1   Vehicle pollution is associated with elevated insect damage to street trees

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7

8   **Abstract**

9   1. Vehicle pollution is a pervasive aspect of anthropogenic change across rural and urban

10   habitats. The most common emissions are carbon- or nitrogen-based pollutants that may

11   impact diverse interactions between plants and insect herbivores. However, the effects of

12   vehicle pollution on plant-insect interactions are poorly understood.

13   2. Here, we combine a city-wide experiment across the Sacramento Metropolitan Area and

14   a laboratory experiment to determine how vehicle emissions affect insect herbivory and

15   leaf nutritional quality.

16   3. We demonstrate that leaf damage to a native oak species (*Quercus lobata*) commonly

17   planted across the western US is substantially elevated on trees exposed to vehicle

18   emissions. In the laboratory, caterpillars preferred leaves from highway-adjacent trees

19   and performed better on leaves from those same trees.

20   4. *Synthesis and applications*. Together, our studies demonstrate that the heterogeneity in

21   vehicle emissions across cities may explain highly variable patterns of insect herbivory

22   on street trees. Our results also indicate that trees next to highways are particularly

23   vulnerable to multiple stressors, including insect damage. To combat these effects, urban

24   foresters may consider installing trees that are less susceptible to insect herbivory along

25   heavily traveled roadways.

26   **Keywords:** global change, herbivory, herbivore, plant-insect interactions, pollution, *Quercus*,

27   urban ecology, urban forest

28

29 **Introduction**

30 Trees provide critical ecosystem services to urban residents, such as local cooling, air

31 purification, and runoff reduction (Bolund & Hunhammar, 1999). Most people now live in cities,

32 and global population continues to grow (United Nations, Department of Economic and Social

33 Affairs, Population Division, 2019). Thus, ecosystem service provisioning within urban areas is

34 increasingly important for human health and wellbeing. In addition to the services trees provide

35 to human residents of cities, they also serve as foundational species that support urban

36 biodiversity. In particular, trees are food for insect herbivores with high biomass (caterpillars)

37 and the vertebrates that rely on that biomass, such as birds and lizards.

38   Herbivores can damage trees by feeding on leaves and reducing photosynthesis (Zangerl

39 et al., 2002) and growth (Zvereva et al., 2012), two functions that are directly correlated with

40 ecosystem services, such as local cooling by trees. Insects can also kill trees (Crawley, 1983),

41 especially when their damage is compounded by abiotic stressors, such as extreme heat and/or

42 drought (Anderegg et al., 2015), which are already prevalent across much of the world's cities

43 (Tuholske et al., 2021; Zhang et al., 2019). It has long been appreciated that urban trees are under

44 threat from stressors associated with both urbanization and climate change, but the extent to

45 which insect damage may also shift over time is poorly characterized.

46   The difficulty in predicting the future of insect herbivory in cities largely stems from a

47 poor understanding of the underlying mechanisms driving highly heterogeneous patterns in

48 insect herbivore occurrences and damage within urban areas. Urban habitats are mosaics of heat,

49 nutrients, water availability, and pollution and thus the effects of individual stressors on insect

50 abundance, diversity, and damage are difficult to parse. Given that urban trees are under threat as

51 the climate warms (Burley et al., 2019; Meineke et al., 2016; Meineke et al., 2013; Monteiro et

52   al., 2017), understanding the specific mechanisms driving herbivory damage to urban trees could

53   better prepare planting programs to protect urban trees. An understanding of these mechanisms

54   could also enhance our ability to target tree planting for more optimal insect conservation and

55   management in cities.

56   Effects of urbanization—and specific aspects of urbanization, such as urban heat—on

57   chewing insects (the most common type of insect damage to plants (Turcotte et al., 2014) are

58   poorly understood. Chewing herbivory increases across some rural to urban gradients (Raupp et

59   al., 2010) and decreases across others. For instance, leaf area damaged by insects was 16.5%

60   higher in rural than in urban areas across several large European cities, an effect attributed to

61   elevated predation by birds and, potentially, ants in city centers (Kozlov et al., 2017). Other

62   studies demonstrate that insect chewing damage is elevated in urban compared to rural areas

63   (Cuevas-Reyes et al., 2013; Dreistadt et al., 1990). Urban to rural gradient studies generally do

64   not reveal the specific mechanisms driving the high heterogeneity of chewing damage within

65   cities.

66   One underexplored potential mechanism (Leonard & Hochuli, 2017) driving herbivory

67   both within cities and along highways in rural areas is vehicle emissions. The most common

68   vehicle-based pollutants that concentrate within a few hundred meters of roadways are nitrogen

69   oxides (NO_x), black carbon, carbon monoxide (CO), and ultrafine particulates (Brugge et al.,

70   2007). Many of these compounds are either nitrogen- or carbon-based, and nitrogen and carbon

71   are the backbones of most nutritional and defensive compounds within leaves for insect

72   herbivores. For instance, soluble sugars that serve as nutritional compounds for insects are

73   carbon-based, but so are tannins, which can reduce feeding by herbivores (Barbehenn &

74   Constabel, 2011; Forkner et al., 2004). Similarly, proteins required by insects are nitrogen-based

4

75   but so are alkaloids, which are compounds that protect against insect herbivory (Macel, 2011;

76   Macel et al., 2005).

77   Past studies hint at the potential role of vehicle pollution as a driver of leaf nutritional

78   quality for chewing herbivores. At one site in the United Kingdom, trees within 100 meters of

79   motorways were much more likely to be severely defoliated than trees at further distances.

80   Elevated herbivory was attributed to elevated nitrogen dioxide (NO_2) along highways (Bignal et

81   al., 2007). Similarly, in the Los Angeles Basin, USA, herbivore communities on oak trees at

82   more polluted natural areas tended to be more dominated by chewing herbivores compared to

83   less polluted natural areas (Jones & Paine, 2006). The specific driver of this regional pattern

84   could have been effects of NO_x or ozone, and the latter is unlikely to accumulate locally along

85   roadways (Brugge et al., 2007).

86   Here, we harness the heterogeneity of vehicle pollution across the Sacramento Valley to

87   investigate its effects on insect damage to trees. We employed a spatially explicit model of

88   vehicle emissions (Gately et al., 2015) to select high and low pollution sites across the region,

89   then measured chewing and mining herbivory on trees at these sites to determine relationships

90   between insect damage and exposure to pollutants. Chewing herbivory on leaves is often caused

91   by mandibulate insects with high biomass, notably caterpillars, that serve as food for higher

92   trophic levels and thus could have disproportionate impacts on food webs and ecosystem

93   functions. In the laboratory, we fed naive caterpillars leaves from trees exposed to various levels

94   of pollution to quantify the effects of leaf origin on insect damage to leaves and insect

95   performance. Our results demonstrate that highly polluted, highway-adjacent habitats are

96   associated with shifts in plant-insect interactions and that this topic may be ripe for future

97   research into how roadside environments may affect insect conservation and plant performance

98   in cities.

99

100   **Materials and Methods**

101   ***Urban field study***

102   *Description of study region*

103   We examined patterns of herbivory on *Quercus lobata* across the Central Valley of northern

104   California, USA. The region has a Mediterranean climate with monthly mean maximum

105   temperatures ranging between 12.1° C and 33.4° C and monthly mean minimum normal

106   temperatures between 3.6° C and 14.7° C (National Oceanic and Atmospheric Administration,

107   2022). Roads are not regularly salted, which can affect plant nutritional quality for insect

108   herbivores (Mitchell et al., 2020). However, Sacramento is heavily impacted by vehicle-based

109   pollutants, the most prevalent of which are particulate matter and ground-level ozone (City of

110   Sacramento, 2022).

111

112   *Focal tree selection and sampling*

113   We chose to focus on an oak species because observational studies suggest that interactions

114   between oaks and their herbivores might be affected by pollutants (Bignal et al., 2007; Jones &

115   Paine, 2006). Valley oak (*Quercus lobata*) was ultimately chosen as a focal species because it

116   native, supports a diverse herbivore community of herbivores (Pearse, 2019), and is commonly

117   planted in urban environments across northern California.

