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

2   Angeles

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19   **Abstract**

20   The urban heat island effect is a worldwide phenomenon that has been linked to species'

21   distributions and abundances in cities. However, effects of urban heat on biotic communities are

22   nearly impossible to disentangle from effects of land cover in most cases because hotter urban

23   sites also have less vegetation and more impervious surfaces than cooler sites within cities. We

24   sampled phorid flies, one of the largest, most biologically diverse families of true flies (Insecta:

25   Diptera: Phoridae), at 30 sites distributed within the central Los Angeles Basin, where we found

26   that temperature and the density of urban land cover are decoupled. Abundance, richness, and

27   community composition of phorids inside urban Los Angeles were most parsimoniously

28   accounted for by mean air temperature in the week preceding sampling. Sites with intermediate

29   mean temperatures had more phorid fly individuals and higher richness. Communities were more

30   even at urban sites with lower minimum temperatures and sites located further away from natural

31   areas, suggesting that communities separated from natural source populations may be more

32   homogenized. Species composition was best explained by minimum temperature. Inasmuch as

33   warmer areas within cities can predict future effects of climate change, phorid fly communities

34   are likely to shift non-linearly under future climates in more natural areas. Exhaustive surveys of

35   biotic communities within cities, such as the one we describe here, can provide baselines for

36   determining the effects of urban and global climate warming as they intensify.

37

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

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Introduction

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41   Urban development is accelerating with uncertain effects on biodiversity. While many

42 species do not persist in urban areas, cities can support a surprising range of native and even

43 threatened taxa [1,2]. Thus, determining conditions within cities that affect species persistence is

44 increasingly a focus of ecological research from fundamental and conservation perspectives [3–

45 5]. However, isolating specific drivers of biodiversity in cities has proven difficult because

46 organisms in cities experience a range of novel conditions that may alter their abundances and

47 distributions [6–8]. Therefore, for most animal taxa, specific mechanisms driving community

48 assembly in cities remain unknown.

49   The urban heat island effect is a prevalent phenomenon in cities, and growing evidence

50 shows that urban heat can alter species richness, abundance, and community composition [9–15].

51 Urbanization causes cities to be as much as 12˚C hotter than adjacent areas [16], which is on par

52 or above warming anticipated by the Intergovernmental Panel on Climate Change over the next

53 several decades [17]. In certain cities, urban warming can also operate at local scales, creating

54 thermal mosaics within the urban matrix (e.g., [18–21]). Despite the short history of research on

55 the biotic effects of urban heat, researchers have found important patterns across diverse taxa

56 [7,10–13,22–24]. For example, remnant native plant communities in urban environments may be

57 altered under warming conditions, favoring more xerophilic species [25,26].

58   Because temperatures in cities match or exceed those expected under future climate

59 change, researchers have suggested that thermal gradients within cities might allow us to predict

60 biotic responses to the future climate warming [27,28]. Cities might be useful proxies for climate

61 warming because urban heat has been in place for decades to centuries, and large scale,

62 controlled warming experiments in more natural areas are often impractical (but see [29,30]).

63   However, urban heat might not be an appropriate proxy for broader climate warming because

64   other aspects of urbanization might also have strong effects on species. Perhaps most

65   importantly, land cover (impervious surfaces, vegetation) and urban heat tend to covary, making

66   it impossible to separate their effects on biological processes. Hot urban environments often have

67   more impervious surface, less vegetation cover, and lower vegetation complexity [31–33]. While

68   researchers have used various useful approaches to determine effects of urban warming alone –

69   e.g., laboratory chamber experiments [11,18] – actually separating effects of land cover and

70   temperature in the city could provide insight into whether biotic responses are more attributable

71   to temperature or other aspects of urbanization. In coastal cities, urban temperatures are often

72   decoupled from landcover, such that sites that are highly urbanized are not necessarily hotter

73   than surrounding sites that are less urbanized because of winds entering from the coast [40]. This

74   offers an experimental opportunity to separate the ecological effects of urbanization and

75   temperature.

76   Insects are highly responsive to temperature, are a foundational component of terrestrial

77   biodiversity, and provide a range of services and disservices within cities [34,35]. As insects are

78   ectotherms, they have elevated metabolic and reproductive rates in response to warming until

79   their thermal maxima are reached [14]. One of the most abundant animals in terrestrial

80   environments are phorid flies [36,37], which are responsive to thermal conditions, but also feed

81   on a wide range of resources and develop and occupy a tremendous variety of microhabitats [38].

