Testing the Accuracy of Vegetation-Based Ecoregions for Predicting the Species Composition of Blow Flies (Diptera: Calliphoridae)

K. Ketzaly Munguía-Ortega,1 Eulogio López-Reyes,1 and F. Sara Ceccarelli2,3

1Museo de Artrópodos, Departamento de Biología de la Conservación, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Baja California, Mexico, 2Museo de Artrópodos, Departamento de Biología de la Conservación, CONACYT-Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Baja California, Mexico, and 3Corresponding author, e-mail: ceccarelli@cicese.mx

Subject Editor: Philippe Usseglio-Polatera

Received 25 June 2020; Editorial decision 5 December 2020

Abstract

To properly define ecoregions, specific criteria such as geology, climate, or species composition (e.g., the presence of endemic species) must be taken into account to understand distribution patterns and resolve ecological biogeography questions. Since the studies on insects in Baja California are scarce, and no fine-scale ecoregions based on the region’s entomofauna is available, this study was designed to test whether the ecoregions based on vegetation can be used for insects, such as Calliphoridae. Nine collecting sites distributed along five ecoregions were selected, between latitudes 29.6° and 32.0°N. In each site, three baited traps were used to collect blow flies from August 2017 to June 2019 during summer, winter, and spring. A total of 30,307 individuals of blow flies distributed in six genera and 13 species were collected. The most abundant species were Cochliomyia macellaria (Fabricius), Phormia regina (Meigen), and Chrysomya rufifacies (Macquart). The composition of the Calliphoridae community was different between the localities and three general groups have been distinguished, based on the species composition similarity (ANOSIM) results: Gulf-Desert, Mountains, and Pacific-Center. The vegetation-based ecoregions only reflect the blow fly species’ distributions to a certain extent, meaning that care must be taken when undertaking ecological biogeographical studies using regionalization based on organisms other than the focal taxa because vegetation does not always reflect fauna species composition.

Key words: biogeography, ANOSIM, Baja California, ecology, Diptera diversity

Ecological biogeography depends on the delimitation of regions based on specific criteria such as geology, climate, or species composition (Escalante 2009, Kreft and Jetz 2013, Vilhena and Antonelli 2015). Furthermore, various methods have been used to identify and delimit biogeographical areas based on species distribution data, such as the non-parametric statistical analysis of similarities (ANOSIM; Shears et al. 2008, Cabrero-Sañudo 2012, Gutjahr et al. 2014, Mercado Casares et al. 2017), methods such as NDM, which search for areas of endemism (Goloboff 1994), methods that analyze the history of taxa over areas (Arias et al. 2011), or track and biogeographic cladistic analysis (Morrone 2006). In his study, Morrone (2006) identified biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeography and cladistics analyses of the entomofauna, in which he recognized the Nearctic and Neotropical regions and the transition zone for Mexico. Subsequently, Morrone et al. (2017) provided a map of 14 biogeographic provinces of Mexico based on climatic, geological, and biotic criteria, recognized five provinces for the Nearctic region, four assigned to the Neotropical region and five corresponding to the Mexican transition zone. The ecoregions proposed by González-Abraham et al. (2010) for the peninsula of Baja California distinguished two regions: Mediterranean and Desert, and 14 ecoregions, of which nine belong to the state of Baja California. These ecoregions were based on the integration of abiotic factors and biogeographical patterns such as vegetation and the spatial scale of micro and macro-geographic processes. The geographical distribution of the indicator plant species was one of the bases to define the ecoregions since vegetation depends on climate, soil type, and geomorphology, helping in recognition of regional borders that work for the definition of the ecoregions. Abiotic factors taken into account were climate information at regional level, physiography, topography, and geology, allowing them to identify where regions change abruptly, transition zones, and ecological limits. In addition, ecoregions were also defined according to the north-south latitudinal axis, which determines the
rainfall recorded in winter in the northern part and the tropical cyclones that affect the southern part of the peninsula, taking into account the proximity to the Gulf of California and the Pacific Ocean along an east-west gradient which determines the air temperature, influence of coastal fogs and the degree of continentality. The ecoregions delimited by González-Abraham et al. (2010) are the best example of fine-scale regionalization available for Baja California.