118   Focal trees were selected in QGIS (QGIS Development Team, 2022) by overlaying the

119   2016 Database of Road Transportation Emissions (DARTE) data layer (Gately et al., 2015) with

120   a shapefile of Sacramento County owned street trees provided by the Sacramento Department of

121   Public Works Urban Forestry Division. The DARTE data layer from 2016 was the latest in a

122   series of one-by-one-kilometer gridded datasets representing vehicle emissions of CO_2 across the

123   continental United States modelled using traffic data. Though DARTE is meant to represent CO_2

124   emissions, the data also represent overall emissions and thus are suitable for describing the

125   emissions of other localized, vehicle-based pollutants.

126   A five-by-five-kilometer grid was then overlaid on these data layers (Fig. 1a). Within

127   each grid cell, we randomly selected one tree within the highest 10% of polluted zones in the

128   DARTE map, and one tree within the lowest 10% (Fig. 1b). Appropriate trees in each pollution

129   category were not available in all grid cells, but the study design still allowed us to achieve a

130   sample that includes trees in high- (n=14) and low- (n=12) pollution areas across urban

131   Sacramento (Fig. 1c).

132   A total of 12 trees from four of the nearest rural sites west of Sacramento were included

133   in the study (Fig. 1c). Three of these trees were from Quail Ridge Reserve and three were from

134   McLaughlin Reserve; these six trees were killed in fires at the end of 2020. In 2021, two

135   additional trees were added to the study from rural regional parks east of Sacramento—which are

136   less likely to be affected by fire—to replace these trees. We added another category of trees we

137   will refer to as highway-adjacent trees, which account for the possibility that resolution of

138   DARTE data (one-by-one kilometer) may not be fine enough to capture the pollution exposure of

139   individual trees because of high levels of air admixture that may dilute pollutants more than a

140   few hundred meters from highways (Brugge et al., 2007). To ensure we included trees exposed

141   to high levels of vehicle pollution in this study, we added 10 focal trees that were accessible from

142   city streets and were within 60 meters of a highway (Fig. 1c). We confirmed with relevant land

143   managers that no focal trees had been treated with pesticides.

144   One bottom, outer branch was collected from each cardinal direction of each tree with a

145   pole pruner, for a total of four branches per tree. Samples were placed in a plant press, and

146   proportion of leaf area removed by herbivory was estimated by eye on ten leaves per branch in

147   the laboratory. To ensure accurate estimation of herbivory, all participants in the study were

148   trained according to established methods (Johnson et al., 2016). Participants were additionally

149   trained by estimating leaf area removed on a given leaf not included in the study and then using

150   ImageJ (Schneider et al., 2012) to measure leaf area removed. This process was repeated until

151   estimates consistently matched measured values with an error rate of five percent or less. If there

152   were more than ten leaves per branch, focal leaves were randomly selected by overlaying a five-

153   by-five-cm grid on each specimen to avoid any biases for or against damaged leaves. Grid cells

154   were randomly selected, and herbivory was quantified on the topmost leaf within the grid cell.

155   After leaves were selected, the percent leaf area removed by chewing herbivores and the percent

156   leaf area mined by leaf miners was estimated.

157

158   *Covariate measurements*

159   *Midday water potential:* Insect herbivore abundance and herbivory can be affected by plant

160   water stress (Dale & Frank, 2017; Gely et al., 2020; Hahn & Maron, 2018; Huberty & Denno,

161   2004; Raupp et al., 2010). To estimate water stress of focal trees, we collected three bottom,

162   outer branches from the north side of each tree with a pole pruner between 11:00 and 14:00

163   between September 15th - 26th, 2021. Branches were placed in a pressure chamber (1515D; PMS

164   Instrument Company, Albany, NY, USA), (Dale & Frank, 2017; Meineke et al., 2016).

165   *Light pollution:* Light pollution can affect herbivory (Mondy et al., 2021) and we measured

166   artificial light at all focal trees. On January 18th - 24th, 2022, we use an illuminance meter (T10A;

167   Konica Minolta, Ramsey, NJ, USA) to measure light pollution (Lux) around focal trees.

168   Measurements were taken after the sun had fully set (after approximately 7:30 PM) until 11:00

169   PM.

170   *Diameter at breast height:* To account for effects of tree size on herbivory, we measured

171   diameter at breast height at 1.4 meters above the ground in October 2021 after leaf fall.

172   *Surface temperature:* Because insects are ectothermic, insect physiology, abundances, and

173   damage are often affected by temperature. To account for effects of local temperature on

174   herbivory in this study, we used a surface temperature raster from Landsat 9 Operational Land

175   Imager 2 (OLI-2) (Cook et al., 2014) from August 25, 2022 to extract mean temperatures within

176   a 50-m buffer around each site. Surface temperature layers from other dates and buffer distances

177   (100 meters, 200 meters, 500 meters, and 1000 meters) were included in preliminary models.

178   Those results are not included here because results among the sampled dates and distances were

179   similar.

180   *Bulk leaf nutrients:* Two leaves per cardinal direction on each tree were collected with a pole

181   pruner, pressed in a plant press, dried and shipped to Brookside Laboratories, INC (New

182   Bremen, Ohio) for analyses of the following nutrients: C, N, P, K, and Na per gm of dry leaf

183   tissue. All nutrients were measured as proportion of leaf weight except for Na, which was

184   measured in parts per million.

185   *Normalized differential vegetation index (NDVI):* To account for effects of surrounding

186   vegetation on herbivory, we extracted NDVI from a 200-meter buffer around each tree using an

187   eMODIS NDVI V6 (Earth Resources Observation And Science (EROS) Center, 2002) dataset

188   from May 2020 and calculated average NDVI per pixel. We chose May as a focal month because

189   NDVI within our study region peaks during this month (Turner et al., 2020). Vegetation data

190   layers from other dates and buffer distances (50 meters, 100 meters, 500 meters, and 1000

191   meters) were included in preliminary models. Results among models with NDVI extracted at

192   other buffer distances were similar to results presented here.

193   *DARTE-derived vehicle pollution data:* We extracted 2016 on-road emissions data within a 200-

194   meter buffer around each tree and calculated average emissions per pixel. On-road emissions

195   data from other buffer distances (50 meters, 100 meters, 500 meters, and 1000 meters) were

196   included in preliminary models. Results among models with on-road emissions extracted at other

197   buffer distances were similar, and thus are not reported here.

198   *Tree proximity to highways;* We manually measured the shortest distance from each tree to an

199   Interstate, U.S., or state highway on Google Maps. This variable was included in a subset of

200   models to determine if 1) distance from a major road can serve as a proxy for exposure to vehicle

201   pollution, and 2) on-road emissions explains additional variation not associated with proximity to

202   roads. For instance, if proximity to highways were significant in models, but on-road emissions

203   were not, we could conclude that some other aspect of highway adjacency unrelated to vehicle

204   pollution drives herbivory.

205   *Leaf proximity to highways*: For highway-adjacent trees, we further characterized leaf exposure

206   to on-road pollution by categorizing each cardinal direction of each tree as "bordering" or "not

207   bordering" the highway.

208

209   *Statistical analyses*

210   We implemented series of Bayesian models in Stan with the *brms* package (Bürkner, 2017) in R

211   (R Core Team, 2019). In all models, mean proportion of leaf area affected by the relevant

212   herbivory type per tree was specified as the response. A beta error structure was specified.