82   Cities can support hyperdiverse communities of phorid flies, with dozens of species recently

83   described from central Los Angeles [39,40]. With a small body size (0.4-6 mm) and presumably

84   short dispersal distances, we would expect phorid fly biodiversity to finely track microclimatic

85   conditions in the urban environment, relative to less ephemeral or larger-sized organisms.

4

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

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109   urbanization, and vegetation [41]. The heterogeneity of the landscape makes predicting climatic

110   differences among sites in Los Angeles particularly difficult [45,46], which reinforces the need

111   for site-specific weather records to reliably compare sites.

112

113   *Study design and insect sampling procedures*

114   We placed a series of Malaise traps [47] (Townes lightweight model Sante Traps,

115   Lexington, KY) in 30 sites throughout central L.A. (Fig. 1). The distribution of the sites was

116   designed to capture a range of biotic and abiotic gradients in the urban environment as part of the

117   BioSCAN (Biodiversity Science: City and Nature) project of the Natural History Museum of Los

118   Angeles County (LACM). The initial findings from this sampling are described by Brown and

119   Hartop [42], who provide a detailed description of each site featured in the study. In a survey,

120   participants whose homes were included in the study were asked if they used pesticides in their

121   yards in areas close to where the traps were located. The survey revealed that none of the sites

122   were treated with pesticides regularly, and only a few hosts used small quantities of pesticides

123   for local control on rare occasions, such as neem oil on a few plants. We decided this incidental

124   treatment would not appreciably affect biodiversity within the yards included in this study.

125   For each of twelve sampling periods (approximately the first week of each month in

126   2014), we collected and identified all phorid flies in samples to species, resulting in a total of

127   42,480 specimens, . Vouchers are deposited in the LACM. Over this year of sampling, the fauna

128   of 99 species was essentially sampled to completion, as richness estimators predicted that

129   additional sampling would be expected to yield perhaps one additional new species [42]. We are

130   confident that this sampling regime represents nearly all the species in this lineage and locality

131   that would be captured using this sampling approach.

132

Abiotic data collection and processing

134 We continuously recorded air temperature, soil temperature, and relative humidity at each site

135 using a weather station adjacent to each trap (Onset HOBO U30 Station, Bourne, MA).

136 Additional details about abiotic data are in the electronic supplementary material.

137

Statistical Analyses

139 **Correlations between environmental and climatic predictors:** To determine the relative

140 contribution of urbanization and topography on microclimates across our study region, we used

141 two simple linear models to test whether impervious surface and/or elevation were predictive of

142 mean average annual air temperature at our sampling sites. In each model, mean average annual

143 temperature was the response variable, and impervious surface or elevation was the sole

144 predictor. We also evaluated whether differences in temperatures across sites were associated

145 with a coastal effect from the Pacific Ocean. Our hypothesis was that urban sites further away

146 from the coast would have warmer mean temperatures [50]. To test this, we also used a simple

147 linear model, with distances from our sites to the Pacific shoreline as the predictor and mean

148 average annual air temperature as the response variable.

149

150 **Phorid fly abundance, richness, and evenness:** We first calculated four response variables that

151 were each used as the responses in the modeling framework described below. First, we

152 calculated the total number of individuals caught per trap per day (abundance), species richness,

153 and Pielou evenness. Because the traps were in place for slightly different amounts of time

154 during some sampling periods, we divided each response variable by the number of days a trap

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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

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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

201 **Community composition:** In addition to the univariate community responses, we also

202 conducted a non-metric multi-dimensional scaling (NMDS) analysis to examine patterns in

203 community composition, and fit environmental vectors to gain insights into drivers of these

204 patterns [55]. For this analysis, we used all captures of phorid flies at a given site, across the

205 whole sampling period. We culled all singletons (species represented by a single sample

206 throughout the entire study), a standard approach because the incidence of a singleton is

207 indistinguishable from a spurious occurrence [56]. The NMDS was conducted on the Bray-Curtis

208 distance calculated from the untransformed matrix of taxon-by-site using abundance values.

209 Environmental fit vectors were selected iteratively by comparing the fit statistics (Global R^2 and

210 p-value) within a group of related, and auto-correlated, parameters (e.g., minimum, maximum

211 and mean air temperatures, etc.).

