# Temperature accounts for the biodiversity of a hyperdiverse group of insects in urban Los Angeles

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**Abstract**

The urban heat island effect is a worldwide phenomenon that has been linked to species' distributions and abundances in cities. However, effects of urban heat on biotic communities are nearly impossible to disentangle from effects of land cover in most cases because hotter urban sites also have less vegetation and more impervious surfaces than cooler sites within cities. We sampled phorid flies, one of the largest, most biologically diverse families of true flies (Insecta: Diptera: Phoridae), at 30 sites distributed across the central Los Angeles Basin, where we found that temperature and the density of urban land cover are decoupled. Abundance, richness, and community composition of phorids were most parsimoniously accounted for by mean air temperature in the week preceding sampling. Sites with intermediate mean temperatures had more phorid fly individuals and higher richness. Communities became more even with lower minimum temperatures and further away from natural areas, suggesting that communities further away from natural source populations may be more homogenized. Species composition was best explained by minimum temperature. Inasmuch as warmer areas within cities can predict future effects of climate change, phorid fly communities are likely to shift non-linearly under future climates in more natural areas. Exhaustive surveys of biotic communities, such as the one we describe here, can provide baselines for determining the effects of urban and global climate warming as they intensify.

Keywords: climate change, species richness, phorid fly, urban heat island

## Introduction

Urban development is accelerating with uncertain effects on biodiversity. While many species do not persist in urban areas, cities can support a surprising range of native and even threatened taxa [1]. Thus, determining conditions within cities that affect species persistence is increasingly a focus of ecological research from fundamental and conservation perspectives [2–4]. However, isolating specific drivers of biodiversity in cities has proven difficult because organisms in cities experience a range of novel conditions that may alter their abundances and distributions [5–7]. Therefore, for most animal taxa, specific mechanisms driving community assembly in cities remain unknown.

The urban heat island effect is a prevalent phenomenon in cities, and growing evidence shows that urban heat can alter species richness, abundance, and community composition [8–14]. Urbanization causes cities to be as much as 12˚C hotter than adjacent areas [15], which is on par or above warming anticipated by the Intergovernmental Panel on Climate Change over the next several decades [16]. In certain cities, urban warming can also operate at local scales, creating thermal mosaics within the urban matrix (e.g., [17–20]). Despite the short history of research on the biotic effects of urban heat, researchers have found important patterns across diverse taxa [6,9–12,21–23]. For example, remnant native plant communities in urban environments may be altered under warming conditions, favoring more xerophilic species [24,25].

Because temperatures in cities match or exceed those expected under future climate change, researchers have suggested that thermal gradients within cities might allow us to predict biotic responses to the future climate warming [26,27]. Cities might be useful proxies for climate warming because urban heat has been in place for decades to centuries, and large scale, controlled warming experiments in more natural areas are often impractical (but see [28,29]).

However, urban heat might not be an appropriate proxy for broader climate warming because other aspects of urbanization might also have strong effects on species. Perhaps most importantly, land cover (impervious surfaces, vegetation) and urban heat tend to covary, making it impossible to separate their effects on biological processes. Hot urban environments often have more impervious surface, less vegetation cover, and lower vegetation complexity [30–32]. While researchers have used various useful approaches to determine effects of urban warming alone – e.g., laboratory chamber experiments [10,17] – actually separating effects of land cover and temperature in the city could provide insight into whether biotic responses are more attributable to temperature or other aspects of urbanization.

Insects are highly responsive to temperature, are a foundational component of terrestrial biodiversity, and provide a range of services and disservices within cities [33,34]. As insects are ectotherms, they have elevated metabolic and reproductive rates in response to warming until their thermal maxima are reached [13]. One of the most abundant animals in terrestrial environments are phorid flies [35,36], which are responsive to thermal conditions, but also feed on a wide range of resources and develop and occupy a tremendous variety of microhabitats [37]. Cities can support hyperdiverse communities of phorid flies, with dozens of species recently described from central Los Angeles [38,39]. With a small body size (0.4-6 mm) and presumably short dispersal distances, we would expect phorid fly biodiversity to finely track microclimatic conditions in the urban environment, relative to less ephemeral or larger-sized organisms.

Here we evaluate the spatial and temporal predictors of phorid fly biodiversity across central Los Angeles, CA, USA, hereafter we refer to as L.A. In this project, species were sampled exhaustively [40], and 30 new species of flies were described from L.A. from this dataset in 2015 [38]. We leverage the complete documentation of this diverse group to determine

effects of urban land development and climate in a city where we found these variables are uniquely decoupled. We sampled phorid flies and site environmental conditions in 30 locations throughout a calendar year to evaluate biodiversity responses to thermal and urbanization gradients in the L.A. metropolitan area. By measuring temperature and moisture variables at a very fine scale to match the habitat occupied by the organisms [41], we achieve a biologically relevant understanding of how local climatic factors vary across an iconic urban habitat.

## Methods

*Study design and insect sampling procedures*

We placed a series of Malaise traps [42] (Townes lightweight model Sante Traps, Lexington, KY) in 30 sites throughout central L.A. (Fig. 1). The distribution of the sites was designed to capture a range of biotic and abiotic gradients in the urban environment as part of the BioSCAN (Biodiversity Science: City and Nature) project of the Natural History Museum of Los Angeles County (LACM). The initial findings from this sampling are described by Brown and Hartop [40], who provide a detailed description of each site featured in the study. For each of twelve sampling periods (approximately the first week of each month), we collected and identified all phorid flies in samples to species, resulting in a total of 42,480 specimens. Vouchers are deposited in the LACM. Over this year of sampling, the fauna was essentially sampled to completion, as richness estimators predicted that additional sampling would be expected to yield perhaps one additional new species [40]. We are confident that this sampling regime represents nearly all the species in this lineage that would be captured using this sampling approach.

*Abiotic data collection and processing*

We continuously recorded air temperature, soil temperature, and relative humidity at each site using a weather station adjacent to each trap (Onset HOBO U30 Station, Bourne, MA). Weather stations were regularly maintained, but like most sensor-based ecological monitoring, gaps in reading due to occasional equipment failure were common [43]. We addressed these gaps through a series of down-sampling and estimation methods. First, data for readings of each type were subjected to quality control to remove impossible values, and flag improbable values for additional scrutiny. Then, to eliminate small gaps in the data, because readings were taken at five-minute intervals, we averaged all readings for each measure by hour. We culled out observations from time periods where fewer than 18 of the 30 sites were reporting data (primarily occurring during experimental set-up and take down). Following this process, null observations (gaps) represented an average of 4% of site-by-hour observations, and 11 of the 30 sites had no gaps.

