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 within 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 inside urban Los Angeles 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 were more even at urban sites with lower minimum temperatures and sites located further away from natural areas, suggesting that communities separated 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 within cities, 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 [1,2]. Thus, determining conditions within cities that affect species persistence is increasingly a focus of ecological research from fundamental and conservation perspectives [3–5]. 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 [6–8]. 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 [9–15]. Urbanization causes cities to be as much as 12˚C hotter than adjacent areas [16], which is on par or above warming anticipated by the Intergovernmental Panel on Climate Change over the next several decades [17]. In certain cities, urban warming can also operate at local scales, creating thermal mosaics within the urban matrix (e.g., [18–21]). Despite the short history of research on the biotic effects of urban heat, researchers have found important patterns across diverse taxa [7,10–13,22–24]. For example, remnant native plant communities in urban environments may be altered under warming conditions, favoring more xerophilic species [25,26].

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 [27,28]. 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 [29,30]).

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 [31–33]. While researchers have used various useful approaches to determine effects of urban warming alone – e.g., laboratory chamber experiments [11,18] – 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. In coastal cities, urban temperatures are often decoupled from landcover, such that sites that are highly urbanized are not necessarily hotter than surrounding sites that are less urbanized because of winds entering from the coast [40]. This offers an experimental opportunity to separate the ecological effects of urbanization and temperature.

Insects are highly responsive to temperature, are a foundational component of terrestrial biodiversity, and provide a range of services and disservices within cities [34,35]. As insects are ectotherms, they have elevated metabolic and reproductive rates in response to warming until their thermal maxima are reached [14]. One of the most abundant animals in terrestrial environments are phorid flies [36,37], which are responsive to thermal conditions, but also feed on a wide range of resources and develop and occupy a tremendous variety of microhabitats [38]. Cities can support hyperdiverse communities of phorid flies, with dozens of species recently described from central Los Angeles [39,40]. 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.

86 Here we evaluate the spatial and temporal predictors of phorid fly biodiversity within
87 urban Los Angeles, CA, USA, hereafter we refer to as L.A. In L.A., urban temperatures are
88 decoupled from land cover, allowing us to investigate the effects of impervious
89 surface,vegetation cover, and temperature,in a system where these aspects of the urban
90 environment are not highly correlated [41]. In this project, species were sampled exhaustively
91 [42], and 30 new species of flies were described from L.A. from this dataset in 2015 [39]. We
92 leverage the complete documentation of this diverse group to determine effects of urban land
93 development and climate in a city where we found these variables are uniquely decoupled. We
94 sampled phorid flies and site environmental conditions in 30 locations throughout a calendar
95 year to evaluate biodiversity responses to thermal and urbanization gradients within the L.A.
96 metropolitan area. By measuring temperature and moisture variables at a very fine scale to match
97 the habitat occupied by the organisms [43], we achieve a biologically relevant understanding of
98 how local climatic factors vary across an iconic urban habitat.
99
100 **Methods**
101 *Study area*
102 The Los Angeles metropolitan area is a highly urbanized region located at 34ºN along the west
103 coast of North America, which has experienced rapid population growth and associated land
104 development over the past 100 years. The climate and flora are characteristically
105 "Mediterranean," and biomes that have given way to development include coastal sage scrub,
106 chaparral, and oak woodlands. Some habitats have only small fragments remaining, including
107 coastal dunes and wetlands [44]. The climate of locations within the city can vary substantially
108 from one another, because of differences in distance from the ocean, elevation, intensity of

urbanization, and vegetation [41]. The heterogeneity of the landscape makes predicting climatic differences among sites in Los Angeles particularly difficult [45,46], which reinforces the need for site-specific weather records to reliably compare sites.

Study design and insect sampling procedures

We placed a series of Malaise traps [47] (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 [42], who provide a detailed description of each site featured in the study. In a survey, participants whose homes were included in the study were asked if they used pesticides in their yards in areas close to where the traps were located. The survey revealed that none of the sites were treated with pesticides regularly, and only a few hosts used small quantities of pesticides for local control on rare occasions, such as neem oil on a few plants. We decided this incidental treatment would not appreciably affect biodiversity within the yards included in this study.