212

213 **Results**

214 **Correlations between environmental variables and urbanization:** Measured mean annual

215 temperatures at our study sites were independent of impervious surface and elevation (Fig. 2;

216 impervious surface: y= -129+9x, $F_{1,28}$=1.12, *p*= 0.30; elevation: y= -45+4.5x, $F_{1,28}$= 0.02, *p*=

217 0.90), suggesting that neither urban land cover nor elevation drove urban temperatures.

218 Therefore, we conclude that, while L.A. may have a largescale urban heat island effect, other

219 unknown factors drive temperatures at the local scale. As expected, NDVI tracked impervious

220 surface, though these values were not closely related to the distance to natural areas (Fig. S1).

221 Contrary to expectations, temperatures measured at weather stations in urban backyards were not

222 significantly associated with their distances from the coast (y= 1.90+1.83e^{-5}, $F_{1,28}$= 0.48, *p*=

223 0.49).

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224

225   **Mean and peak biotic responses:** Abundance and richness of phorid fly communities

226   throughout the city were best explained by air temperature (Table 1; Fig. 3). No other climatic

227   parameters had significant predictive value, aside for a lesser effect of relative humidity on

228   species richness (Table 1), and humidity slightly tracked temperature (Fig. S3). Phorid fly

229   abundance and richness responses to environmental conditions were nonlinear, with peaks at

230   intermediate mean weekly temperatures (Fig. S1). The factors affecting the abundance of the

231   most common species, *M. agarici*, were the same factors affecting total abundance (Table 1).

232   Evenness of phorid fly communities was weakly explained by mean minimum weekly

233   temperature and distance to natural areas, such that phorid fly communities in areas with lower

234   minimum temperatures and those that were further away from natural were more even (Table 1).

235   Latitude and longitude were associated with abiotic conditions (Figs. S4, S5), but spatial

236   autocorrelation was limited. Among all dates where sufficient data existed for autocorrelation

237   analysis (10 dates), one date (Week 6 of 2014) had significant spatial autocorrelation ($p = 0.037$),

238   suggesting that autocorrelation is rare in this system and may have been observed by chance.

239   Thus, after we accounted for spatial similarity of sites using latitude and longitude as described

240   above, no additional correction for spatial autocorrelation was needed.

241

242   **Community composition:** The effects of NDVI and mean minimum weekly temperature on

243   species composition were orthogonal, with a much greater effect of temperature (Fig. 4). Mean

244   minimum weekly temperature had the only significant vector, which also had the greatest

245   magnitude ($r^2 = 0.26$, $p = 0.02$)

246

Discussion

247

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.

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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

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293   species showed large spikes in abundance. Among those with known life histories (as listed in

294   Fig. 4: *Chonocephalus bentacaisei*, *M. agarici*, *M. halterata*, *M. marquezi*, *M. nigra*, and *M.*

295   *pleuralis*) fungus-feeding larvae are overwhelmingly common. Sporophore eruptions can

296   produce hundreds of flies relatively quickly, as Brown & Hartop [58,59] estimated a single

297   mushroom cap contained 500 larvae of *M. marquezi*. We suspect abundance peaks for these

298   species are associated with the mass production of fungal sporophores in close proximity to our

299   sampling area, which are common after rain. However, we also suspect that very wet climates

300   may increase fungal disease incidence [60,61], such that highest phorid fly richness occurs at

301   intermediate relative humidity.

302   Urban landscapes are rarely designed to sustain biodiversity, though this is often an

303   idealized goal informed by research [62]. At very high levels of heat, abundance and diversity

304   declines, which is consistent with other studies suggesting that the urban heat island effect has

305   negative effects on many species [14,63,64]. As the global temperature increases, many of the

306   sites we sampled may also warm and therefore no longer support diverse phorid fly

307   communities, though this will depend on how quickly phorid flies can adapt to changing thermal

308   conditions. Even on short timescales, it is possible that the thermal limits of species have

309   evolved, so that animals in the warmer parts of the city are capable of tolerating warmer

310   conditions independent of ecotypic acclimation [65]. Given the rapid evolution of thermal

311   tolerance in other arthropods [65–67], and the short generation times of phorid flies, rapid

312   adaptation to climate change might be possible.

313   Our work was designed to test how the urban matrix surrounding sites in urban Los

314   Angeles affects insect biodiversity. Our analyses suggest that temperature is a more important

315   variable than surrounding urban land cover (impervious surface and NDVI densities) for

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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-

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339   term data for describing species' long-term responses to urbanization and climate change

340   [75,76].