The vegetation in Baja California is well-studied (Rehman and Roberts 2012) as opposed to other groups of organisms, such as insect species. Considering the ecological importance of insects (Triplehorn and Johnson 2005, Hung et al. 2018) and their declining status (Hallmann et al. 2017, Lister and Garcia 2018, Habel et al. 2019), there is an urgent need for more studies. An ecologically important group of insects are the species belonging to the fly family Calliphoridae, which has recently undergone several taxonomic revisions whereby subfamilies such as Mesembrinellidae, Rhiniidae, and Polleniidae have been elevated to family status based on morphological and molecular data, leaving approximately 932 species described for the family Calliphoridae (Kutty et al. 2010; Pape et al. 2011; Marinho et al. 2012, 2017; Cerretti et al. 2017, 2019; Kutty et al. 2019; Whitworth and Yussef-Vanegas 2019; Gisondi et al. 2020). This family is very diverse with regards to morphology, ecology, and behavior (Pape et al. 2011, Yang et al. 2014). Most blow fly species have scavenger and decomposer feeding habits, but some species are known to cause myiasis in birds, amphibians, and mammals, including humans (de Azeredo-Espin and Lessinger 2006, Stevens et al. 2006, Stevens and Wallman 2006, Marshall 2012). Some calliphorids are biointicators of the state of conservation of ecosystems (Nuorteva 1963; Vasconcelos et al. 2015), the adults of some species are pollinators (Dag and Gazit 2001, Pérez-Bañoñ et al. 2003) and recently, the use of several species in forensic sciences and larval therapy has been increasing (Amendt et al. 2004, Byrd and Castner 2010, Echeverri et al. 2010, Benbow et al. 2015).

Given the fact that sampling efficiency must be maximized in ecological studies, it is important to select the minimum number of sites (at least one site per ecoregion) that will yield an accurate estimate of the beta diversity of the model organisms in a study region. Since there is a paucity of studies on insects in Baja California and no fine-scale ecoregions based on the region’s entomofauna, this study was designed to test whether the ecoregions based on vegetation can be used for other groups of organisms, such as calliphorid flies, and to propose a framework for alternative ecoregions.

**Material and Methods**

Nine collecting sites were selected based on a grid system, between latitudes 29.6° and 32.0°N. The collecting sites fall into five of the nine ecoregions of Mexico’s Baja California state (Fig. 1). Collections in the field were carried out between August 2017 and June 2019 during summer, winter and spring (for more details, see Supp Table S1 of Appendix I and Fig. S1 of Appendix II [online only]). In each site, three baited traps (two NTP-80 modified traps and a modified Blendon butterfly net trap), left for five hours, were used to collect blow flies (for more details, see Supp Fig. S2 Appendix II [online only]). The temperature and relative humidity were recorded with a data sensor (LASCAR electronics, EasyLog EL-USB-2). Rainy or excessively cold days were avoided, as suggested by Saloña Bordas et al. (2009). The individuals collected were recovered in 80% ethanol and brought to the laboratory for counting, curation, and taxonomic identification.

Calliphorid specimens were identified to the species level based on specialized taxonomic keys (Whitworth 2006, 2014; Tantawi et al. 2017; Jones et al. 2019) and identifications were verified by Dr. Terry L. Whitworth (Washington State University). The characters of some Calliphora (Robineau-Desvoidy) species’ genitalia were dissected for further identification. Representative voucher specimens for each species were dried and pinned, labeled, and deposited in the Collection of Baja California Arthropod Museum in Ensenada Center for Scientific Research and Higher Education (MABC; CICESE), Mexico, and the Orma J. Smith Museum of Natural History at The College of Idaho (CIDA). The remaining specimens were stored in 80% ethanol in the Collection of Baja California Arthropod Museum.