For each of twelve sampling periods (approximately the first week of each month in 2014), 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 of 99 species was essentially sampled to completion, as richness estimators predicted that additional sampling would be expected to yield perhaps one additional new species [42]. We are confident that this sampling regime represents nearly all the species in this lineage and locality 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). Additional details about abiotic data are in the electronic supplementary material.

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 average annual air temperature at our sampling sites. In each model, mean average annual temperature was the response variable, and impervious surface or elevation was the sole predictor. We also evaluated whether differences in temperatures across sites were associated with a coastal effect from the Pacific Ocean. Our hypothesis was that urban sites further away from the coast would have warmer mean temperatures [50]. To test this, we also used a simple linear model, with distances from our sites to the Pacific shoreline as the predictor and mean average annual air temperature as the response variable.

Phorid fly abundance, richness, and evenness: We first calculated four response variables that were each used as the responses in the modeling framework described below. First, 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

155 was left out, i.e., the total amount of time flies had access to a trap. One species, *M. agarici*,
156 constituted a substantial number of specimens in samples at many sites (and about one-quarter of
157 all individuals collected). Therefore, we included total individuals of this species captured per
158 trap per day as an additional response variable. (Many of the species in this study were only
159 recently described and their biology remains poorly known, and the current state of knowledge
160 [51] prevents us from using taxon-specific data, such as phylogeny, diet, as factors in the models
161 described below.)

162 As a preliminary step, we used model selection to minimize overfitting in the final
163 models. Specifically, we used model selection to identify the most parsimonious independent
164 variables describing effects of temperature, humidity, and urbanization on each response
165 variable. For each response, we built a series of linear mixed effects models in the *nlme* package
166 in R [52]. In each case below, we compared models with tightly correlated predictors describing
167 similar aspects of the urban environment and selected the parameter in the model with the lowest
168 AICc score to include in full models used for inference, i.e., to choose the response variable most
169 closely associated with the response. For each response variable, we compared three sets of
170 models. One set included mean RH (relative humidity), maximum RH, minimum RH, and no
171 humidity predictor. The second set of models selected from included mean temperature,
172 maximum temperature, minimum temperature, and no temperature predictor, and the final set
173 compared mean soil temperature, mean maximum soil temperature, mean minimum soil
174 temperature, and no temperature predictor. All climatic predictors represented average conditions
175 one week before sampling to represent the conditions most likely to affect phenology [53]. We
176 decided, depending on the shape of the response, whether to include a squared term to account
177 for non-linear responses of phorid flies to environmental variables. In all models built for final

178 model selection, we included latitude, longitude, and distance to the nearest natural, protected
179 area were included as fixed effects, and site was included as a random effect to account for
180 repeated sampling of flies at each site. To account for the composition of the matrix surrounding
181 each study site and to describe urbanization, we compared models that included impervious
182 surface cover, NDVI – each measured at a 50-m buffer as described above – and neither of these
183 (null model).

184 After selecting parameters for each response variable (species richness, *M. agarici*
185 abundance, total abundance, and evenness), we built one full model for each, for a total of four
186 models. In these models, we included each parameter chosen to represent urbanization,
187 temperature, and humidity, along with latitude, longitude, and distance to the nearest natural area
188 as fixed effects. Site was included as a random effect in all models. To determine if the effects of
189 temperature depended on water availability, and vice versa, we included an interaction between
190 the best temperature predictor and the best relative humidity predictor; these were subsequently
191 removed from all models because they were not significant. We did not include any interaction
192 effects that were not associated with explicit *a priori* hypotheses, because these interaction
193 effects often can be explained more directly by main effects of environmental variables, and
194 including these variables would be redundant and reduce the power of analyses of our main
195 effects. To determine if site proximity rather than environmental conditions may account for
196 responses we observed, we performed an analysis to test if spatial autocorrelation was observed
197 among sample sites. We examined abundance of phorid flies by date, for every date where >5
198 sites reported data, using Moran's I, applied to an inverse distance matrix of site co-ordinates as
199 the weighting factor [54].
200

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 [55]. 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 [56]. 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; impervious surface: y= -129+9x, $F_{1,28}$=1.12, p= 0.30; elevation: y= -45+4.5x, $F_{1,28}$= 0.02, p= 0.90), suggesting that neither urban land cover nor elevation drove urban temperatures. Therefore, we conclude that, while L.A. may have a largescale urban heat island effect, other unknown factors drive temperatures at the local scale. As expected, NDVI tracked impervious surface, though these values were not closely related to the distance to natural areas (Fig. S1). Contrary to expectations, temperatures measured at weather stations in urban backyards were not significantly associated with their distances from the coast (y= 1.90+1.83e^{-5}, $F_{1,28}$= 0.48, p= 0.49).

