Fig. 3) matches the known distribution of these fleas (Fig. 1). The known distribution of *Rhadinopsylla* subspecies occurs in Utah & California U.S.A. (*R. heiseri*), Lebanon & Syria (*R. syriaca*), and Japan (*R. rectofrontia*) (Fig. 2). The possible geographic ranges of the subspecies overlap when these localities are compared to predicted niche breadth. The predicted niche of *R. syriaca* allows it to occur in areas of the Middle East and the western coastline of North America (Fig. 4). The predicted niche of *R. rectofrontia* allows it to occur in eastern Asia and Japan, the far western portion of North America, and northern Europe (Fig. 5). The predicted niche of *R. heiseri* allows it to occur in western North America, northern Africa, and parts of the Middle East and western Asia (Fig. 6). Comparing the MaxEnt predictions with known distributions (Fig. 2), the known localities of these *Rhadinopsylla* subspecies occur in the areas of the predicted fundamental niches. The results reveal the geographic ranges of *Rhadinopsylla* subspecies when considering their predicted fundamental niches (Fig. 4-6). The common areas in which the fundamental niches of *R. syriaca*, *R. rectofrontia*, and *R. heiseri* overlapped were western North America, the Middle East, and eastern Asia. These areas were also found to be occupied by the realized niches of the subspecies in (Fig. 2).

Discussion:

The areas in which the *Rhadinopsylla* subspecies occurred have similar climates and niche conditions year-round. The *Rhadinopsylla* subspecies samples were collected in Kyoto, Japan, Beirut, Lebanon, and Tooele, Utah, U.S.A. The yearly climate of these areas has similar humidity, median temperature, and precipitation. Specifically, *R. rectofrontia* subspecies occur in western Japan, where the yearly temperature ranges from 33°F-88°F (*Climate-Data.org* 2021). This area of Asia is very humid and has an annual precipitation of 66.0 inches. *R. syriaca* subspecies occur in western Lebanon, where the temperature ranges from 50°F-81°F, and the annual precipitation is 28.6 inches (*Climate-Data.org* 2021). Finally, *R. heiseri* subspecies occur in the western United States, where the yearly temperature ranges from 30ºF-80ºF, and the annual precipitation is 20.9 inches (*Climate-Data.org* 2021). Although the yearly precipitation is higher in Japan, these areas have similar temperature ranges in which the fleas can tolerate. Since temperature is a factor that influences where survival is permissible, the temperature range of species affects their niche breadth (Monahan 2009). Considering the similar temperature ranges in the regions where the subspecies are found, and the effect temperature has on niche breadth, we can conclude that the data support that *R. syriaca*, *R. rectofrontia*, and *R. heiseri* have equivalent niches. As *Rhadinsopsylla* temperature tolerances are influential in predicting their niche and geographic range, we must consider how these tolerances and adaptations evolve. Earlier, we discussed how parasite-host relationships influence the niche breadth of parasites. As fleas rely on their small rodent hosts for food and shelter, their relationship will ultimately determine the flea's geographical distribution. Therefore, we must look further into the host-specificity of fleas and their small rodent hosts. Again, *Rhadinopsylla* fleas are "nesting fleas," which means they are associated with their host for their entire lifespan (Medvedev et al. 2020). According to the categories of host-specificity above, *Rhadinopsylla* is classified as host-specific because they rely on small rodents for shelter and food. Therefore, *Rhadinopsylla* subspecies are expected to have the same geographic ranges and tolerances as their rodent hosts, as this outcome correlates with highly specialized parasites (Krasnov et al. 2005). As this specialized relationship is crucial to the geographic range of *Rhadinopsylla*, we must look further into the small rodent with which the subspecies travel on and interact with. A typical small rodent host of *R. syriaca* is the gerbil, specifically Tristram's jird (*Meriones tristrami*). Common small rodent hosts of *R. rectofrontia* are flying squirrels and voles; the samples did not specify the species from which *R. rectofrontia* was collected on. The usual rodent hosts of *R. heiseri* are squirrels, specifically, the white-tailed antelope squirrel (*Citellus leucurus*). Since squirrels are hosts of two of the *Rhadinopsylla* subspecies, we will look further into their evolutionary dispersal. Today, tree and flying squirrels occur across the world with their peak species richness in Asia, central and north Africa, and North America. The *Squiride* likely spread to its current distribution from the Nearctic and Northern Hemisphere (Koprowski & Nandini 2008). As these small rodents are non-aquatic, non-flying mammals, they can't cross large bodies of water readily. We must consider another route of dispersal because of the physiological limitations of squirrel, voles, and gerbils. A recent study by Medvedev et al. discovered that the distribution of *Rhadinpsylla* in the Nearctic and Palearctic is likely due to land bridges (Medvedev et al. 2020). They found land bridges as likely modes of dispersal because the number of *Rhadinopsylla* fleas increased from south to north; this is a trend that reflects dispersal via a land bridge. The current distribution is thought to have been achieved in three ways: from the northeastern Palearctic via the north Asian route, over the Beringia land bridge, and via the East-Central-Turano-Iranian route (Medvedev et al. 2020). Not only would these specific land bridges allow the dispersal of *Rhadinopsylla* subspecies via small rodents, but these routes would disperse to the areas in which our study discovered these subspecies. The Beringia land bridge connected North America and eastern Asia, while the Iranian route connected Asia to the Middle East during the Pleistocene. These routes align with our findings as *R. heiseri* is found in western North America, and *R. rectofrontia* is found in eastern Asia and Japan, then *R. syriaca* is present in Lebanon and Syria. Our first hypothesis was that *R. rectofrontia*, *R. heiseri*, and *R. syriaca* have similar fundamental niches and geographical ranges. This hypothesis is supported by our findings within MaxEnt (Fig. 3-6), which provide evidence that the fundamental niche of these subspecies allows them to survive in the localities in which they occurred in the ArcGIS mapping system (Fig. 1,2). Our second hypothesis is also supported, as the *Rhadinopsylla* subspecies are found on small rodent hosts like squirrels, gerbils, and voles. The presence of land bridges between North America, Asia, and the Middle East allowed for the global distribution of these small mammals. These dispersal patterns offer a mechanism for the distribution of *R. rectofrontia*, *R. heiseri*, and *R. syriaca* and the formation of similar fundamental niches.