To corroborate morphology-based identifications, the nucleotide sequences of fragments of the ‘Bar Code’ gene (cytochrome oxidase C1) were obtained (Supp Table S2, Appendix I [online only]). Tissue from 22 individuals was sent to the CIBNOR node in La Paz, Baja California Sur of the MEXBOL (Mexican thematic network for the Barcode of Life project) for DNA extraction and fragment amplification. The amplified product was sent for Sanger sequencing to Macrogen, Korea. The sequences were deposited in the GenBank database (https://www.ncbi.nlm.nih.gov/genbank/). The BLAST search engine was used to compare the sequence identity of the specimens studied herein with sequences available in the GenBank database.

To test the significance of differences among the ecoregional groups of localities, based on calliphorid species composition, an ANOSIM was carried out, which is a non-parametric multivariate analysis based on the R statistic, which has values of −1 to 1 and a value of significance (P). The null hypothesis (R = 0) establishes that there is no difference between-groups and within-group similarities. Positive values indicate more similarity within groups than between groups (i.e., the groups differ), and negative values suggest more similarity between groups than within groups (Anderson and Walsh 2013). To carry out the ANOSIM analysis, the similarity matrices were constructed using the Bray–Curtis coefficient of similarity and the matrix data were previously treated to standardize the abundance of each species by the sampling effort in each ecoregion; that is, the total abundance was divided by the number of traps per ecoregion. A dendrogram was also constructed with the Bray–Curtis coefficient of similarity, using the unweighted pair-group average (UPGMA) algorithm. The dendrogram and ANOSIM analysis were performed in the PAST v 3.25 program (Hammer and Harper 2006). Finally, the percentage similarity analysis (SIMPER) was performed to evaluate which taxa best contributed to the differences between groups in the samples (Clarke 1993). This analysis has been used with the same Bray–Curtis similarity matrix, to support the results of the ANOSIM (Kavazos and Wallman 2012, Martin-Vega and Baz 2013, Dupek et al. 2019). To explore the possibility of delineating new ecoregions based on calliphorid species composition and areas of endemism, an analysis was carried out in NDM/VNDM (version 3.1; Szumik et al. 2002, Goloboff 2004; Szumik and Goloboff 2004) using distribution data for the 14 species known from Baja California. For the data on species distributions, the coordinates of the sampling sites for each individual caught during this study were used, along with data obtained from different sources (the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/); CICESE collection; CEAM—Colección Entomológica Colegio de Postgraduados, Texcoco, México; Whitworth and Rognes
The analysis was run 100 times using edge proportions, saving sets with one or more endemic species and keeping the remaining default settings. A consensus of the areas was then created with a cutoff of 75% similarity.

Results

Abundance and Richness

A total of 30,307 individual blow flies distributed in six genera and 13 species were collected in the nine localities (Supp Table S3 Appendix I [online only]). Cochliomyia macellaria (Fabricius) was the most abundant species (77.11%), followed by Phormia regina (Meigen) (16.37%) and Chrysomya rufifacies (Macquart) (2.95%). These three species make up 96.43% of all individuals collected in this study. The least abundant species was Compsomyiops callipes (Bigot) with only two specimens collected.

Two species found in all nine localities were Chrysomya rufifacies and Cochliomyia macellaria. Most of the Calliphora species were distributed in a narrow area. Furthermore, the six species of Calliphora were collected in Sierra Juarez and Sierra San Pedro Martir. However, Calliphora latifrons (Hough) was the only species in this genus that occurred in eight of the nine localities. The species that were only found in Sierra Juarez and Sierra San Pedro Martinez were Calliphora grahami (Aldrich), C. terraenovae (Macquart), C. vomitoria (L), and Compsomyiops callipes. Lucilia cuprina (Wiedemann) was found in five of the nine localities. The locality with the highest total abundance of calliphorids was San Felipe, where C. macellaria predominated, followed by Sierra Juarez, where P. regina was the most abundant, and Punta Final and El Mogor, where C. macellaria predominated (Supp Table S3 Appendix I [online only]).