Mean and peak biotic responses: Abundance and richness of phorid fly communities throughout the city were best explained by air temperature (Table 1; Fig. 3). No other climatic parameters had significant predictive value, aside for a lesser effect of relative humidity on species richness (Table 1), and humidity slightly tracked temperature (Fig. S3). Phorid fly abundance and richness responses to environmental conditions were nonlinear, with peaks at intermediate mean weekly temperatures (Fig. S1). The factors affecting the abundance of the most common species, *M. agarici*, were the same factors affecting total abundance (Table 1). Evenness of phorid fly communities was weakly explained by mean minimum weekly temperature and distance to natural areas, such that phorid fly communities in areas with lower minimum temperatures and those that were further away from natural were more even (Table 1).

Latitude and longitude were associated with abiotic conditions (Figs. S4, S5), but spatial autocorrelation was limited. Among all dates where sufficient data existed for autocorrelation analysis (10 dates), one date (Week 6 of 2014) had significant spatial autocorrelation (p= 0.037), suggesting that autocorrelation is rare in this system and may have been observed by chance. Thus, after we accounted for spatial similarity of sites using latitude and longitude as described above, no additional correction for spatial autocorrelation was needed.

Community composition: The effects of NDVI and mean minimum weekly temperature on species composition were orthogonal, with a much greater effect of temperature (Fig. 4). Mean minimum weekly temperature had the only significant vector, which also had the greatest magnitude (r^2= 0.26, p= 0.02)

247 **Discussion**

248 We found that urbanization and climate are uniquely decoupled across the L.A. Basin.
249 Consistent with an earlier study [41], urban land cover does not influence local temperatures at
250 the fine scale of our sampling Because of this decoupling, we were able to independently assess
251 effects of local climate and urban land cover on phorid fly communities. We found that air
252 temperature had the most robust influence on the assembly of the phorid fly community, but that
253 different aspects of temperature were most closely associated with species abundance, richness,
254 and evenness. Local impervious surface and vegetation cover (NDVI), which represent
255 urbanization, did not outperform null models. We conclude that local climate, not urban land
256 cover, is the strongest driver of phorid fly community assembly across Los Angeles.

257 Higher mean temperatures were associated with increased phorid fly richness, until
258 around 20°C, where richness declined. We predicted that cooler sites would harbor more species
259 because warmer areas would be associated with reduced persistence of heat-intolerant species.
260 However, we find evidence that intermediate temperatures may support both heat-tolerant and -
261 intolerant species, and thus most phorid species in L.A. Many of the species in our study (e.g.,
262 *M. halterata*, *M. nigra*, and *M. pleuralis*) are probably introduced from areas of northern Europe
263 with cooler thermal conditions than L.A., which could also account in part for the loss of
264 abundance at higher mean temperatures. However, in general, the relative contributions of non-
265 native and native species to the patterns we observed are unclear. While we know that many
266 species of phorids in L.A. are native based on their species interactions and/or distributions (i.e.,
267 found only in certain parts of North America in well-studied groups), knowledge about phorid
268 fly distributions is inadequate to inform us to what extent non-native species contribute to the
269 patterns we observe.