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Authors' Contributions

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

344   flies was conducted by BVB and EAH. Data curation and analyses were conducted by EKM and

345   CAB. Spatial data for analyses and maps were provided by EL. The manuscript was written by

346   TPM, with contributions from EKM, BVB, BJA, EL, and CAB.

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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

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

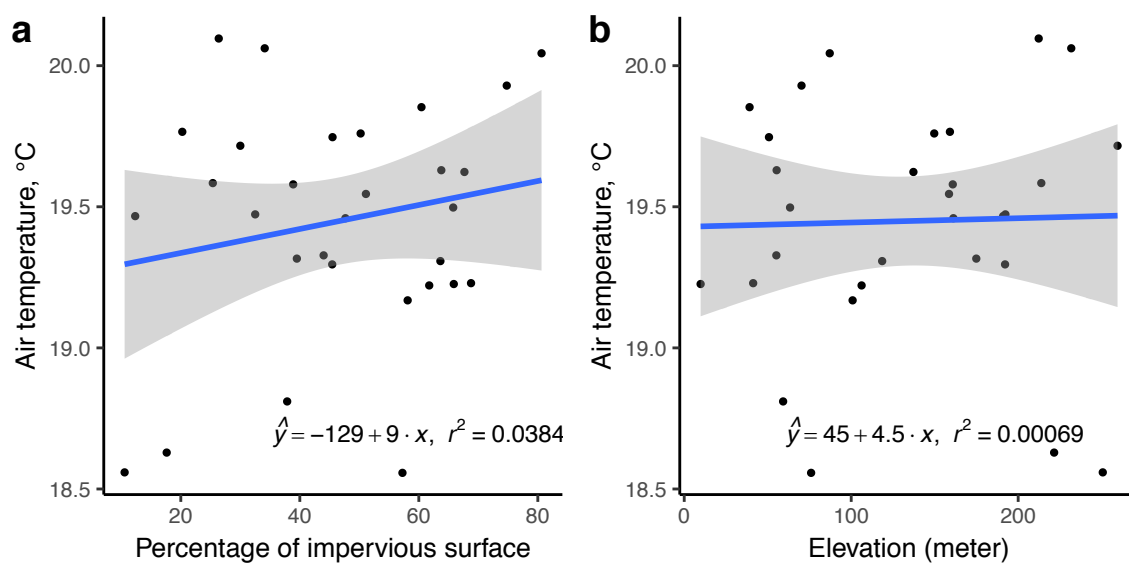559   Dot size represents mean daily phorid fly species caught in traps, and color represents mean

560   annual air temperatures.

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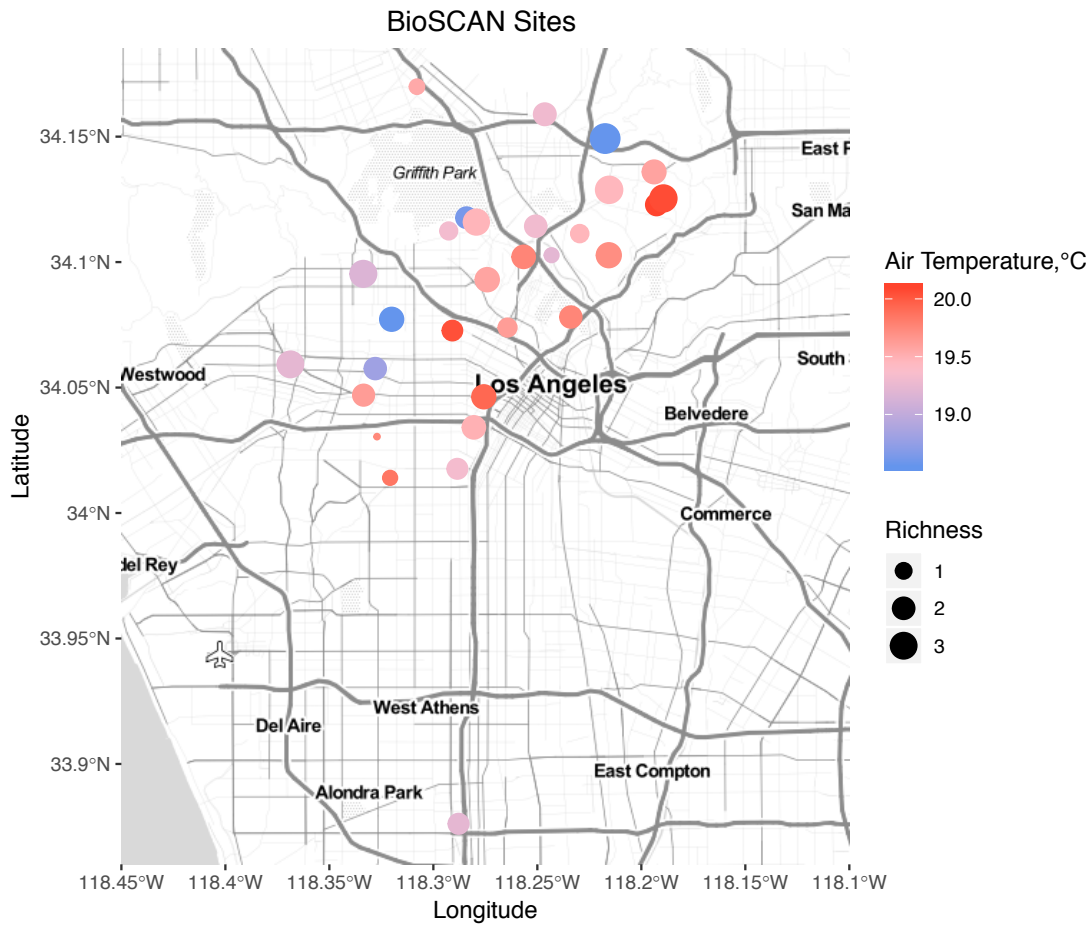
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565 **Figure 2. Thermal responses to landscape characteristics.** Mean annual air temperature is not