The localities with the highest species richness were Sierra Juarez and Sierra San Pedro Martinez, where 12 of the 13 species were found, but they slightly differed in species composition: Chrysomya megacephala (Fabricius) was found only in Sierra Juarez and Compsomyiops callipes only in Sierra San Pedro Martinez. Rio Hardy and El Mogor exhibited eight species with different species composition. The localities with the lowest species richness were Santa Catarina and Río Hardy with four species but different composition of species.

Spatial Variability by Localities

The composition of the Calliphoridae community differed between the localities (\( R_{global} = 0.3758 \), \( P < 0.001 \)). Two similar localities in terms of species composition were San Felipe and Punta Final with no significant difference between the species found in either locality (\( R = 0.087, P = 0.138 \) (Table 1, Fig. 2)). These localities also belong to the same ecoregion, San Felipe Desert (Eco 5). The species composition of Santa Catarina and Rio Hardy were also not significantly different (\( R = 0.037, P = 0.289 \)) and the two localities...
grouped together, despite belonging to different ecoregions, where Santa Catarina is part of the Central Desert ecoregion and Río Hardy is part of San Felipe Desert. 

El Mogor, which belongs to the transitional zone Chaparral/Coastal Sage Scrub (Eco 1), had species composition that was not significantly different from Santa Catarina, Cerro Santo Tomás, Río Hardy and Punta Colonet. El Mogor formed a group in the dendrogram with Punta Colonet, located in Coastal Succulent Scrub (Eco 2). Cerro Santo Tomás had nonsignificantly different species composition from the localities El Mogor and Punta Colonet, although it belongs to the Central Desert (Eco 4) and should therefore have similar species composition as Santa Catarina, but in the dendrogram it does not group with any other locality. Sierra Juárez and Sierra San Pedro Mártir belong to the same ecoregion of California Mountains (Eco 3) and are similar (R = 0.048, P = 0.255) in terms of species composition, while being distinct from all of the other localities. When comparing the groupings on the dendrogram (Fig. 2) with the ANOSIM R-values (Table 1), it is clear that some of the localities early split in the dendrogram, do not appear to have significantly different species compositions based on the ANOSIM R-values. Therefore, the approach taken here has been to use the dendrogram as a visual guide, but to discuss the general groupings based on the ANOSIM R-values.

**Table 1.** R-values provided by the ANOSIM test for community similarities of Calliphoridae in nine localities of Baja California, Mexico, between August 2017 and June 2019

|      | EIM | PC  | SJ  | SSPM | SC  | CST | RH  | SF  |
|------|-----|-----|-----|------|-----|-----|-----|-----|
| EIM  | -0.049 |     |     |      |     |     |     |     |
| PC   | 0.594** | 0.565** |     |      |     |     |     |     |
| SJ   | 0.716** | 0.562** | 0.048 |      |     |     |     |     |
| SSPM | 0.031 | 0.175 | 0.268 | 0.449** | 0.719** | 0.017 | 0.017 | 0.797** |
| SC   |       | 0.031 | 0.268 | 0.017 | 0.719** | 0.017 | 0.797** | 0.344* |
| CST  | 0.104 | 0.706** | 0.037 | 0.748** | 0.344* | 0.319* |       |     |
| RH   | 0.421** | 0.994** | 0.153* | 0.949** | 0.344* | 0.319* | 0.413** | 0.319* |
| SF   | 0.388** | 0.954** | 0.078 | 0.949** | 0.344* | 0.319* | 0.413** | 0.087 |
| PF   |       |       |       |       |       |       |       |     |

*R < 0.05, **P < 0.01.

**Fig. 2.** UPGMA dendrogram by localities and map with the clusters color-coded as in the dendrogram. EIM: El Mogor; PC: Punta Colonet; SJ: Sierra Juárez; SSPM: Sierra San Pedro Mártir; SC: Santa Catarina; CST: Cerro Santo Tomás; RH: Río Hardy; SF: San Felipe; PF: Punta Final.
In the SIMPER analysis, an overall dissimilarity percentage of 67.58% was obtained. The species that contributed most to the dissimilarity between localities were Cochliomyia macellaria (41.38%), Calliphora latifrons (19.60%), Phormia regina (11.44%), and Chrysomya rufifacies (8.11%) (Table 2). The search for areas of endemism returned zero areas (Supp Appendix II, Fig. 5).