270 While species richness was tied to mean temperature, evenness was weakly explained by
271 minimum temperature and distance to natural areas. The latter was included in the analysis
272 because it is well established that some species have habitat requirements involving larger
273 patches of land that are less urbanized. For example, the ant-decapitating guild of phorid flies are
274 only found within and adjacent to natural areas because these are locations in L.A. where their
275 hosts (species of *Camponotus*, *Crematogaster*, *Liometopum*, *Neivamyrmex*, *Pheidole,* and
276 *Solenopsis*) are found. Elsewhere, the host ants are typically displaced by invasive Argentine
277 ants [42,57]. We expected that species richness would drop with distance from natural areas, as
278 certain native species would be removed from the species pool. Instead, we found that species
279 evenness might be the result of a more complex process, in which communities become less even
280 further from natural areas, but not because of the loss of species from communities – distance
281 from natural areas did not predict richness – but rather because relative abundances may shift.
282 Our results suggest that a subset of species may benefit from living further from natural areas,
283 where perhaps there is less competition from species that may locally disperse into more
284 urbanized environments from source populations in more natural areas. While we predict this
285 may be the cause of less even communities further from natural, protected areas, further studies
286 on population genomics and niche overlap of phorid flies are needed to determine mechanisms
287 driving this pattern. In addition, sites with lower minimum temperatures support compositionally
288 different and more even communities than areas with higher minimum temperatures. We may
289 observe this pattern because a few species in the region have disproportionate fitness benefits
290 from warmer minima.
291 Species richness was also higher at intermediate relative humidities, and we suspect this
292 results from the benefits and drawbacks of wet climates for insects. Throughout the year, many

species showed large spikes in abundance. Among those with known life histories (as listed in Fig. 4: *Chonocephalus bentacaisei*, *M. agarici*, *M. halterata*, *M. marquezi*, *M. nigra*, and *M. pleuralis*) fungus-feeding larvae are overwhelmingly common. Sporophore eruptions can produce hundreds of flies relatively quickly, as Brown & Hartop [58,59] estimated a single mushroom cap contained 500 larvae of *M. marquezi.* We suspect abundance peaks for these species are associated with the mass production of fungal sporophores in close proximity to our sampling area, which are common after rain. However, we also suspect that very wet climates may increase fungal disease incidence [60,61], such that highest phorid fly richness occurs at intermediate relative humidity.

Urban landscapes are rarely designed to sustain biodiversity, though this is often an idealized goal informed by research [62]. At very high levels of heat, abundance and diversity declines, which is consistent with other studies suggesting that the urban heat island effect has negative effects on many species [14,63,64]. As the global temperature increases, many of the sites we sampled may also warm and therefore no longer support diverse phorid fly communities, though this will depend on how quickly phorid flies can adapt to changing thermal conditions. Even on short timescales, it is possible that the thermal limits of species have evolved, so that animals in the warmer parts of the city are capable of tolerating warmer conditions independent of ecotypic acclimation [65]. Given the rapid evolution of thermal tolerance in other arthropods [65–67], and the short generation times of phorid flies, rapid adaptation to climate change might be possible.

Our work was designed to test how the urban matrix surrounding sites in urban Los Angeles affects insect biodiversity. Our analyses suggest that temperature is a more important variable than surrounding urban land cover (impervious surface and NDVI densities) for

316 determining fly abundance and richness. However, a more detailed analysis of the specific
317 habitat types between potential source communities in protected, more natural sites and urban
318 sites might reveal patterns we have not tested for. Specifically, we predict that if protected areas
319 are source populations for urban fly biodiversity, protected areas and urban sites with more
320 hospitable habitat between (more NDVI, for example), may have higher fly diversity. Assessing
321 the specific land cover types between protected areas and urban sites is an important area for
322 future studies. We also note that our study did not take into account plant species composition,
323 including the amount of native vs. non-native plant cover. Prior work has shown that the amount
324 of native vegetation [68], vegetation complexity [69,70], and plant diversity [71] can drive urban
325 insect diversity. Investigating plant species composition of the matrix around sites and intra-
326 urban corridors among sites may help explain patterns in diversity that are not accounted for in
327 our analyses.Exhaustive biodiversity sampling has reaped substantial rewards in understanding
328 how environmental change across space affects biodiversity [72,73]. While labor intensive, our
329 approach created a foundational understanding of which species occur in the phorid fly
330 community, a presumably informative subset of the entire insect community. Baseline
331 knowledge of insect communities is a prerequisite for generating expected responses to
332 continued global change. These data are rare, but sampling programs like the one we describe
333 here could be replicated in other cities to build baselines that allow us to determine how biotic
334 change varies across background climates and habitat types. However, our robust sampling of
335 the L.A. Basin relied on collaboration between scientists and the public. Members of the
336 community hosted Malaise traps in their backyards, increasing the range of urban environments
337 available for sampling, and, importantly, reducing the resources and labor required for this
338 intensive sampling [74]. With continued public support, efforts such as ours could create long-

term data for describing species' long-term responses to urbanization and climate change [75,76].