213   Models were each fit with 2000 iterations in four chains, and the initial 1000 iterations were

214   decarded after warm-up. We assumed convergence when Rhat values were equal to one and

215   assessed model fit to the observed data using posterior predictive checks in *brms.* We also

216   calculated the variance explained, i.e., the Bayesian R^2, for each model using the bayes_R2

217   function in *brms*. In all models, tree-level covariates included latitude, longitude, DBH, NDVI,

218   water potential, surface temperature, and light pollution.

219   We generated four sets of models, one of which characterizes herbivory across the

220   categories used to select focal trees (rural, urban low pollution, urban high pollution, highway-

221   adjacent). The second set identified specific mechanisms driving herbivory across these

222   categories. In a third model, we assessed the potential for highly localized effects of pollution on

223   herbivory by testing for the effect of highway adjacency within trees (for details, see below). The

224   fourth set of models focused on leaf nutrients. All continuous predictors were centered on zero to

225   allow comparison between effect sizes within models. For all models that included data from

226   multiple years, we included an interaction effect for year and pollution metric to determine

227   whether the effects of pollution depended on year. We subsequently built separate models for

228   each year. Models were generally structured as described in the formula here with slight

229   deviations as described below.

230

231   *Mean proportion of leaf area damaged ~ Beta(p_i, n)*

232   $f(p_i) = \square + \beta_1 pollution\_metric_i \times \beta_2 year_i + \beta_3 DBH_i + \beta_4 latitude_i +$

233

234     $\beta_5 longitude_i + \beta_6 NDVI_i + \beta_7 light\_pollution_i +$

235     $\beta_8 surface\_temp_i + \beta_9 water\_potential_i + u_i$

236   Where *mean proportion of leaf area damaged* is the number of grid cells with chewing damage

237   by mandibulate herbivores p on tree i. We modelled p_i as a function of the intercept (a),

238   *pollution_metric,* the pollution metric i depending on the specific model (see below), *year,* the

239   year in which herbivory was sampled (2020 or 2021) on tree i, environmental and spatial

240   covariates associated with each tree i, and u_i, a grouping factor (random effect) of individual tree

241   characteristics accounting for repeated herbivory sampling in 2020 and 2021.

242

243   Model Set 1. *Category-based herbivory models:* We assessed the effects of covariates and

244   sampling category on proportion of leaves affected by chewing and mining by insect herbivores.

245   In these models, 'pollution _metric' in the model above is specified as the sampling category of

246   each tree.

247

248   Model Set 2. *Mechanistic herbivory models:* We assessed the effects of vehicle pollution and

249   environmental and spatial covariates on insect herbivory. In two models—one with mining and

250   one with chewing herbivory as response variables—we included all covariates listed in the

251   formula above and DARTE-derived vehicle pollution data as the "pollution_metric". In another

252   set of two models, we assessed the effects of proximity to highways on each type of herbivory.

253   In these models, distance from the closest major highway was specified as the

254   "pollution_metric", and all covariates were included.

255

256 Model Set 3. *Within-tree highway adjacency model*: To determine whether leaves that bordered

257 highways were more or less eaten by insects than leaves on the same trees not bordering

258 highways, we subset the full datasets from each year to include only highway-adjacent trees. In

259 these models, we determined whether the "pollution_metric" of bordering highways (binary:

260 yes/no) affected leaf area removed by mandibulate herbivores in each year. This was the sole

261 fixed effect included in the models. Tree was included in each model as a random effect to

262 account for multiple replicates per tree.

263

264 Model Set 4. *Leaf nutrient models:* To assess effects of on-road pollution on leaf nutrients, and

265 C:N ratios (Lincoln et al., 1986; Schädler et al., 2007) we built separate models for each

266 nutrient following the basic structures of Models 1-2 above. Because C, N, P, and K were

267 measured as proportion of leaf composed of each nutrient, beta error structures were specified

268 for these models. A Gaussian error structure was specified for C:N and the model of Na because

269 it was measured as parts per million. For all leaf nutrient models, the "pollution_metric"

270 specified was DARTE-derived vehicle pollution data as it is the most direct measurement of leaf

271 exposure to pollutants.

272

273 ***Laboratory studies***

274 To determine effects of pollution on caterpillar preference and performance, we collected several

275 hundred individuals of the locally abundant western tussock moth (*Orgyia vetusta*) from Bodega

276 Marine Reserve on July 16, 2021. While the species is a generalist feeder, the populations we

277 collected from feed on coastal bush lupine (*Lupinus arboreus*), are naïve feeders on *Q. lobata*,

278 and are therefore unlikely to possess adaptations to particular *Q. lobata* phenotypes. During

13

279 transport, caterpillars were fed *Q. lobata* leaves from local trees on the UC Davis campus. They

280 were then starved for 24 hours before the experiments described below, which were performed

281 on July 19-20, 2021 at ambient temperature and humidity in the lab.

282

283 *Choice assays*

284 To determine the extent to which caterpillars choose to feed on leaves from polluted or less

285 polluted trees, we placed 20 caterpillars in 20 mesh bag arenas with one leaf from each of the

286 trees in the rural, urban low pollution, and highway-adjacent sampling categories. To reduce

287 field effort and ensure feasibility, we chose to eliminate the urban high pollution category.

288 Leaves were labeled by tree with sharpies. After 24 hours, leaves were harvested from the bags

289 and placed in a plant press. We then used ImageJ (Schneider et al., 2012) to quantify proportion

290 of leaf area removed by caterpillars. Any prior damage to leaves was also quantified before the

291 leaves were included in mesh bags, though all leaves chosen for the study were undamaged or

292 minimally damaged by herbivores.

293

294 *No choice assays*

295 To determine caterpillar performance on leaves from polluted and less polluted trees, we placed

296 a leaf from each tree described in the 'Choice Trials' in its own individual petri dish. Wet cotton

297 was fastened to the petiole of each leaf to ensure they remained hydrated, and the cotton was re-

298 wetted throughout the experiment. One caterpillar was placed in each petri dish. We repeated this

299 setup on five replicates per focal tree. Caterpillars were weighed at the beginning of the

300 experiment and then after 24 hours of feeding *ad libitum.* Any leaf damage present before

14

301   caterpillars began to feed was recorded categorically, i.e., as presence of mines, galls, chewing,

302   or scale insects and sooty mold.

303

304   *Statistical analyses*

305   To test our hypotheses, we implemented a series of Bayesian models in Stan with the *brms*

306   package (Bürkner, 2017) in R (R Core Team, 2019). Models were each fit as specified for the

307   field experiment.

308

309   *Choice assays*

310   *Mean proportion of leaf area damaged ~ overdispersed Beta(p_{ij}, n)*

311    $f(p_{ij}) = \square + \beta_1 tree\_category_i + u_j$

312   To assess effects of pollution on herbivory in choice trials, we modelled p_{ij} as a function of the

313   intercept (*a*), *tree_category* of tree *i* (rural, urban low emissions, highway adjacent), and arena

314   specified as a random effect (u_j). The response variable was specified as total proportion of leaf

315   area removed by caterpillars. We chose a zero-inflated (over-dispersed) beta error structure to

316   account for leaves that remained un-eaten; beta error structures require non-zero values.

317

318   *No choice assays*

319   *Caterpillar weight change ~ Gaussian(p_{ij}, n)*

320    $f(p_{ij}) = \square + \beta_1 tree\_category_i + B_2 prior\_herbivory_{ij} + u_i$

321   To assess the effects of pollution on leaf nutritional quality for caterpillars, we modelled p_{ij} as a

322   function of the intercept (*a*), *tree_category* of tree *i* (rural, urban low emissions, highway

323   adjacent). The response variable was specified as caterpillar weight change from the beginning to

324   the end of the experiment. We included *prior_herbivory* on leaf *j* put in petri dishes as a

325   categorical effect with the following categories: no prior herbivory on leaves, chewing, mining,

326   galls, scale insects/sooty mold. A random effect of tree was included to account for multiple

327   replications per study tree (u_i).