Discussion

Of the 13 species belonging to the Calliphoridae family found in this study, seven have been previously registered in Baja California (Tantawi et al. 2017), Lyle Stotelmyre (personal communication, 2019). However, Lucilia mexicana, a species known in the region according to the literature and collected by Whitworth (2014) and Lyle Stotelmyre (personal communication, 2019), was not collected in this study. Furthermore, seven species are newly reported to occur in the State of Baja California (Calliphora coloradensis, C. grahami, C. livida, C. terraenovae, C. vomitoria, Compsomyiops callipes, and Phormia regina) and two of them are newly reported in Mexico (Calliphora livida and C. terraenovae).

Based on the most recent revision of the Nearctic species of the genus Calliphora, 13 species are described for North America (Tantawi et al. 2017), six of which were collected in this study. Of these six species, Calliphora coloradensis and C. livida are endemic to North America, C. terraenovae has a Holarctic distribution, while C. grahami, C. latifrons and C. vomitoria are distributed in other regions as well (Pont 1980, Verves 2005, Kurahashi 1989, Tantawi et al. 2017). Calliphora colonodensis is widespread throughout the western United States (Hall 1948, Whitworth 2006, Jones et al. 2019) and in northwestern and central Mexico (Vergara-Pineda et al. 2012, Tantawi et al. 2017). Calliphora livida and C. terraenovae are newly reported from Mexico (Munguia-Ortega et al. 2020, unpublished data), the former commonly found in Canada and southern United States (Tantawi et al. 2017, Jones et al. 2019) and the latter widespread from Alaska to Southern California, and has even been reported from eastern Greenland (Whitworth 2006). Calliphora grahami is endemic to the western Palearctic and Oriental regions and was introduced to Hawaii and western United States (Tantawi et al. 2017, Jones et al. 2019). Finally, Calliphora vomitoria is common throughout the Holarctic Nearctic regions, including Mexico (James 1955, Delfinado and Hardy 1977, Molina-Chavez et al. 2012, Tantawi et al. 2017).

The genus Chrysomya, known to cause myiasis (Whitworth 2006) contains 12 species, four of which are found in the Nearctic and Neotropical regions (Dear 1985, Carmo et al. 2018) and two, C. megacephala and C. rufifacies, in this study. Both species were originally only found in the southern United States and throughout Mexico (Gagné 1981, Baumgartner and Greenberg 1994, Castañeda-Vildózola et al. 1999, Greenberg and Kunich 2002, Whitworth 2006, Pérez-Balaz et al. 2012, Vergara-Pineda et al. 2012, Huerta Jiménez 2015, Mañas-Jordá et al. 2017, Jones et al. 2019). However, the distributional ranges of these two species are currently expanding since they have also been reported from Canada during the summer (Rosati and VanLaeerhoven 2007, Whitworth 2019, personal communication).

The genus Cochliomyia is endemic to America with four species described so far. The only species of this genus found in this study, C. macellaria, is widespread in the Nearctic and Neotropical regions (Whitworth 2010) and has been recorded from several states throughout Mexico (Dear 1985, Whitworth 2010, Vergara-Pineda et al. 2012, Wolff and Kosmann 2016, Yusseff-Vanegas and Aagnarsson 2016). Compsomyiops callipes is a predominately Neotropical species, also found in the Nearctic region in the southwestern United States (Whitworth 2006, Brundage and Byrd 2016, Jones et al. 2019) and in central and southern Mexico (Dear 1985, Huerta Jiménez 2015). Phormia regina is a monotypic genus with a Holarctic distribution, widespread and very common in North America. In Mexico, it has been found as far south as Mexico City (Hall 1948, Molina-Chávez et al. 2012, Vergara-Pineda et al. 2012) and Veracruz (personal observation by Jaume-Schinkel and Ibáñez-Bernal 2020).