Because many sites were near to each other and behaved similarly (although not identically) from an environmental standpoint, we estimated missing data first by using principal component analysis to rank sites, pairwise, by their similarity. Then, for each site with missing values for a given environmental response variable, we ran a linear model between that variable and the same variable from the most similar site. Then, based on the regression parameters observed, we estimated the values of the missing data, and substituted them for the missing value code into the weather data frame. We repeated this process for each site and variable combination where missing values were observed, and in the rare occasion where this process did not address all the gaps, we repeated this process by pairing the site with missing data from the second most similar site.

We estimated distance to the closest natural area by calculating the distance to the nearest boundary of an area recorded in the California Protected Area Database (CPAD). CPAD contains lands protected under conservation easements and open space, such as national/state/regional parks, forests, preserves, and wildlife areas. As estimates of urbanization, we used 2016 -2017 U.S. Geological Survey Landsat 7 surface reflectance and the National Land Cover Database 2011 Percent Developed Imperviousness Layer to calculate the average Normalized Difference Vegetation Index (NDVI) and the percentage of impervious surface at each site. A 50-meter buffer was used for data extraction to represent the local environment.

*Statistical Analyses*

**Correlations between environmental and climatic predictors:** To determine the relative contribution of urbanization and topography on microclimates across our study region, we used two simple linear models to test whether impervious surface and/or elevation were predictive of mean annual air temperature at our sampling sites.

**Phorid fly abundance, richness, and evenness:** As the first set of response variables, we calculated the total number of individuals caught per trap per day (abundance), species richness, and Pielou evenness. Because the traps were in place for slightly different amounts of time during some sampling periods, we divided each response variable by the number of days a trap was left out. One species, *M. agarici*, constituted a substantial number of specimens in samples at many sites (and about one-quarter of all individuals collected). Therefore, we included total individuals of this species captured per trap per day as an additional response variable. Many of the species in this study were only recently described and their biology remains poorly known,

151 and the current state of knowledge [44] prevents us from using taxon-specific data (such as
152 phylogeny, diet) as factors in the model.

153 To minimize overfitting, we conducted model selection to identify the most parsimonious
154 independent variables describing effects of temperature, humidity, and urbanization on each
155 response variable. For each response, we built a series of linear mixed effects models in the *nlme*
156 package in R [45]. In all models, latitude, longitude, and distance to the nearest natural, protected
157 area were included as fixed effects, and site was included as a random effect to account for
158 repeated sampling of flies at each site. In each case below, we compared models with tightly
159 correlated predictors describing similar aspects of the urban environment and selected the
160 parameter in the model with the lowest AICc score to include in full models used for inference
161 (see below). We decided, depending on the shape of the response, whether to include a squared
162 term to account for non-linear responses of phorid flies to environmental variables. To describe
163 urbanization, we compared models that included impervious surface cover, NDVI – each
164 measured at a 50-m buffer as described above – and neither of these (null model). For each
165 response, we also compared models including mean RH (relative humidity), maximum RH,
166 minimum RH, and no humidity predictor. Similarly, we compared separate models including
167 mean temperature, maximum temperature, minimum temperature, and no temperature predictor,
168 and we compared another set of models of mean soil temperature, mean maximum soil
169 temperature, mean minimum soil temperature, and no temperature predictor. All climatic
170 predictors represented average conditions one week before sampling to represent the conditions
171 most likely to affect phenology [46].

172 After selecting parameters, we built one full model for each response variable (species
173 richness, *M. agarici* abundance, total abundance, and evenness) for a total of four models. In

these models, we included each parameter chosen to represent urbanization, temperature, and humidity, along with latitude, longitude, and distance to the nearest natural area as fixed effects. Site was included as a random effect. To determine if site proximity rather than environmental conditions may account for responses we observed, we performed an analysis to test if spatial autocorrelation was observed among sample sites. We examined abundance of phorid flies by date, for every date where >5 sites reported data, using Moran's I, applied to an inverse distance matrix of site co-ordinates as the weighting factor [47].

**Community composition:** In addition to the univariate community responses, we also conducted a non-metric multi-dimensional scaling (NMDS) analysis to examine patterns in community composition, and fit environmental vectors to gain insights into drivers of these patterns [48]. For this analysis, we used all captures of phorid flies at a given site, across the whole sampling period. We culled all singletons (species represented by a single sample throughout the entire study), a standard approach because the incidence of a singleton is indistinguishable from a spurious occurrence [49]. The NMDS was conducted on the Bray-Curtis distance calculated from the untransformed matrix of taxon-by-site using abundance values. Environmental fit vectors were selected iteratively by comparing the fit statistics (Global $R^2$ and p-value) within a group of related, and auto-correlated, parameters (e.g., minimum, maximum and mean air temperatures, etc.).

## Results

**Correlations between environmental variables and urbanization:** Measured mean annual temperatures at our study sites were independent of impervious surface and elevation (Fig. 2;

197 impervious surface: y= -129+9 x, $F_{1,28}$=1.12, *p*= 0.30; elevation: y= -45+4.5x, $F_{1,28}$= 0.02, *p*=
198 0.90), suggesting that neither urban land cover nor elevation drove urban temperatures.
199 Therefore, we conclude that, while L.A. may have a large scale urban heat island effect, other
200 unknown factors drive temperatures at the local scale. As expected, NDVI tracked impervious
201 surface, though these values were not closely related to the distance to natural areas (Fig. 3)
202
203 **Mean and peak biotic responses:** Abundance and richness of phorid fly communities
204 throughout the city were best explained by air temperature (Table 1). No other climatic
205 parameters had significant predictive value, aside for a lesser effect of relative humidity on
206 species richness (Table 1), and humidity slightly tracked temperature (Fig. S1). Phorid fly
207 abundance and richness responses to environmental conditions were nonlinear, with peaks at
208 intermediate mean weekly temperatures (Fig. 4). The factors affecting the abundance of the
209 most common species, *M. agarici*, were the same factors affecting total abundance (Table 1).
210 Evenness of phorid fly communities was weakly explained by mean minimum weekly
211 temperature and distance to natural areas, such that phorid fly communities in areas with lower
212 minimum temperatures and those that were further away from natural were more even (Table 1).
213 Latitude and longitude were associated with abiotic conditions (Figs. S2, S3), but spatial
214 autocorrelation was limited. Among all dates where sufficient data existed for autocorrelation
215 analysis (10 dates), one date (Week 6 of 2014) had significant spatial autocorrelation (*p*= 0.037),
216 suggesting that autocorrelation is rare in this system and may have been observed by chance.
217 Thus, after we accounted for spatial similarity of sites using latitude and longitude as described
218 above, no additional correction for spatial autocorrelation was needed.
219