328

329   **Results**

330   ***Urban field study***

331   *Chewing herbivory:* In all models, pollution metrics had a significant positive effect on chewing

332   herbivory. In the categorical model (Model Set 1), highway-adjacent trees displayed more

333   herbivory than trees from any other category (Fig. 2; Table 1a; $\beta= 1.46$, $CI_{95} = 0.87– 2.05$), with

334   urban trees in low-emissions and high emissions categories displaying intermediate levels of

335   herbivory while rural trees displayed the least, though these values were not statistically

336   distinguishable (Fig. 2; Table 1a). Mechanistic models (Model Set 2) demonstrated positive

337   effects of both on-road vehicle pollution (Fig.3a; Fig. S1a; Table 1b; $\beta= 0.042$, $CI_{95} = 0.09–$

338   0.75) and tree proximity to highways (Fig. 3c; Fig. S1c; Table 1c; $\beta= -1.02$, $CI_{95} = -2.01– -0.04$)

339   on herbivory, such that trees in higher pollution zones and trees closer to highways displayed

340   more chewing damage. Further, leaves from the sides of individual highway-adjacent trees

341   bordering a highway displayed more herbivory than the sides of trees not bordering a highway

342   (Model Set 4; Fig. 4; 2020: $\beta= 0.35$, $CI_{95} = 0.04– 0.67$; 2021: $\beta= 0.33$, $CI_{95} = -0.03– 0.67$),

343   though the effect was not as strong in 2021. Chewing herbivory was higher overall in 2020 than

344   in 2021 across all models (Fig. 3; Table 1). In most cases, there were not strong interactive

345   effects between year and pollution metric, indicating that effects of pollutants were similar in

346   2020 and 2021. However, effects of highway-adjacency in categorical models were higher in

16

347   2020 (Table 1a; year × highway-adjacent: β= -0.39, CI_{95} = -0.73– -0.05), as was the effect of on-

348   road pollution, though this effect was not as pronounced (Fig. S2a-b; year × on-road emissions:

349   β= -0.07, CI_{95} = -0.20– 0.05). Results from models run separately for each year are included in

350   Tables S1-2. No environmental or spatial covariates explained patterns in chewing herbivory

351   except NDVI and tree size, such that larger trees surrounded by less vegetation displayed more

352   herbivory (Fig. 3a,c; Fig. S1; Table 1).

353   *Mining herbivory:* Mining and chewing herbivory were of similar magnitudes with an average

354   across all trees of four percent of leaf area mined and five percent of leaf area chewed in 2020,

355   and 0.3 percent of leaf area mined and two percent of leaf area chewed in 2021. Models of

356   mining herbivory did not display strong effects of vehicle pollution. However, trends pointed to

357   potential negative effects of pollution on leaf mining. While neither sampling category (Table

358   2a) nor distance from highways affected mining herbivory (Table 2c; Fig. S3c-d), on-road

359   emissions had a marginally negative effect on mining (Table 2b; Fig. S3a-b; β= -0.26, CI_{95} = -

360   0.59– 0.08). Results from models run separately for each year are included in Table S3-4. No

361   additional covariates explained patterns in mining herbivory (Fig. S3; Table 2).

362   *Leaf nutrients:* We found no evidence for effects of pollution metrics on leaf nutrients (Model

363   Set 4; Fig. S4). The sole covariate with effects on leaf nutrient concentrations was surface

364   temperature, such that trees at sites with higher surface temperatures had marginally lower

365   nitrogen content (Fig. S4d; Table S5a; β= -0.08, CI_{95} = -0.20– 0.03), and higher C:N ratios (Fig.

366   S4f; Table S5b; β= 2.07, CI_{95} = 0.03– 4.07).

367   ***Laboratory studies***

17

368   In choice assays, highway adjacent trees were eaten more than trees from rural areas (Fig. 5a; $\beta=$

369   -0.39, CI_{95} = -0.64– -0.14) and low emissions zones within cities (Fig. 5a; $\beta=$ -0.44, CI_{95} = -0.65–

370   -0.22). In no-choice assays, most caterpillars lost weight from the beginning to the end of the

371   experiment, but individuals fed leaves from highway-adjacent trees lost less weight than those

372   from rural areas (Fig. 5b; $\beta=$ -0.01, CI_{95} = -0.03– 0.00) and low emissions zones within cities

373   (Fig. 5b; $\beta=$ -0.01, CI_{95} = -0.03– 0.01), though the latter trend had less support than the former as

374   the credible interval overlapped zero. There was no effect of previous leaf herbivory on

375   caterpillar weight change during the course of the assay.

376

377   **Discussion**

378   Vehicle pollution was strongly associated with elevated insect chewing herbivory across all

379   models. Trees in high-pollution areas displayed more chewing herbivory than trees in urban

380   areas with low levels of pollution or rural areas: On highway-adjacent trees, leaves from

381   branches bordering highways were eaten more than branches not bordering highways. In

382   laboratory assays, leaves from highway-adjacent trees were both more attractive and more

383   nutritious for generalist caterpillars, providing evidence for plant-mediated elevation of insect

384   chewing herbivory in response to on-road pollution. Effects of pollution on leaf mining, in

385   contrast, were weaker but trended toward less leaf mining in more polluted areas.

386   We assessed effects of pollution on herbivory using four metrics: a categorical

387   representation of how focal trees were selected (from rural, highway-adjacent, urban low

388   emissions, and urban high emissions sites), a continuous metric of tree proximity to highways, a

389   categorical metric of whether a branch was collected from a side of a tree bordering a highway,

390   and—the metric that arguably serves as the most direct measure of pollution from vehicles—on-

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391   road emissions from the DARTE database (Gately et al., 2015). Across every model assessing

392   effects of these predictors, pollution was associated with elevated leaf chewing, and differences

393   between these predictors reveal additional information about the specific drivers of herbivory.

394   On-road pollution derived from the DARTE database had the strongest effect of any continuous

395   predictor, supporting our hypothesis that vehicle pollution is a key driver of insect chewing on

396   leaves. Effects of distance from a major road on herbivory were slightly weaker and more

397   variable, but trees nearer to highways still clearly displayed more herbivory than those further

398   away, suggesting that distance from highways may serve as an adequate proxy for tree exposure

399   to on-road pollution. This proxy could be useful in a management context—for instance, if on-

400   road emissions data are not available to aid in decision making about where to plant herbivory-

401   resistant tree species and cultivars.

402   The metric that explained the most variation in chewing herbivory was sampling

403   category, such that highway-adjacent trees displayed more herbivory than any other trees, and

404   rural trees experienced the lowest amount of herbivory. Urban trees from high- and low-

405   emissions zones displayed herbivory levels that fell between these other two categories, though

406   'high emissions' trees did not display higher herbivory than 'low emissions' trees. This might be

407   because, in some cases, trees may not fall into these categories reliably on-the-ground because

408   DARTE data are at a one-by-one-km resolution, and levels of pollution can vary more locally.

409   Elevated levels of on-road pollutants are often localized to a few hundred meters from roadways,

410   at most, because pollutants are quickly dispersed (Brugge et al., 2007, but see Cobley & Pataki,

411   2019). Highly localized pollution is consistent with the strong effects of highway-adjacency on

412   herbivory that we documented. We note, however, that even though DARTE may not capture

413   on-road pollution reliably when included categorically, it was representative enough in our

414   models to serve as a strong continuous predictor of herbivory.