The genus Lucilia includes 12 species described for North America, cosmopolitan and mostly synanthropic (Whitworth 2006). Of the two species found in this study, L. cuprina is found from the southern United States through Central America to northern

### Table 2. Percentage contribution of each species of Calliphoridae to dissimilarities in nine localities of Baja California, Mexico, between August 2017 and June 2019

| Species                      | Av. dissim | Contrib. % | Cumulative % | ELM   | PC   | SJ   | SSPM | SC   | CST  | RH   | SF   | PF   |
|------------------------------|------------|------------|--------------|-------|------|------|------|------|------|------|------|------|
| Cochliomyia macellaria       | 27.97      | 41.38      | 41.38        | 0.464 | 0.513| 0.054| 0.000| 0.783| 0.238| 0.71 | 0.996| 0.984|
| Calliphora latifrons         | 13.25      | 19.60      | 60.99        | 0.143 | 0.204| 0.24 | 0.464| 0.132| 0.116| 0.000| 0.000| 0.000|
| Phormia regina               | 11.44      | 16.92      | 77.91        | 0.002 | 0.643| 0.349| 0.018| 0.028| 0.000| 0.000| 0.002|
| Chrysomya rufifacies         | 8.115      | 12.01      | 89.92        | 0.342 | 0.104| 0.030| 0.003| 0.084| 0.206| 0.032| 0.002| 0.012|
| Lucilia sericata             | 2.634      | 3.897      | 93.82        | 0.037 | 0.18 | 0.009| 0.004| 0.000| 0.000| 0.000| 0.000|
| Chrysomya megacephala        | 1.675      | 2.479      | 96.30        | 0.009 | 0.008| 0.000| 0.037| 0.098| 0.001| 0.000| 0.000|
| Calliphora livida            | 1.674      | 2.477      | 98.77        | 0.004 | 0.008| 0.132| 0.000| 0.000| 0.000| 0.000| 0.000|
| Calliphora coloradensis      | 0.268      | 0.396      | 99.17        | 0.000 | 0.000| 0.016| 0.000| 0.006| 0.000| 0.000| 0.000|
| Calliphora grahami           | 0.247      | 0.365      | 99.53        | 0.000 | 0.000| 0.020| 0.000| 0.000| 0.000| 0.000| 0.000|
| Lucilia cuprina              | 0.186      | 0.276      | 99.81        | 0.001 | 0.000| 0.007| 0.000| 0.000| 0.008| 0.000| 0.000|
| Calliphora vomitoria         | 0.063      | 0.093      | 99.90        | 0.000 | 0.001| 0.004| 0.000| 0.000| 0.000| 0.000| 0.000|
| Calliphora terraenovae       | 0.061      | 0.090      | 99.99        | 0.000 | 0.000| 0.004| 0.000| 0.000| 0.000| 0.000| 0.000|
| Compsomyiops callipes        | 0.005      | 0.007      | 100.00       | 0.000 | 0.000| 0.000| 0.000| 0.000| 0.000| 0.000| 0.000|
Argentina and Peru (Whitworth 2006, 2010; Jones et al. 2019; personal communication Yusseff-Vanegas 2019), with records from the Mexican states of Mexico City and Veracruz (Molina-Chávez et al. 2012, Whitworth 2014) and L. serrata can be found from southern Canada to Argentina (Hall 1948, Mello 1961, Whitworth 2014), recorded in four Mexican states (Vergara-Pineda et al. 2012, Molina-Chávez et al. 2012, Valdés-Perezgasga and García-Espinoza 2014, Mañas-Jordá et al. 2017).

A new regionalization for Baja California, based on calliphorid species, could not be obtained in this study since these species are widespread and there are no endemic species in our focal area. Furthermore, given that the fact that the main aim of this study was not to propose new ecoregions, but rather, to evaluate the fit of vegetation-based ecoregions for blow flies, the discussion will focus on the results of the analyses carried out using ANOSIM and the UPGMA-based cluster analysis.