**Community composition:** The effects of NDVI and mean minimum weekly temperature on species composition were orthogonal, with a much greater effect of temperature (Fig. 5). Mean minimum weekly temperature had the only significant vector, which also had the greatest magnitude ($r^2$= 0.26, $p$= 0.02)

## Discussion

We found that urbanization and climate are uniquely decoupled across the L.A. Basin. While distance to the coast appears to affect air temperature (see Fig. 1), urban land cover does not influence local temperatures at the fine scale of our sampling [50]. Because of this decoupling, we were able to independently assess effects of local climate and urban land cover on phorid fly communities. We found that air temperature had the most robust influence on the assembly of the phorid fly community, but that different aspects of temperature were most closely associated with species abundance, richness, and evenness. Local impervious surface and vegetation cover (NDVI), which represent urbanization, did not outperform null models. We conclude that local climate, not urban land cover, is the strongest driver of phorid fly community assembly across Los Angeles.

Higher mean temperatures were associated with increased phorid fly richness, until around 20°C, where richness declined. We predicted that cooler sites would harbor more species because warmer areas would be associated with reduced persistence of heat-intolerant species. However, potentially because temperatures in L.A. appear to be driven by a natural gradient (distance to coast) rather than urbanization and has therefore been in place for a long time, we find evidence that intermediate temperatures may support both heat-tolerant and -intolerant species, and thus most phorid species in L.A. Many of the species in our study (e.g., *M.*

243 *halterata*, *M. nigra*, and *M. pleuralis*) are probably introduced from areas of northern Europe
244 with cooler thermal conditions than L.A., which could also account in part for the loss of
245 abundance at higher mean temperatures. However, in general, the relative contributions of non-
246 native and native species to the patterns we observed are unclear. While we know that many
247 species of phorids in L.A. are native based on their species interactions and/or distributions (i.e.,
248 found only in certain parts of North America in well-studied groups), knowledge about phorid
249 fly distributions is inadequate to inform us to what extent non-native species contribute to the
250 patterns we observe.

251 While species richness was tied to mean temperature, evenness was weakly explained by
252 minimum temperature and distance to natural areas. The latter was included in the analysis
253 because it is well established that some species have habitat requirements involving larger
254 patches of land that are less urbanized. For example, the ant-decapitating guild of phorid flies are
255 only found within and adjacent to natural areas because these are locations in L.A. where their
256 hosts (species of *Camponotus*, *Crematogaster*, *Liometopum*, *Neivamyrmex*, *Pheidole,* and
257 *Solenopsis*) are found. Elsewhere, the host ants are typically displaced by invasive Argentine
258 ants [40,51]. We expected that species richness would drop with distance from natural areas, as
259 certain native species would be removed from the species pool. Instead, we found that species
260 evenness might be the result of a more complex process, in which communities become less even
261 further from natural areas, but not because of the loss of species from communities – distance
262 from natural areas did not predict richness – but rather because relative abundances may shift.
263 Our results suggest that a subset of species may benefit from living further from natural areas,
264 where perhaps there is less competition from species that may locally disperse into more
265 urbanized environments from source populations in more natural areas. While we predict this

266 may be the cause of less even communities further from natural, protected areas, further studies
267 on population genomics and niche overlap of phorid flies are needed to determine mechanisms
268 driving this pattern. In addition, sites with lower minimum temperatures support compositionally
269 different and more even communities than areas with higher minimum temperatures. We may
270 observe this pattern because a few species in the region have disproportionate fitness benefits
271 from warmer minima.

272 Species richness was also higher at intermediate relative humidities, and we suspect this
273 results from the benefits and drawbacks of wet climates for insects. Throughout the year, many
274 species showed large spikes in abundance. Among those with known life histories (as listed in
275 Fig. 5: *Chonocephalus bentacaisei*, *M. agarici*, *M. halterata*, *M. marquezi*, *M. nigra*, and *M.*
276 *pleuralis*) fungus-feeding larvae are overwhelmingly common. Sporophore eruptions can
277 produce hundreds of flies relatively quickly, as Brown & Hartop [52,53] estimated a single
278 mushroom cap contained 500 larvae of *M. marquezi.* We suspect abundance peaks for these
279 species are associated with the mass production of fungal sporophores in close proximity to our
280 sampling area, which are common after rain. However, we also suspect that very wet climates
281 may increase fungal disease incidence [54,55], such that highest phorid fly richness occurs at
282 intermediate relative humidity.

283 Urban landscapes are rarely designed to sustain biodiversity, though this is often an
284 idealized goal informed by research [56]. At very high levels of heat, abundance and diversity
285 declines, which is consistent with other studies suggesting that the urban heat island effect has
286 negative effects on many species [13,57,58]. As the global temperature increases, many of the
287 sites we sampled may also warm and therefore no longer support diverse phorid fly
288 communities, though this will depend on how quickly phorid flies can adapt to changing thermal

289 conditions. Even on short timescales, it is possible that the thermal limits of species have
290 evolved, so that animals in the warmer parts of the city are capable of tolerating warmer
291 conditions independent of ecotypic acclimation [59]. Given the rapid evolution of thermal
292 tolerance in other arthropods [59–61], and the short generation times of phorid flies, rapid
293 adaptation to climate change might be possible.