415   Low amounts of herbivory at rural trees may indicate that both pollution and other factors

416   drive differences in herbivory differences between urban and rural sites. Our models accounted

417   for NDVI as a measure of surrounding vegetation, and chewing herbivory on trees from rural

418   areas was still statistically distinguishable from the three urban sampling categories; thus, we

419   suggest that rural sites have additional factors protecting trees from high levels of mandibulate

420   herbivory, such as elevated biological control in rural compared to urban habitats (Raupp et al.,

421   2010; Shrewsbury & Raupp, 2006) and/or above or belowground conditions that aid in tree

422   defense against herbivores (Moreira et al., 2019).

423   Along these lines, laboratory assays demonstrated that rural trees are less palatable and

424   are of poorer nutritional quality for caterpillars than leaves from urban, highway-adjacent

425   habitats. Without these assays, it would be impossible to tell whether higher herbivory rates on

426   polluted trees were a result of higher or lower leaf quality at those sites; more feeding on

427   polluted plants could indicate that leaves were more nutritious for herbivores, or less , i.e., that

428   individual insects had to eat more polluted leaf material to meet their nutritional needs (Lincoln

429   et al., 1986, 1993; Schäedler et al., 2007). Contrary to this possibility, lower weight loss by

430   highway-adjacent caterpillars in laboratory assays indicates that leaves from polluted sites are

431   actually of higher quality for herbivores. Though caterpillars were attracted to leaves from

432   highway-adjacent trees and lost less weight when fed those leaves, all caterpillars in the

433   laboratory trial lost weight, which is not surprising; *Q. lobata* is a novel food source for this

434   caterpillar population, and its leaves are much tougher than those of their host lupine. Our focal

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435   caterpillar species exhibits very limited dispersal and gene flow, and it might as a result be

436   locally adapted to its host plant even though it can feed on other species (Harrison, 1997).

437   Together, our data support a scenario in which leaves from highway adjacent trees are

438   both more attractive and nutritious to generalist herbivores, and fitness of these herbivores may

439   be higher on polluted trees. However, more herbivory on more polluted trees could result from

440   multiple proximate mechanisms between which we cannot distinguish in this study; higher

441   herbivory on highway-adjacent trees, for instance, may be a result of unique insect communities

442   at these sites, higher feeding rates by individual insects, higher abundance due to the

443   attractiveness of leaves to adult moths who lay eggs, and/or higher abundance due to elevated

444   insect fitness on more polluted trees. Our study provides evidence for the potential importance of

445   the latter three mechanisms.

446   We did not find evidence that on-road pollution is associated with changes in elemental

447   nutrients that could explain patterns in herbivory. Instead, it is possible that pollution affects

448   specific nutritional or defensive compounds, and future studies will be required to identify these

449   compounds. It is also possible that elemental leaf nutrient changes at different points during the

450   season are affected by vehicle pollution, but that these changes were masked by effects of the

451   herbivores on elemental leaf composition. For instance, leaf miners may artificially elevate leaf

452   nitrogen content. We chose minimally damaged leaves for nutrient analyses, and we therefore

453   find this explanation unlikely. Instead, we suspect that vehicle pollution depresses defensive

454   pathways within trees and reduces the concentrations of key compounds that protect against

455   herbivore damage (Moreira et al., 2019). Evidence for this scenario emerged in laboratory

456   assays, wherein caterpillars only very rarely chose to feed on leaves from rural trees in 'choice'

457   trials. Moreover, even when rural leaves were the only food available to caterpillars in 'no

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458   choice' trials, they avoided feeding on rural leaves, a mechanism that might have driven more

459   weight loss in these caterpillars compared to those fed leaves from highway-adjacent trees.

460   We included a wide range of measured covariates in models to test alternative hypotheses

461   about what may drive patterns of herbivory on urban trees across pollution gradients. Perhaps

462   surprisingly, light pollution, surface temperature, and tree water stress were not implicated as

463   drivers of herbivory on urban *Q. lobata*. Accounting for these variables provided more support

464   that on-road pollution is a key mechanism driving herbivory. Tree size and NDVI were the only

465   covariates that explained additional variation in chewing herbivory, such that bigger trees and

466   trees surrounded by less vegetation were eaten more by chewing herbivores (though no

467   covariates affected leaf mining). Our work adds to mounting evidence that surrounding

468   vegetation has a protective effect on trees, potentially through the provision of biological control

469   services that are supported by additional plant cover, diversity, and/or complexity (Korányi et al.,

470   2022; Nighswander et al., 2021; Philpott & Bichier, 2017; Shrewsbury & Raupp, 2006). We

471   suspect that larger trees were eaten more than smaller trees because they are older and have

472   therefore had more years to accumulate herbivores that are sedentary and tend to mate and lay

473   eggs on the same tree year after year. Larger trees may also be more apparent to herbivores

474   (Feeny, 1976).

475   Though our study points to the key importance of bottom-up processes on insect

476   herbivory across urban pollution gradients, top-down effects may also partially explain why

477   highway-adjacent leaves were eaten more. Airborne pollutants may disrupt or dilute chemical

478   signals to predators and parasitoids (Blande, 2021). Highway-associated noise could also

479   discourage foraging by birds, potentially because traffic noise precludes their communication or

480   otherwise deters them from being present on highway-adjacent trees (Grade & Sieving, 2016).

481　More studies are also needed to determine if top-down processes work in tandem with bottom-up

482　processes we identified to elevate chewing herbivory on polluted trees.

483　　　Chewing herbivory was lower in 2021 than in 2020 despite lower urban vehicle traffic

484　across the USA in 2020 that has been linked to reduced pollution (Pitiranggon et al., 2022). This

485　pattern that at first glance is contrary to our hypothesis that chewing herbivory is elevated on

486　some trees compared to others because of on-road pollution. While differences in pollution

487　exposure among trees located in different areas may predict levels of herbivory, other factors

488　may be more important in driving how much plants are eaten from year to year. This underscores

489　the need for more long-term studies on insect herbivory in cities to promote a temporally explicit

490　understanding of the major drivers of plant-insect herbivore interactions (Ossola et al., 2021).

491　　　Regardless, our study highlights the importance of planting decisions along major

492　roadways. The concept of "right tree, right place" has long stated that tree selection should be

493　aimed at maximizing the performance in urban areas (Minckler, 1941; Morakinyo et al., 2020;

494　Wang et al., 2022). *Quercus lobata* and other species that are highly susceptible to herbivores

495　may provide ecosystem services sub-optimally along highways, and may have shorter lifespans

496　due to chronic damage promoted by on-road pollution (Pearse et al., 2015). Identifying tree

497　species that are robust to pollution, and resistant to insects that may benefit from pollution, could

498　be a novel consideration in planting decisions. This consideration may become even more

499　important as many cities become drier and hotter, and insect herbivores have disproportionate

500　impacts on tree growth (Meineke & Frank, 2018). Because city-owned trees are planted and

501　cannot themselves evolve in response to climate change, we may be required to develop new

502　cultivars to promote robust trees along roadways.

503   Our research also has implications for other cultivated and wild plant communities

504   worldwide. In most countries, it is difficult to locate land that is more than one mile from a

505   roadway (Riitters & Wickham, 2003). Initiatives such as those spearheaded by the former First

506   Lady Claudia "Lady Bird" Johnson to plant native wildflowers along state and federal highways

507   (Gould, 1996) have the potential to contribute to local biodiversity (O'Sullivan et al., 2017).

508   However, these same plants may take up pollutants from vehicles, with unknown consequences

509   for interactions between plants, insects, and higher trophic levels. Our research suggests that on-

510   road pollution ca have consequences for plant-insect interactions, which deserve to be studied

511   further in the contexts of plant performance and services, biological conservation, and climate

512   change. Our research also adds to a now growing chorus of studies (Lahr et al., 2018;

513   Youngsteadt et al., 2015, 2017) demonstrating the scientific value of intra-urban gradients of

514   particular variables (heat, pollution, surrounding vegetation). These specific gradients move

515   beyond urban-to-rural gradients to isolate particular mechanisms shaping ecological functions in

516   rural and urban habitats.