566 associated with a) impervious surface, nor with b) elevation.
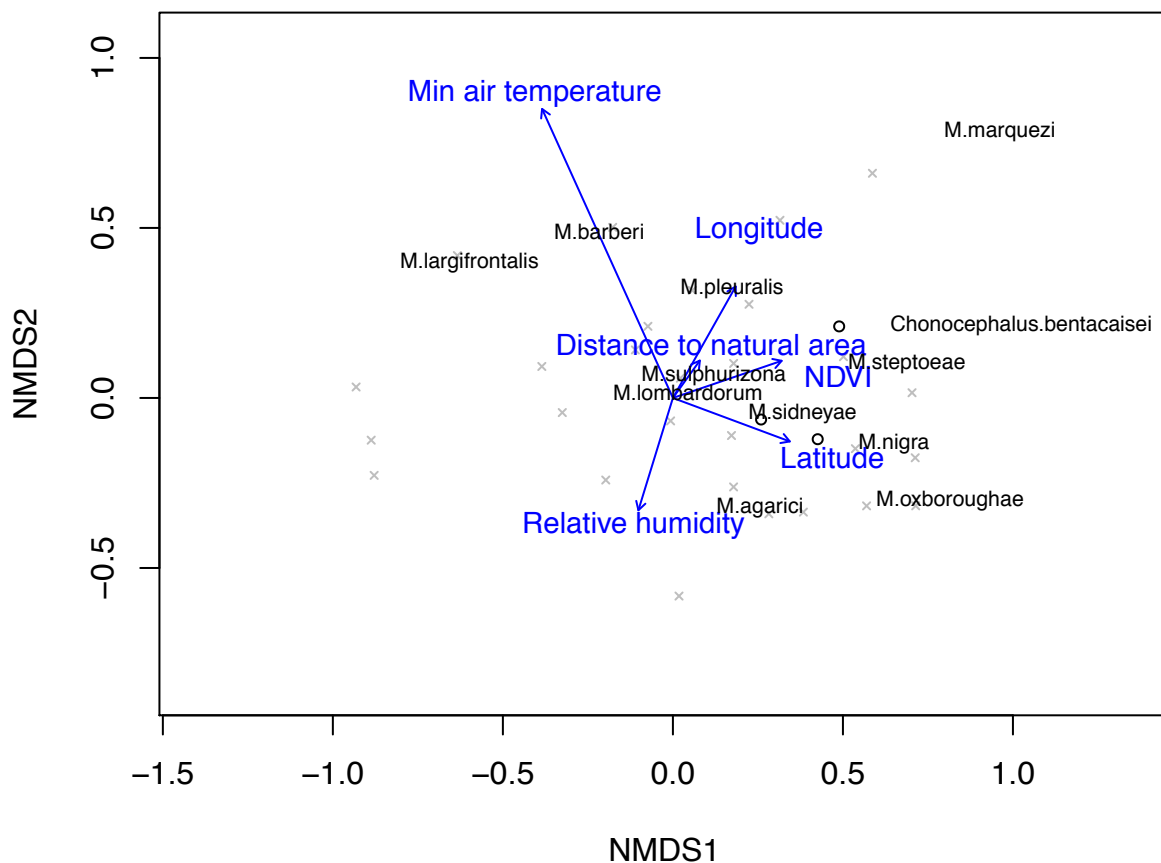