Authors' Contributions

The BioSCAN project was conceived and operated by BVB, and taxonomy and identification of 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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555
556 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

557

558 **Figure 1. Map of BioSCAN sites where phorid flies and climatic variables were sampled.**

559 Dot size represents mean daily phorid fly species caught in traps, and color represents mean

560 annual air temperatures.

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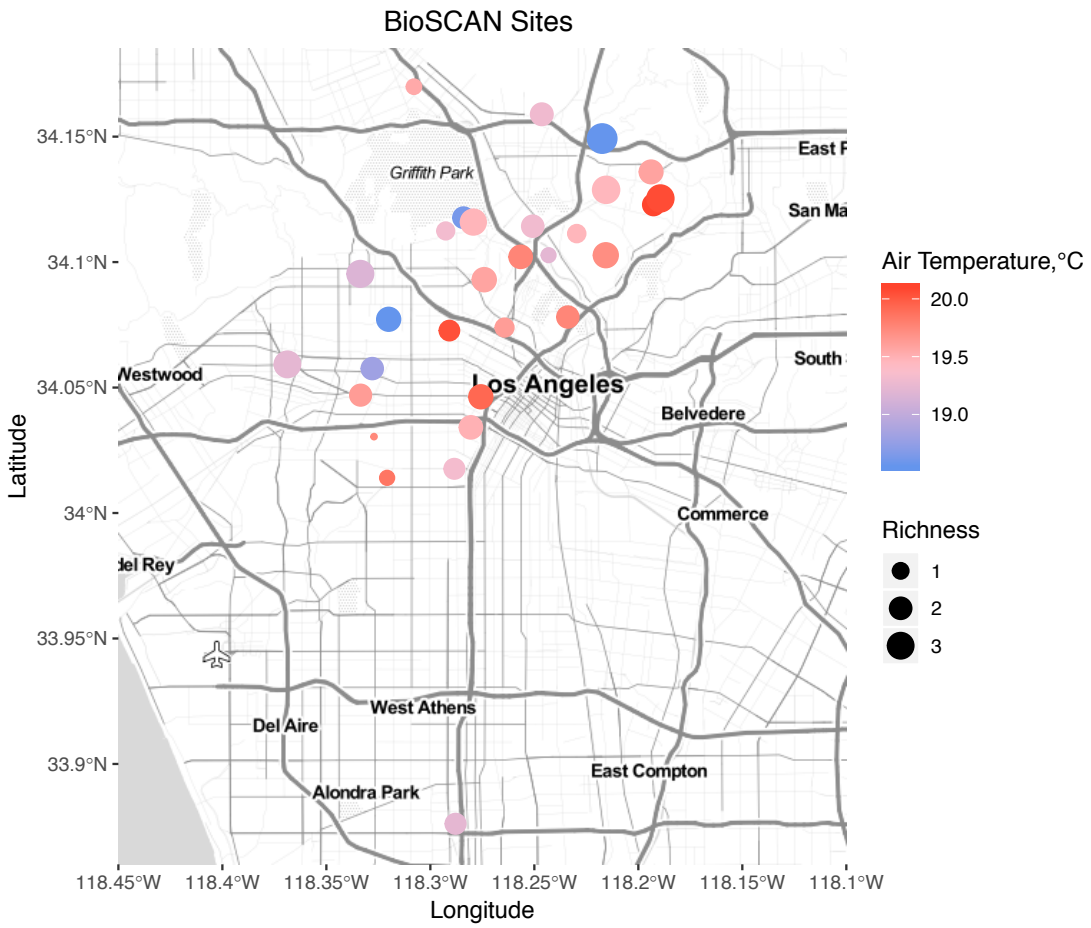