For the nine localities studied here, the Calliphoridae species composition was similar in two of the three localities of the San Felipe Desert ecoregion (Eco 5), reflecting the homogeneity in environmental factors of these coastal desert localities. However, Rio Hardy, which—based on vegetation—also belongs to Eco 5, was more similar to the locality Santa Catarina (Eco 2) in terms of Calliphoridae species composition, possibly due to the fact that both localities had a higher relative humidity than other localities. The other two localities which belong to different ecoregions, but grouped together based on fly species, are Punta Colonet and El Mogor. These localities are found in neighboring regions, where González-Abraham et al. (2010) mentioned as main discrepancy zones for the biological regionalization of the Baja California peninsula. Punta Colonet is located in Coastal Succulent Scrub ecoregion and El Mogor belongs to the transitional zone Chaparral/Coastal Sage Scrub. However, both localities are near the Pacific coast and only separated from each other by 157 km, which confers very similar climatic conditions.

The California Mountains ecoregion, which includes the localities Sierra Juárez and Sierra San Pedro Mártir, also formed a group based on calliphorid species composition, significantly different from the composition of all other localities studied. Even though Sierra San Pedro Mártir and Sierra Juárez had similar species compositions, a more in-depth study of the California Mountains ecoregion might yield interesting results, given that these two localities differ in species composition for other groups as well, such as Hesperocyparis montana (Wiggins), Sphaeromeria martirensis (Wiggins), Oncorhynchus mykiss nelsoni (Everman), and Tamiasciurus mearnsi (Townsend) which are endemic to Sierra San Pedro Mártir (Minnich et al. 1997, Rebmam and Roberts 2012, Ramos-Lara et al. 2013, Rebmam et al. 2016) and Hesperocyparis reveliana (Silba) and Verbena occidentiana (Perry) which are endemic of Sierra Juárez (Rebmam et al. 2016). Furthermore, Riemann and Ezcurre (2007) mentioned that high levels of micro-endemics were found in Sierra San Pedro Mártir. The distinctiveness of these mountains was previously recognized in other studies (e.g., Morrone 2017) and is reflected by the fact that the California Mountains ecoregion belongs to the California biogeographic province, while the remainder of the peninsula belongs to the Baja California province.

Cerro Santo Tomás is the locality that did not form a group in the dendrogram with any of the other localities, although it belongs to the Central Desert (Eco 4), as does Santa Catarina, where the greatest abundance and richness of species was found. On the other hand, the collections in Cerro Santo Tomás were characterized by a lack of specimens, which could be associated both with the adverse conditions that occurred throughout the collections, with wind during the three sampling seasons, extreme temperatures and low humidity. Furthermore, even though Cerro Santo Tomás belongs to the Central Desert ecoregion and the Valle de los Cirios protected area, it could be considered a ‘sky island’, with an ecosystem different to its surrounding areas. We recommend the Valle de los Cirios protected area for further studies, especially given the fact that populations of the invasive genus Chrysomya were found in sympathy with native species such as C. macellaria, whereas previous studies in other areas have reported displacement of C. macellaria by expanding populations of Chrysomya (Baumgartner and Greenberg 1984, Baumgartner 1993, Godoy 2007, Rosati and VanLaeethoven 2007, Moretti and Godoy 2013).

Although in the dendrogram the localities formed five clusters, some of these clusters were not separated based on the calliphorid species composition analysis (ANOSIM). Therefore, considering both sources of information, but lending more weight to the R-values, three general groups have been distinguished: Gulf-Desert, Mountains and Pacific-Center. The Gulf-Desert group is conformed by San Felipe and Punta Final, two of the three localities in the San Felipe Desert ecoregion. The Pacific-Central group formed by El Mogor, Punta Colonet, Rio Hardy, Santa Catarina and Cerro Santo Tomás, which belong to three vegetation-based ecoregions, and the Mountains group conformed by Sierra Juárez and Sierra San Pedro Mártir which belong to the California Mountains ecoregion.