294 Exhaustive biodiversity sampling has reaped substantial rewards in understanding how
295 environmental change across space affects biodiversity [62,63]. While labor intensive, our
296 approach created a foundational understanding of which species occur in the phorid fly
297 community, a presumably informative subset of the entire insect community. Baseline
298 knowledge of insect communities is a prerequisite for generating expected responses to
299 continued global change. These data are rare, but sampling programs like the one we describe
300 here could be replicated in other cities to build baselines that allow us to determine how biotic
301 change varies across background climates and habitat types. However, our robust sampling of
302 the L.A. Basin relied on collaboration between scientists and the public. Members of the
303 community hosted Malaise traps in their backyards, increasing the range of urban environments
304 available for sampling, and, importantly, reducing the resources and labor required for this
305 intensive sampling [64]. With continued public support, efforts such as ours could create long-
306 term data for describing species' long-term responses to urbanization and climate change
307 [65,66].

308

309 **Authors' Contributions**

310 The BioSCAN project was conceived and operated by BVB, and taxonomy and identification of
311 flies was conducted by BVB and EAH. Data curation and analyses were conducted by EKM and

CAB. Spatial data for analyses and maps were provided by EL. The manuscript was written by TPM, with contributions from EKM, BVB, BJA, EL, and CAB.

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496 Table 1. Full model evaluation of phorid fly biodiversity across 30 sites in urban Los Angeles.

| Response variable | Model parameter | Estimate | SEM | DF | T | p |
|---|---|---|---|---|---|---|
| Abundance | (Intercept) | 87.751 | 488.103 | 313 | 0.18 | 0.857 |
| | log(min RH^2) | 0.000 | 0.000 | 313 | -0.22 | 0.827 |
| | min RH | -0.009 | 0.017 | 313 | -0.49 | 0.622 |
| | log(min soil T^2) | 0.000 | 0.002 | 313 | -0.19 | 0.849 |
| | min soil T | 0.048 | 0.065 | 313 | 0.74 | 0.459 |
| | log(mean air T^2) | -0.019 | 0.003 | 313 | -5.79 | <0.0001 |
| | mean air T | 0.673 | 0.133 | 313 | 5.07 | <0.0001 |
| | Latitude | 1.805 | 2.857 | 25 | 0.63 | 0.533 |
| | Longitude | 1.293 | 3.728 | 25 | 0.35 | 0.732 |
| | distance to protected area | 0.000 | 0.001 | 25 | 0.21 | 0.839 |
| Richness | (Intercept) | 337.215 | 501.628 | 313 | 0.67 | 0.502 |
| | log(mean RH^2) | -0.001 | 0.000 | 313 | -3.27 | 0.001 |
| | mean RH | 0.109 | 0.034 | 313 | 3.25 | 0.001 |
| | log(min soil T^2) | -0.003 | 0.002 | 313 | -1.33 | 0.185 |
| | min soil T | 0.078 | 0.068 | 313 | 1.15 | 0.251 |
| | log(mean air T^2) | -0.017 | 0.003 | 313 | -4.88 | <0.0001 |
| | mean air T | 0.637 | 0.141 | 313 | 4.53 | <0.0001 |
| | Latitude | 2.883 | 2.936 | 25 | 0.98 | 0.336 |
| | Longitude | 3.745 | 3.831 | 25 | 0.98 | 0.338 |
| | distance to protected area | 0.000 | 0.001 | 25 | -0.08 | 0.935 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Evenness | (Intercept) | 107.709 | 58.598 | 222 | 1.84 | 0.067 |
| | I(temp_air_min^2) | 0.001 | 0.001 | 222 | 1.70 | 0.091 |
| | temp_air_min | -0.024 | 0.012 | 222 | -1.98 | 0.049 |
| | Latitude | -0.306 | 0.348 | 25 | -0.88 | 0.388 |
| | Longitude | 0.818 | 0.446 | 25 | 1.83 | 0.079 |
| | distance to protected area | -0.00014 | 0.00007 | 25 | -2.15 | 0.042 |
| | | | | | | |
| *M. agarici* abundance | (Intercept) | -72.628 | 390.116 | 313 | -0.19 | 0.852 |
| | log(min RH^2) | 0.000 | 0.000 | 313 | 0.71 | 0.476 |
| | min RH | -0.013 | 0.014 | 313 | -0.89 | 0.375 |
| | log(min soil T^2) | -0.002 | 0.002 | 313 | -1.05 | 0.296 |
| | min soil T | 0.025 | 0.053 | 313 | 0.47 | 0.640 |
| | log(mean air T^2) | -0.014 | 0.003 | 313 | -5.13 | <0.0001 |
| | mean air T | 0.532 | 0.109 | 313 | 4.90 | <0.0001 |
| | impervious surface | 0.885 | 0.721 | 24 | 1.23 | 0.232 |
| | Latitude | 2.631 | 2.351 | 24 | 1.12 | 0.274 |
| | Longitude | 0.178 | 3.070 | 24 | 0.06 | 0.954 |
| | distance to protected area | 0.000 | 0.000 | 24 | 0.66 | 0.513 |

**Figure 1. Map of BioSCAN sites where phorid flies and climatic variables were sampled.** Dot size represents mean daily phorid fly species caught in traps, and color represents mean annual air temperatures.