517

518   **Authors' contributions**

519   EKM conceived of the urban field study, collaborated with RK and DSE on design of the

520   palatability studies, led statistical analyses, and co-wrote the manuscript. DSE collected data,

521   helped manage undergraduate research activities, and helped edit the manuscript. RK helped

522   design and collect data for palatability studies and co-wrote the manuscript.

523

524   **Data availability statement**

525   Upon publication, all data from this project will be made available on the Dryad database with a

526   corresponding DOI. All code and data will additionally be made available on the Meineke Lab

527   website at a designated URL.

528

529   **Conflict of Interest**

530   We declare no conflicts of interest.

531

532   **Acknowledgements**

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Figures and Figure captions
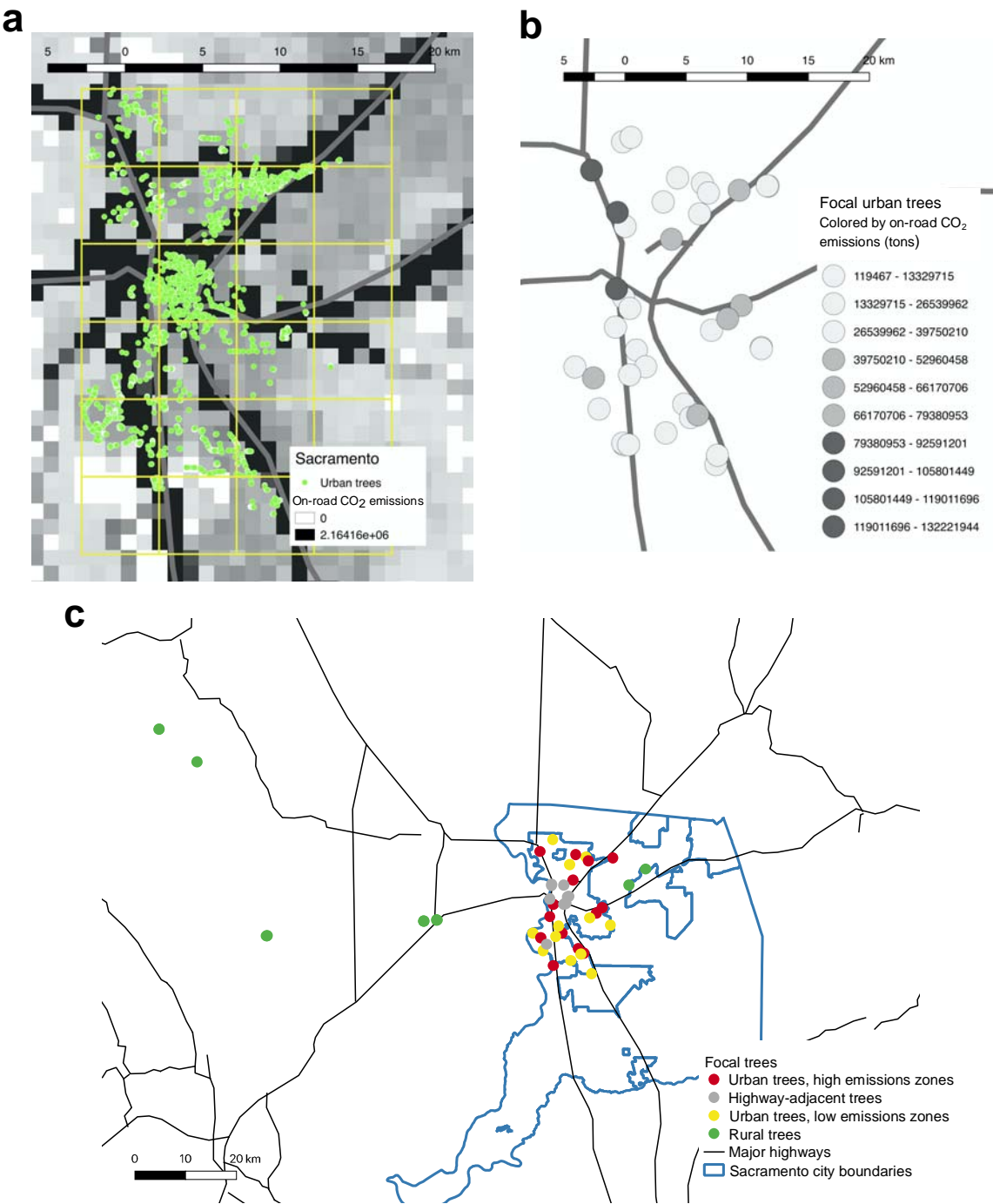
Fig. 1. Study system and tree selection in Sacramento, CA. a) The DARTE on-road CO_2

emissions base layer overlaid with street trees owned by the city of Sacramento City and a 5×5-

km grid from which trees in high (top 10%) and low (bottom 10%) vehicle emissions zones were

755   randomly selected. b) Urban focal trees selected from a) and colored by on-road CO_2 emissions,

756   and c) All focal individuals, including highway-adjacent and rural trees added to study design.