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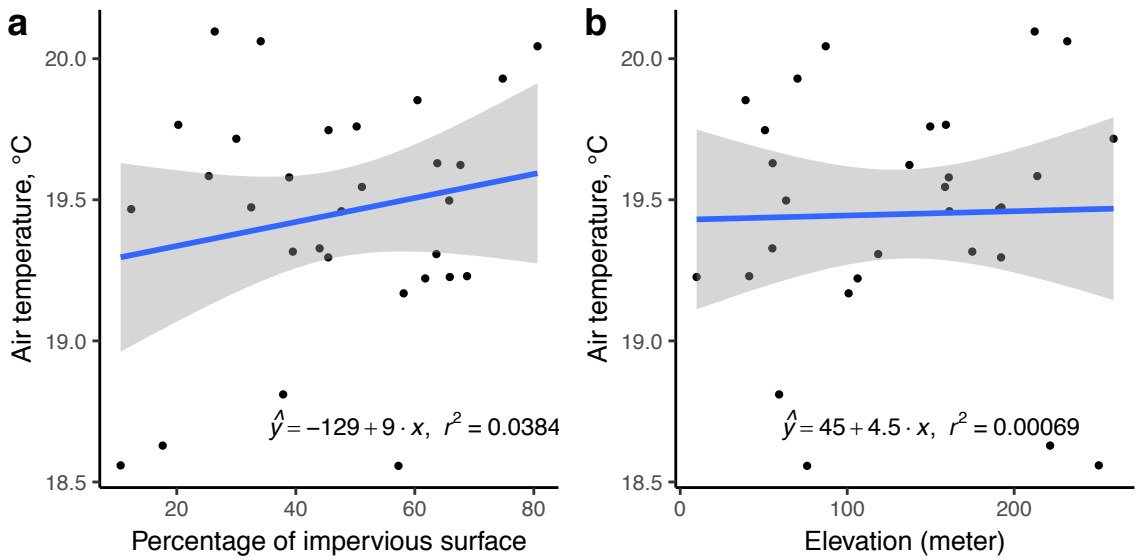
Figure 2. Thermal responses to landscape characteristics. Mean annual air temperature is not associated with a) impervious surface, nor with b) elevation.



569 **Figure 3. Phorid fly abundance and richness responses to temperature**. a) Total abundance