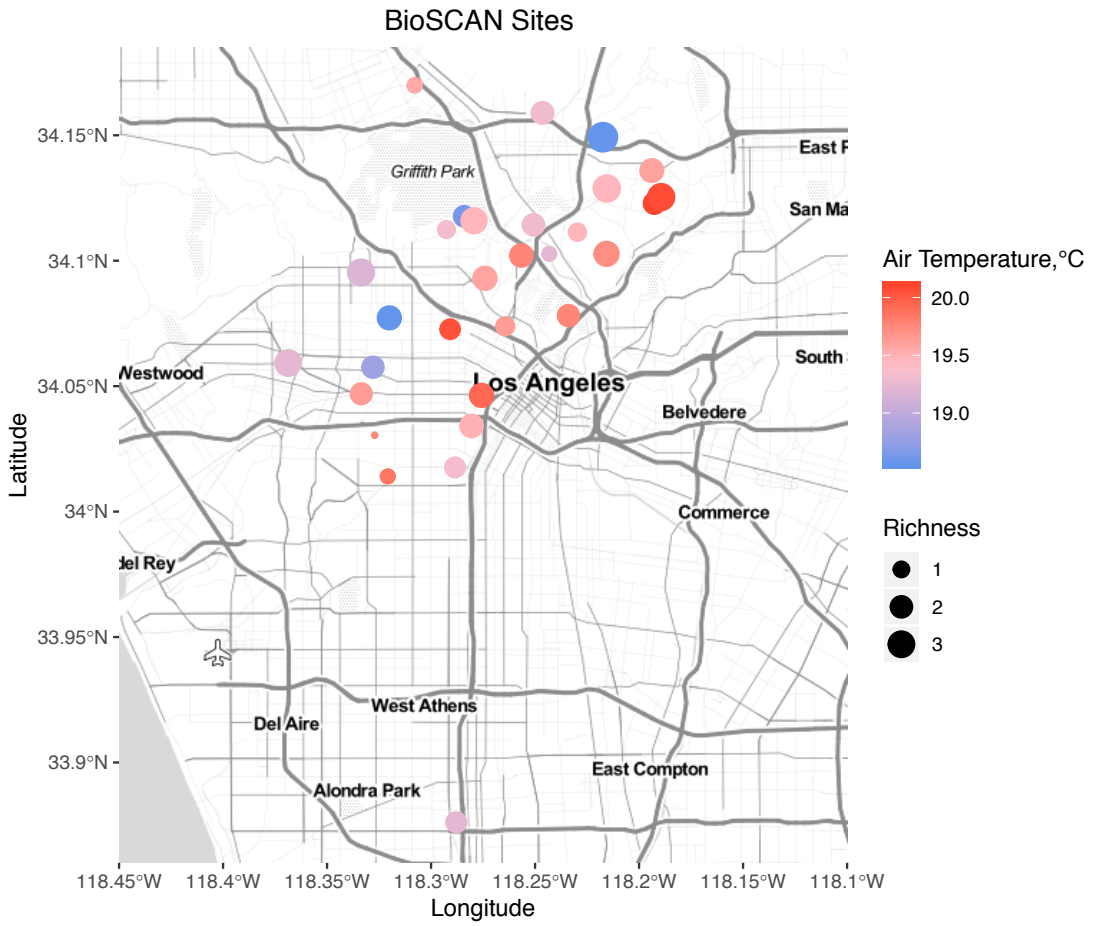
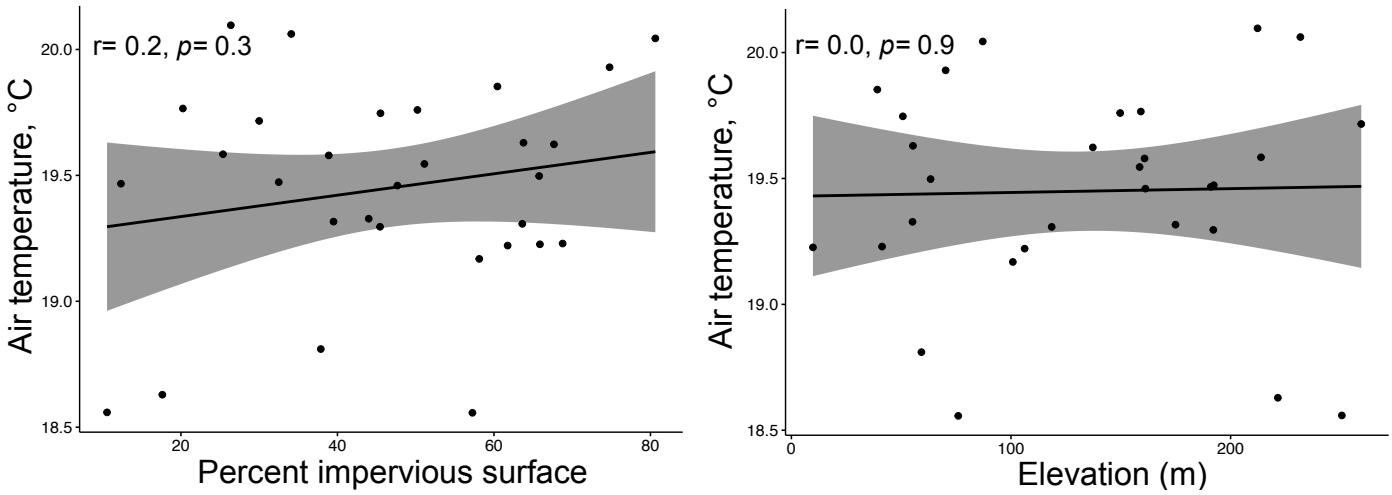


**Figure 2. Thermal responses to landscape characteristics.** Mean annual air temperature is not associated with a) impervious surface, nor with b) elevation.



508 **Figure 3. Scatterplot matrix showing correlations between environmental and**

509 **microclimatic predictors:** Mean weekly air temperature, average normalized difference