757
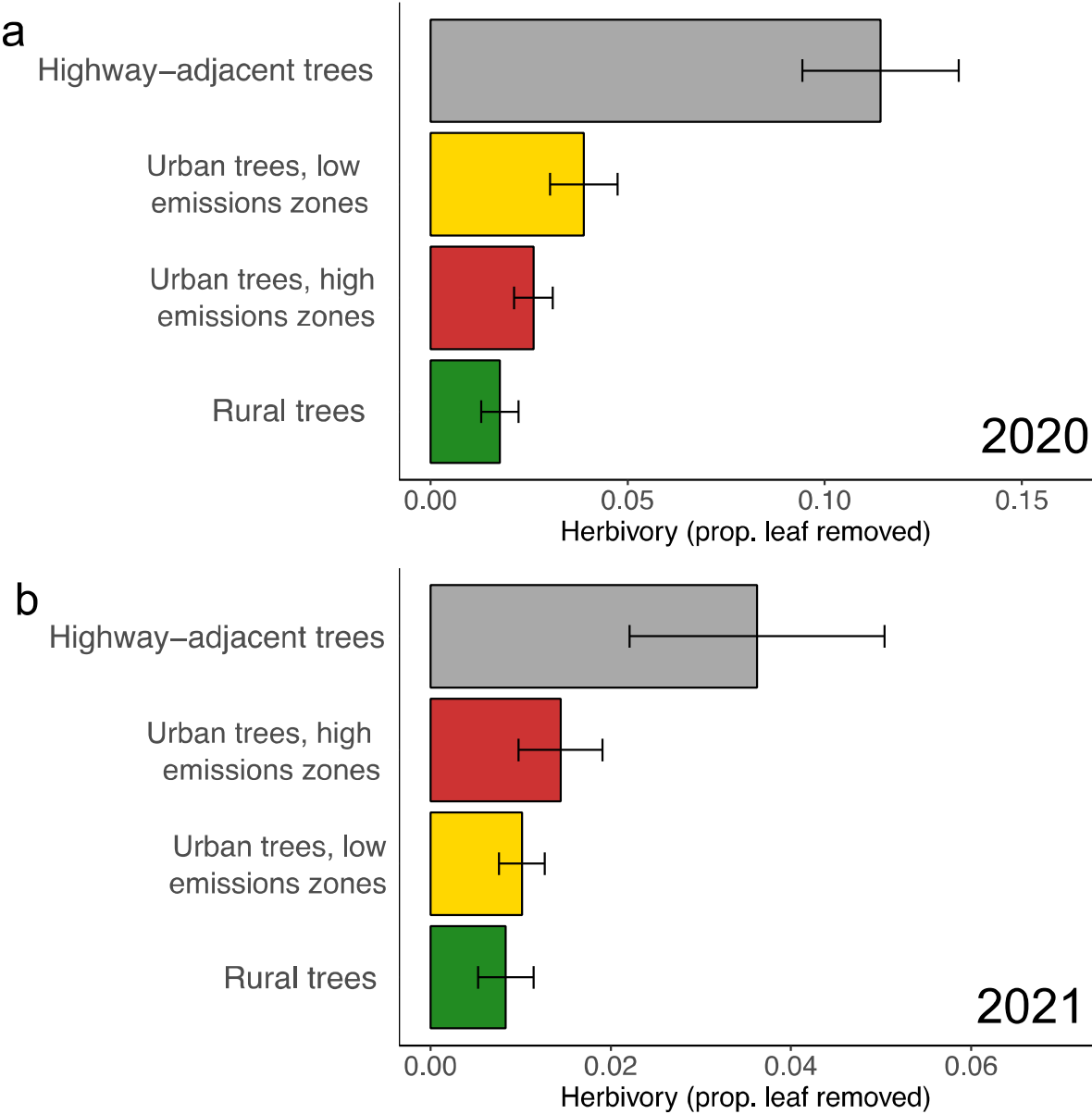
Fig. 2. Effects of vehicle-derived pollution on insect herbivory on valley oak (*Quercus lobata*). Chewing herbivory by insect herbivores with mandibles as it relates to categories of pollution exposure.
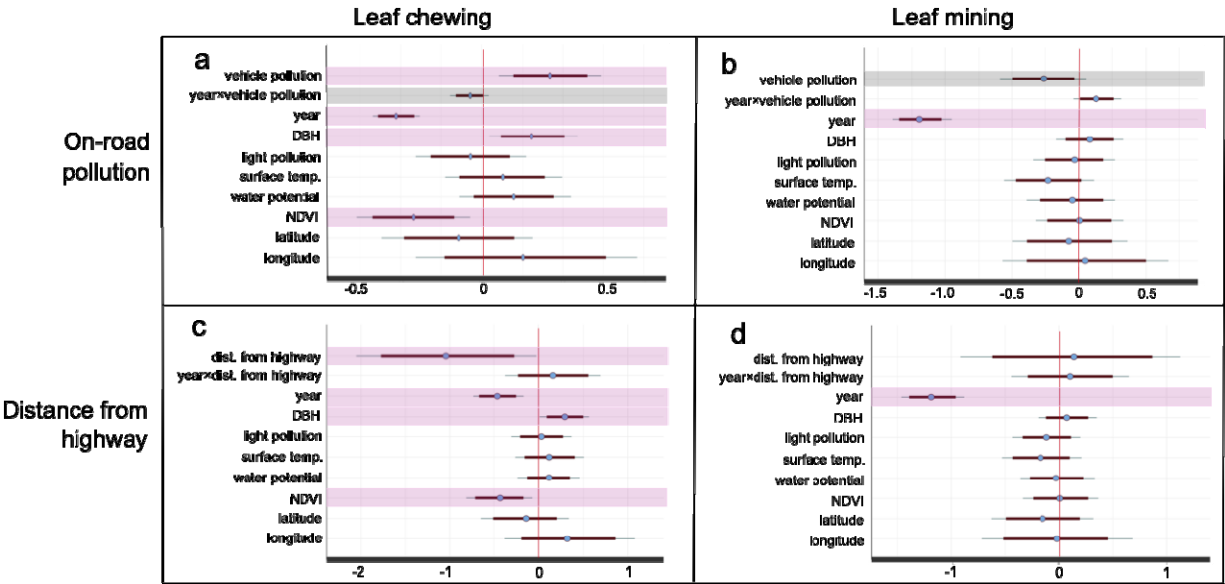
Fig. 3. Model estimates showing the predicted effects of pollution, location, and environmental variables on insect damage to leaves. Bold lines represent 85% credibility intervals, and narrow lines represent 95% credibility intervals. Predictors with 85% credibility intervals not crossing zero are highlighted in grey, and those with 95% credibility intervals not crossing zero are highlighted in purple.

a

b
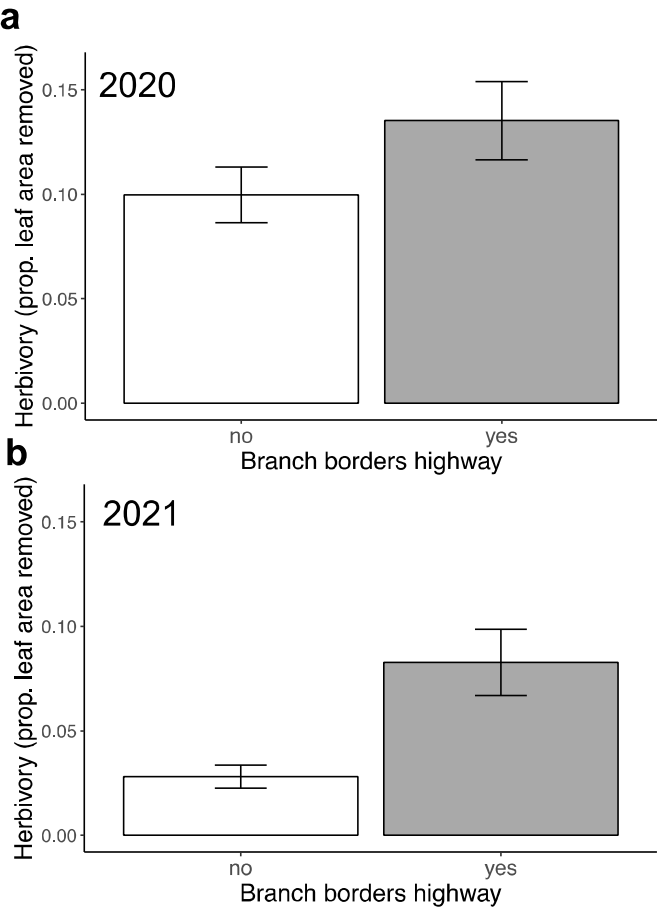
Fig. 4. Effects of branch proximity to highways on herbivory. Branches from the sides of individual trees bordering highways displayed higher rates of herbivory than leaves from the same trees not bordering highways.
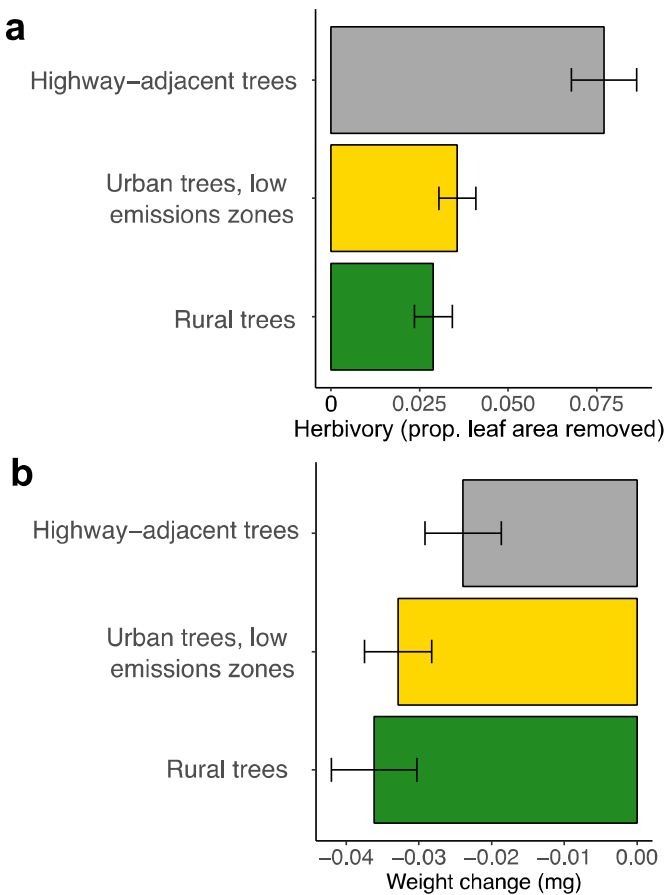
Fig. 5. Effects of tree exposure to highways on insect damage to leaves and insect performance. a) Chewing herbivory by naive insect herbivores in the laboratory as it relates to categories of pollution exposure in trials that gave insects the choice to feed on leaves within the category of their choosing, and b) weight change in caterpillars in no-choice trials fed leaves from one pollution exposure category.