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569   **Figure 3. Phorid fly abundance and richness responses to temperature**. a) Total abundance

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
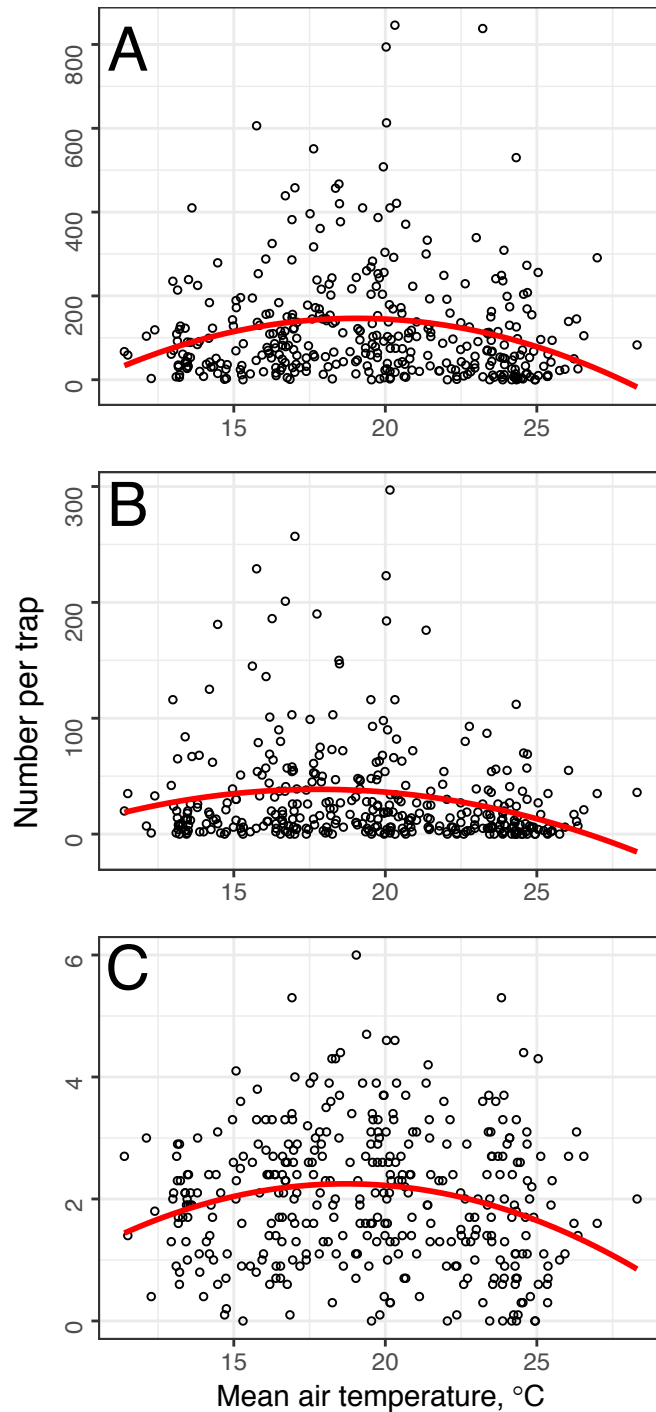
574 **Figure 4. Non-metric multidimensional scaling of phorid fly communities from urban Los**

575 **Angeles backyard sampling stations**. The species are superimposed with environmental fit

576 vectors for minimum air temperature ($r^2= 0.26$, $p= 0.02$), normalized difference vegetation index

577 within a 50-meter radius of the site (NDVI; $r^2= 0.03$, $p= 0.65$), distance to the nearest natural

578 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

579 longitude ($r^2= 0.04$, $p= 0.56$). Most common species names are plotted (with captures >500

580 individuals). NMDS 2D stress= 0.13.

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