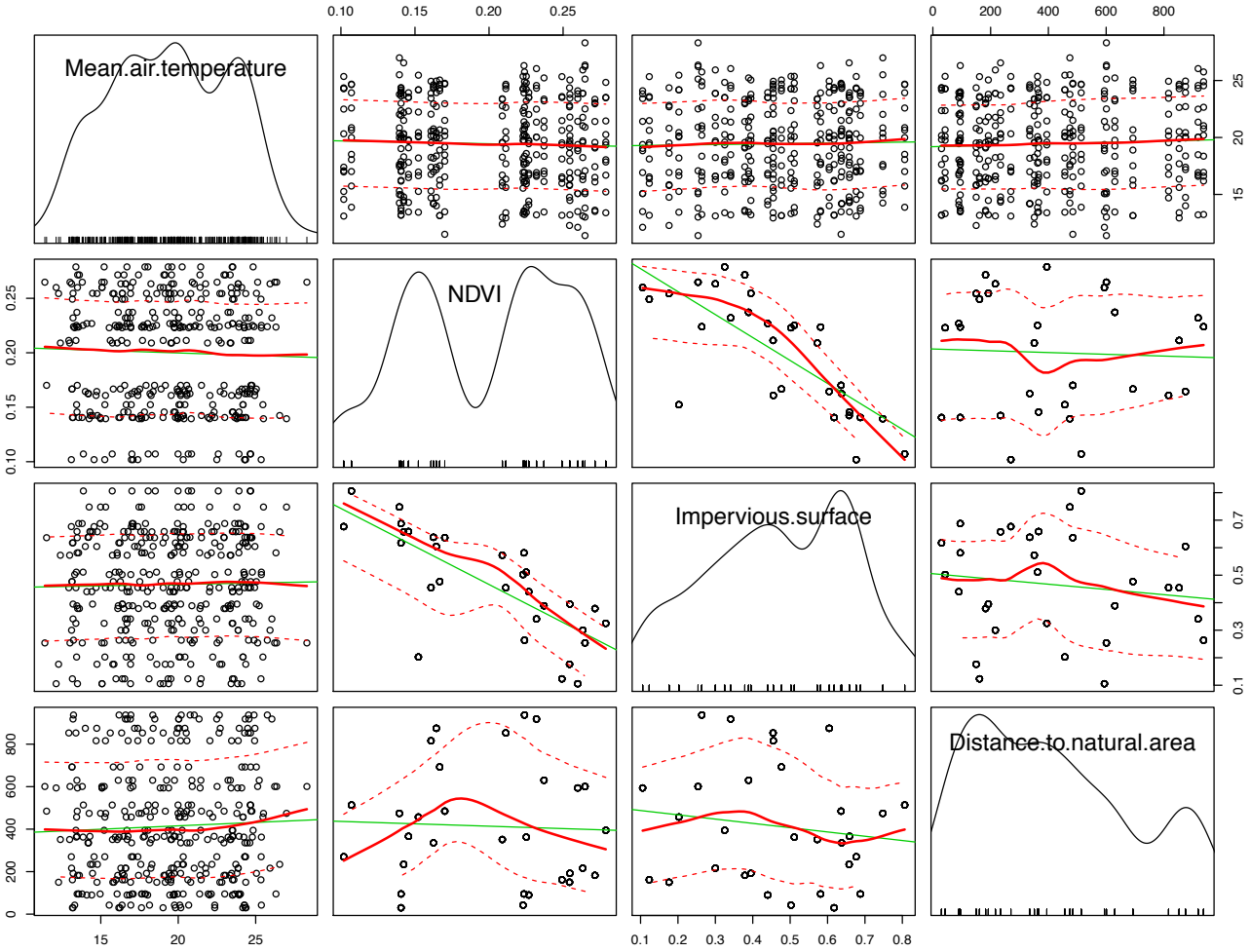
510 vegetation index for a circle with radius of 50 meters surrounding each site (NDVI), percent

511 impervious groundcover in that same area and distance to nearest natural area, in meters. Straight

512 pale green lines represent the robust-regression line between the variable pairs, and the curved

513 red lines represent a GAM (generalized additive model) smoother and their respective

514 confidence intervals.



515 **Figure 4. Phorid fly abundance and richness responses to temperature**. a) Total abundance

516 of phorid flies caught in each trap per sampling period, b) abundance of the most prevalent

517 species, *M. agaraci*, and c) total species richness per sampling period. The x-axis represents

518 mean air temperature the week prior to sampling, and regression lines represent best fits.

519

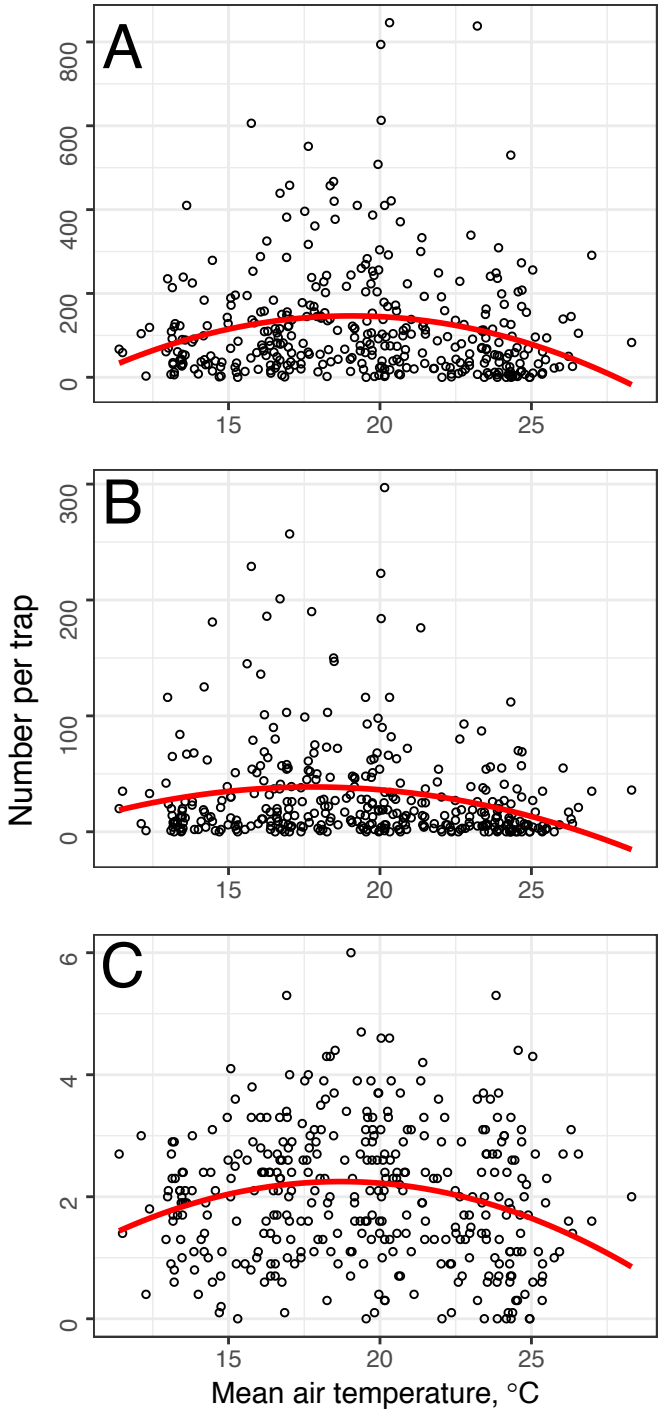


**Figure 5. Non-metric multidimensional scaling of phorid fly communities from urban Los Angeles backyard sampling stations**. The species are superimposed with environmental fit vectors for minimum air temperature ($r^2$= 0.26, *p*= 0.02), normalized difference vegetation index within a 50-meter radius of the site (NDVI; $r^2$= 0.03, *p*= 0.65), distance to the nearest natural area ($r^2$= 0.01, *p*= 0.92), relative humidity ($r^2$= 0.04, *p*= 0.63), latitude ($r^2$=0.04, p=0.61) and longitude ($r^2$= 0.04, *p*= 0.56). Most common species names are plotted (with captures >500 individuals). NMDS 2D stress= 0.13.