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

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

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

573

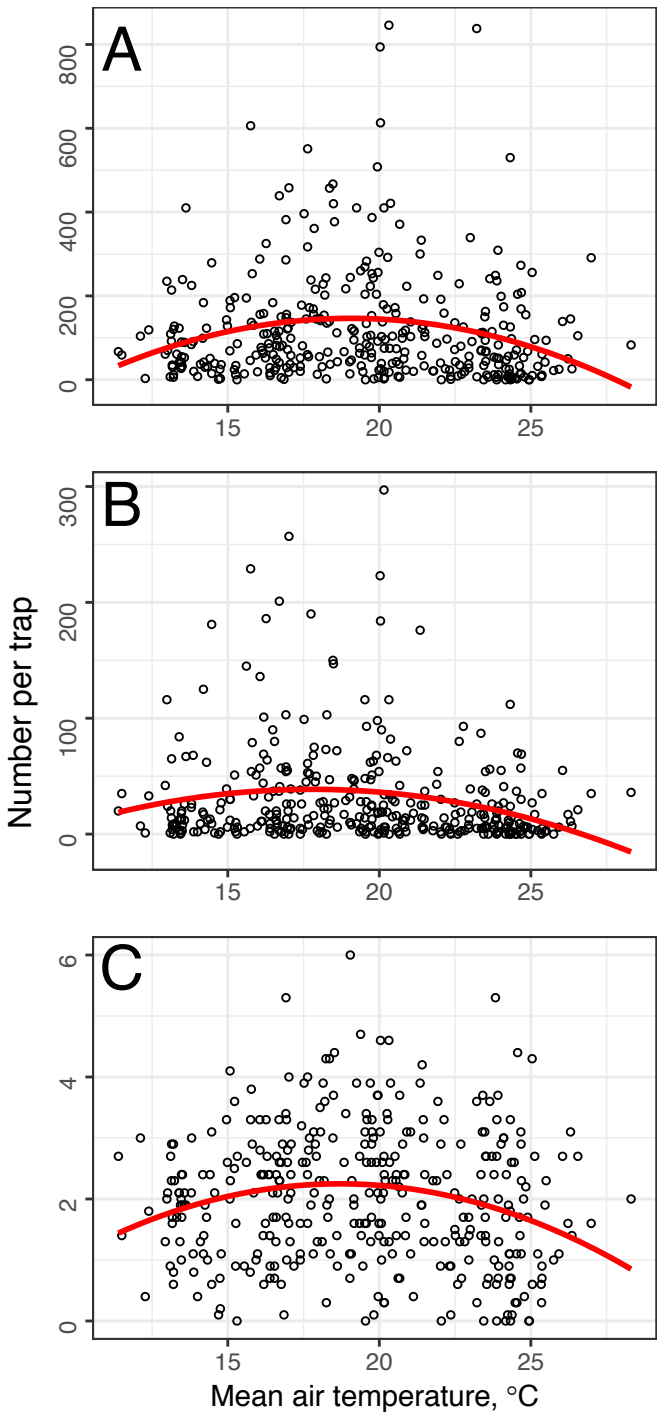
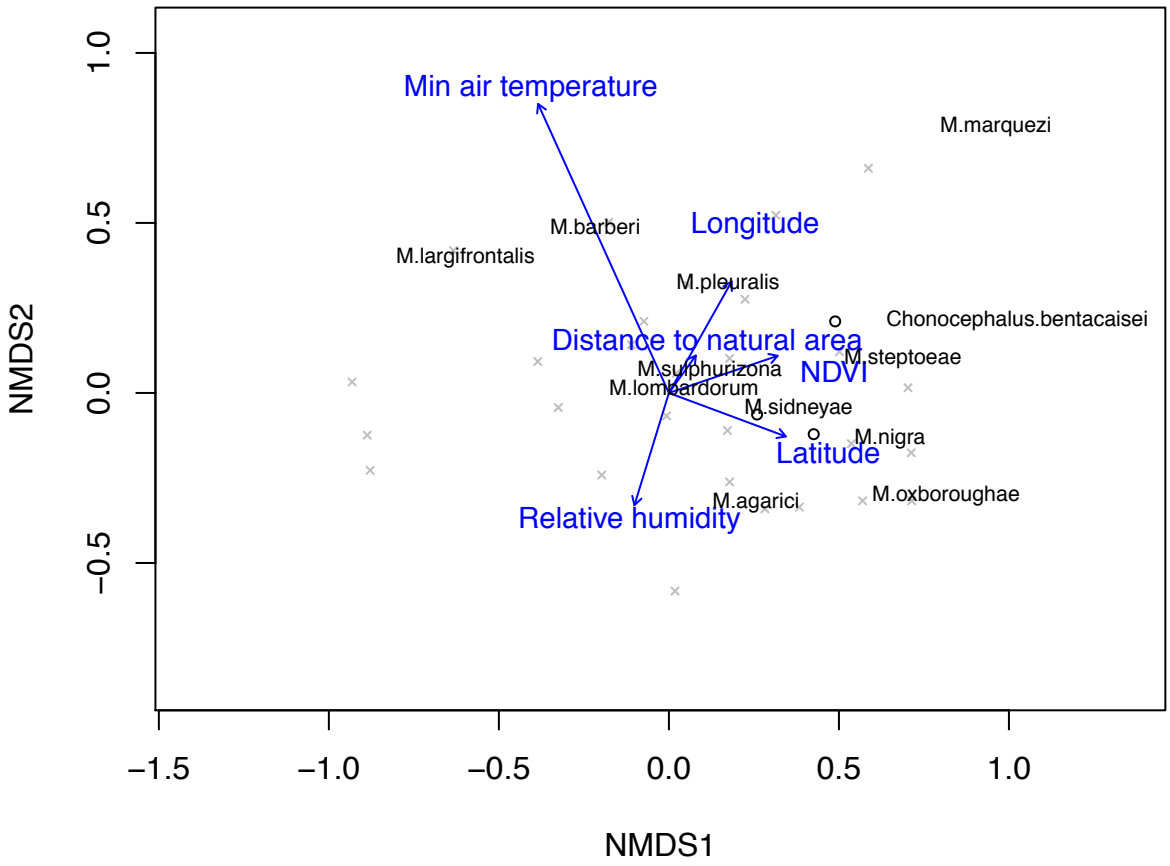



Figure 4. Non-metric multidimensional scaling of phorid fly communities from urban Los Angeles backyard sampling stations. The species are superimposed with environmental fit vectors for minimum air temperature (r^2= 0.26, *p*= 0.02), normalized difference vegetation index within a 50-meter radius of 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.