Therefore, one can infer that in the case of calliphorid flies, the vegetation-based ecoregions only reflect the fly species’ distributions to a certain extent and care must be taken when undertaking ecological biogeographical studies using regionalization based on organisms other than the focal taxa. Perhaps, in the case of herbivorous insects with host-plant specificity, the distribution of the insects mirrors that of vegetation more closely. But given that calliphorids display a wide range of different habits and strategies, it would be of better use delimiting their own ecoregions. Unfortunately, the factors determining these fly species’ distributional range are still not clear. Previous studies have provided different explanations for calliphorid fly distribution, including biotic and abiotic factors such as time of year, geographic position, environmental characteristics, and micro-habitats (Anderson 1995, Hwang and Turner 2005, Lomolino et al. 2006, Fremdt and Amedendt 2014, Mañas-Jordá et al. 2017, Feddern et al. 2018). Thus, temporal fluctuations in calliphorid populations are difficult to model, due to the complexity of predicting resource availability, interspecific competition, climate, habitat structure, and their effects (Kavazos and Wallman 2012). Based on the approximate grouping of the localities in this study, one important factor could be altitude, followed by humidity. Another factor that could be taken into account in future studies is the degree of urbanization of certain localities, especially for the more synanthropic species. Since carrion is an ephemeral resource in the ecosystem, these ‘ecological islands’ (Beaver 1977) are characterized by intense resource competition (Hanski 1987). Therefore, it is not surprising that blowfly species distribution often does not match vegetation categories or ecoregions since factors such as food availability are mostly animal-based. Since this is the first study in the State of Baja California, we recommend more extensive collecting throughout each ecoregion, which would improve the understanding of blow fly populations in the entire region.

Supplementary Data

Supplementary data are available at Journal of Insect Science online.
Acknowledgments

We thank the Sánchez-Piñuelas family and their cousin Simón Peralta, for granting us permission and logistics support to collect in Cerrro Santo Tomás. We thank Sierra San Pedro Mártir National Park for their help during our stay in the Park. We thank the many volunteers and students from CICESE and UABC who participated in the field work: Ramiro Santos Cobos, Carlos González Vera, Diego González Zamora, Victor Aguilera Molina, Edgar Lima, Rodrigo Arce Valdés, Heriberto Pérez Murillo, Bryan Meza Macias, Jorge Sánchez Solís, Cipatli Jiménez Vera, Stephen Bullock, Mario Salazar (who also helped us resolve questions about endemic flora), Jaime Luévano, and Mario Mendoza. Special thanks to William H. and Mary Clark for all the lab materials and help during the development of this research, for joining us during fieldwork and for letting us stay in their home while working in the Desert. We are most grateful to Terry L. Whitworth for helping us with specimen identifications, research stay and comments to improve the research and the manuscript. We thank Jesús Romero Nápoles and Alejandro Estrada for the records data from the Museum Colección Entomológica Colegio de Postgraduados (CEAM), Texcoco, Mexico. We thank Sohath Zamira Yussef Vanegas, Arn Rytter Jensen, Juan José Morrison, Philippe Usseglio-Polatara and an anonymous reviewer for the constructive comments on the manuscript.

We are grateful to William H. Clark from the Orma J. Smith Museum of Natural History at The College of Idaho (CIDA), who provided valuable feedback in the early English version of the essay and which greatly improved the final version of the manuscript. This research was supported by the Jiji Foundation fund of the International Community Foundation awarded to FSC (award number 20180127), Fondo Sectorial de Investigación para la Educación SEP-CONACYT Investigación Científica Básica 2017–2018 grant A1-S-15134 to FSC, and by the postgraduate grant from the Consejo Nacional de Ciencia y Tecnología (CONACyT, grant number 634579) to KMO.

Author Contributions

F.S.C., K.M.O. and E.L.R. conceived and designed the study. K.M.O. and E.L.R. collected the data through field and laboratory work. K.M.O. and F.S.C. analyzed the data and led the writing. All authors contributed to the editing of the final version of the manuscript.

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