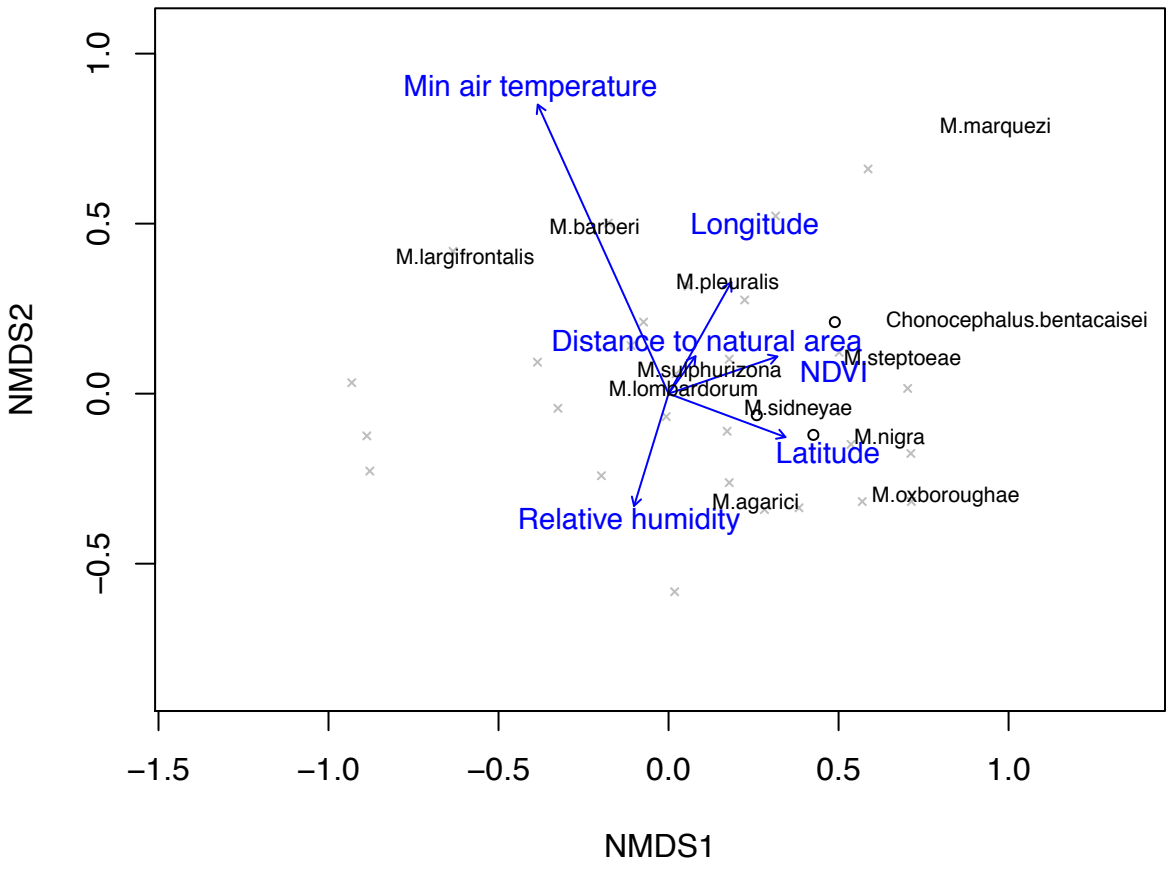


Figure S1. Scatterplot matrix of relative humidity, minimum soil temperature at 1-cm depth, mean weekly air temperature, and distance to nearest natural, protected area, in meters. Straight pale green lines represent the robust-regression line between the variable pairs, and the curved red lines represent a GAM smoother and their respective confidence intervals.

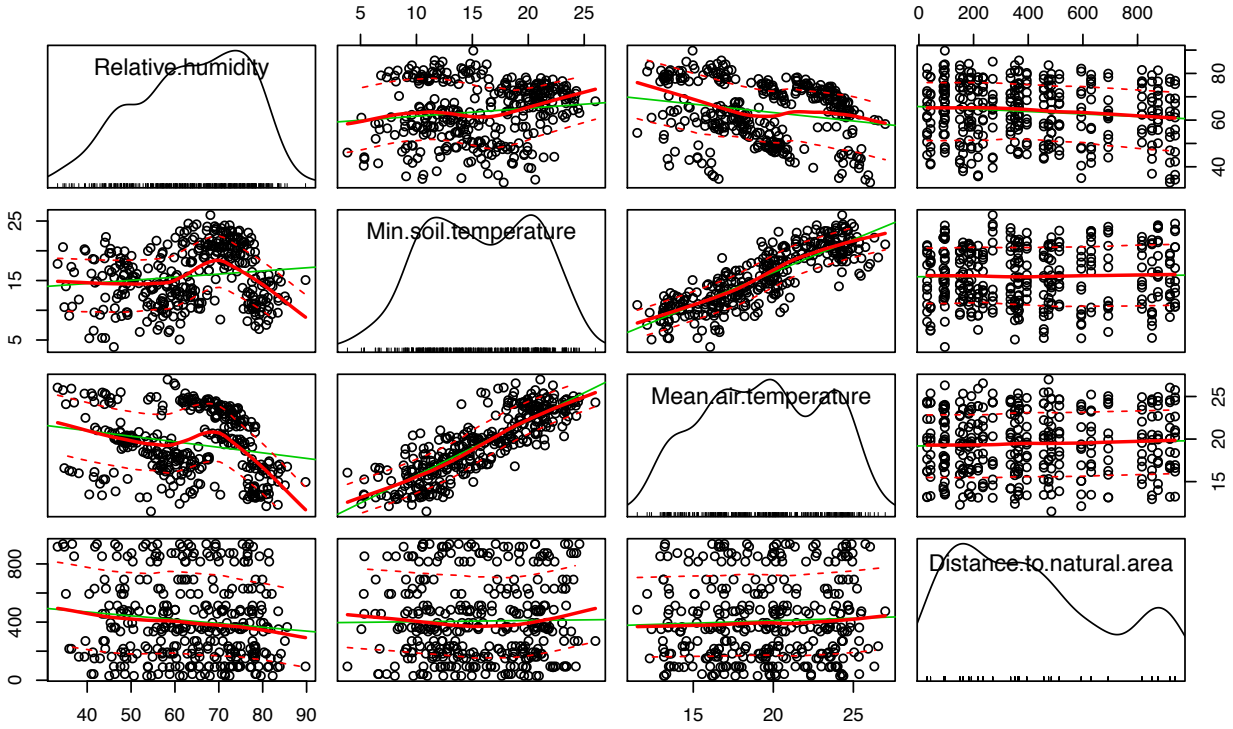


Figure S2. Scatterplot matrix of latitude, longitude, relative humidity, minimum soil temperature at 1-cm depth, and mean air temperature. Straight pale green lines represent the robust-regression line between the variable pairs, and the curved red lines represent a GAM smoother and their respective confidence intervals.

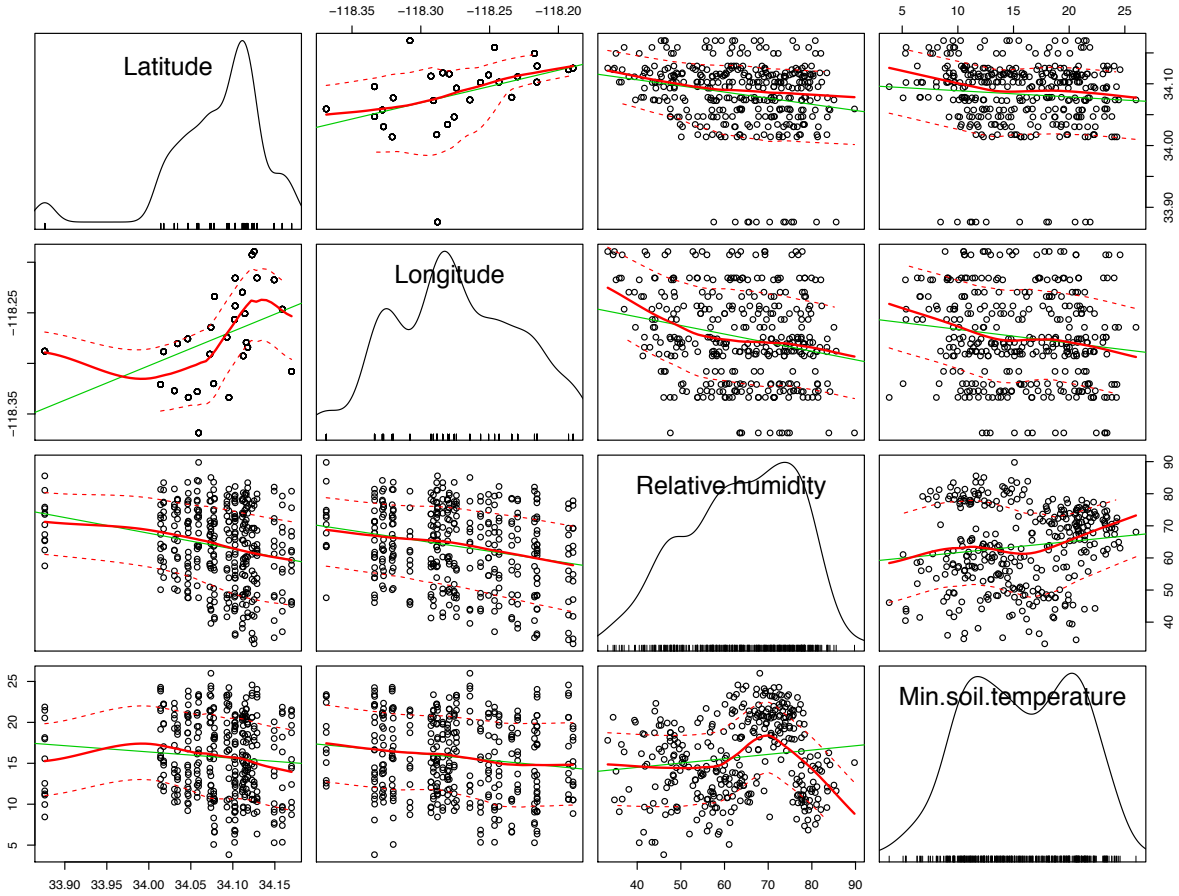
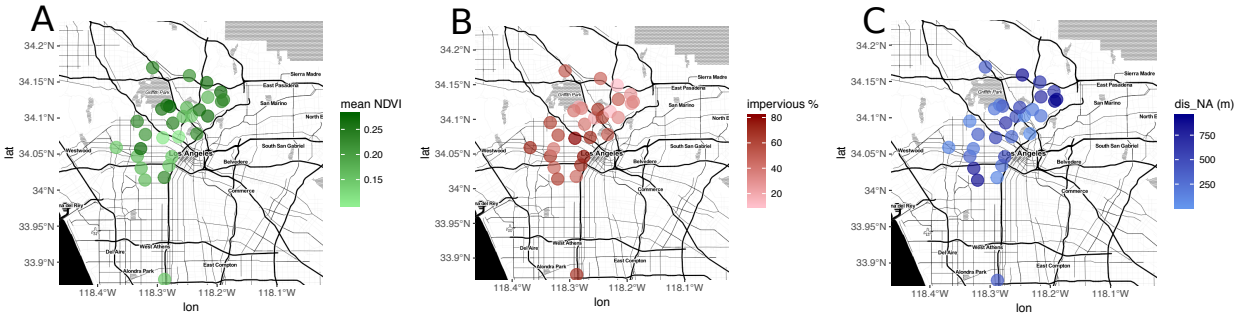


Figure S3.

Site maps of abiotic variables analyzed, including a) NDVI (50-meter buffer), b) impervious surface (50-m buffer), and c) distance to closest natural, protected area.