785   **Table 1. Effects of key predictors on insect chewing herbivory.** Bayesian models predicting

786   the effects of a) vehicle emissions category, b) distance from the nearest major highway, c) on-

787   road CO_2 emissions, along with covariates included in all models: light pollution (illuminance),

788   surface temperature, stem water potential (tree water stress), tree size (diameter at breast height),

789   and latitude and longitude of individual focal trees on proportion of leaf area removed by

790   mandibulate herbivores during the 2020 growing season. For each parameter, β_{avg} is the

791   estimated average effect on insect chewing herbivory. Values of each continuous variable were

792   scaled prior to analysis. Thus, larger deviations of β_{avg} values from zero indicate a larger effect of

793   the parameter, and these effects can be compared across parameters. The effective sample size is

794   indicated by n_{eff}, and Rhat = 1 indicates convergence.

795
796   *a. Model with pollution exposure categories ($R^2 = 0.78$)*

Variable	β_{avg}	SE	2.5%	97.5%	n_{eff}	Rhat
Intercept	-4.11	0.30	-4.71	-3.50	2375	1.00
Highway-adjacent	1.46	0.30	0.87	2.05	2200	1.00
Urban, low emissions	0.41	0.33	-0.25	1.05	2558	1.00
Rural	-0.14	0.50	-1.15	0.77	2684	1.00
Illuminance	0.04	0.13	-0.20	0.29	3125	1.00
Surface temperature	-0.11	0.16	-0.42	0.20	2834	1.00
Water potential	0.20	0.14	-0.07	0.47	2415	1.00
Tree size	0.22	0.10	0.01	0.42	3172	1.00
Latitude	-0.01	0.23	-0.46	0.44	2467	1.00
Longitude	-0.07	0.45	-0.99	0.79	2365	1.00
NDVI	-0.52	0.14	-0.81	-0.24	2941	1.00
Year	-0.28	0.13	-0.54	-0.01	2478	1.00
Highway-adjacent × Year	-0.39	0.17	-0.73	-0.05	2894	1.00
Urban, low emissions × Year	-0.39	0.20	-0.78	0.01	3166	1.00

	β_{avg}	SE	2.5%	97.5%	n_{eff}	Rhat
Rural × Year	-0.16	0.26	-0.68	0.35	3837	1.00

797 *b. Mechanistic model including on-road vehicle emissions ($R^2 = 0.75$)*

Variable	β_{avg}	SE	2.5%	97.5%	n_{eff}	Rhat
Intercept	-3.83	0.22	-4.29	-3.39	1862	1.00
On-road CO_2 emissions	0.42	0.17	0.09	0.75	1726	1.00
Illuminance	-0.07	0.18	-0.45	0.29	1868	1.00
Surface temperature	0.12	0.18	-0.24	0.46	2261	1.00
Water potential	0.19	0.18	-0.15	0.54	1943	1.00
Tree size	0.31	0.14	0.04	0.59	1939	1.00
Latitude	-0.15	0.24	-0.61	0.32	1708	1.00
Longitude	0.28	0.36	-0.41	1.02	1791	1.00
NDVI	-0.41	0.18	-0.76	-0.07	2124	1.00
Year	-0.53	0.08	-0.67	-0.38	3076	1.00
On-road CO_2 emissions × Year	-0.07	0.06	-0.20	0.05	4316	1.00

798 *c. Mechanistic model including distance from nearest major highway ($R^2 = 0.73$)*

Variable	β_{avg}	SE	2.5%	97.5%	n_{eff}	Rhat
Intercept	-4.19	0.29	-4.77	-3.64	2033	1.00
Distance from highway	-1.02	0.50	-2.01	-0.04	1968	1.00
Illuminance	0.03	0.17	-0.29	0.37	1892	1.00
Surface temperature	0.12	0.19	-0.25	0.48	2129	1.00
Water potential	0.11	0.18	-0.23	0.46	1889	1.00
Tree size	0.30	0.14	0.02	0.60	1902	1.00
Latitude	-0.15	0.25	-0.65	0.34	1893	1.00
Longitude	0.33	0.37	-0.38	1.07	2008	1.00
NDVI	-0.44	0.19	-0.81	0.08	1958	1.00
Year	-0.46	0.14	-0.74	-0.17	2198	1.00
Distance from highway × Year	0.16	0.27	-0.37	0.69	2473	1.00

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801 **Table 2. Effects of key predictors on insect leaf mining herbivory.** Bayesian models

802 predicting the effects of a) vehicle emissions category, b) distance from the nearest major

803 highway, c) on-road CO_2 emissions, along with covariates included in all models: light pollution

804 (illuminance), surface temperature, stem water potential (tree water stress), tree size (diameter at

805 breast height), and latitude and longitude of individual focal trees on proportion of leaf area

806 removed by mining herbivores during the 2020 growing season. For each parameter, β_{avg} is the

807 estimated average effect on insect mining herbivory. Values of each continuous variable were

808 scaled prior to analysis. Thus, larger deviations of β_{avg} values from zero indicate a larger effect of

809 the parameter, and these effects can be compared across parameters. The effective sample size is

810 indicated by n_{eff}, and Rhat = 1 indicates convergence.

811
812 *a. Model with pollution exposure categories (R^2 = 0.85)*

Variable	β_{avg}	SE	2.5%	97.5%	n_{eff}	Rhat
Intercept	-4.43	0.41	-5.24	-3.64	2407	1.00
Highway-adjacent	-0.32	0.41	-1.14	0.47	2638	1.00
Urban, low emissions	0.17	0.41	-0.67	0.98	2325	1.00
Rural	-0.21	0.65	-1.57	0.99	2713	1.00
Illuminance	-0.07	0.15	-0.36	0.22	2744	1.00
Surface temperature	-0.22	0.19	-0.58	0.15	2591	1.00
Water potential	0.06	0.18	-0.30	0.39	2354	1.00
Tree size	0.09	0.13	-0.17	0.35	3012	1.00
Latitude	0.03	0.27	-0.49	0.55	2192	1.00
Longitude	-0.26	0.59	-1.49	0.87	2609	1.00
NDVI	0.02	0.17	-0.31	0.38	2787	1.00
Year	-1.20	0.15	-1.51	-0.90	2145	1.00
Highway-adjacent × Year	0.34	0.23	-0.10	0.78	3676	1.00
Urban, low emissions × Year	-0.21	0.20	-0.61	0.18	3911	1.00

44

Variable	β_{avg}	SE	2.5%	97.5%	n_{eff}	Rhat
Rural ✕ Year	-0.07	0.22	-0.52	0.36	3663	1.00

813 *b. Mechanistic model including on-road vehicle emissions ($R^2 = 0.83$)*

Variable	β_{avg}	SE	2.5%	97.5%	n_{eff}	Rhat
Intercept	-4.57	0.23	-5.01	-4.10	1105	1.00
On-road CO_2 emissions	-0.26	0.17	-0.59	0.08	2557	1.00
Illuminance	-0.04	0.15	-0.34	0.26	2298	1.00
Surface temperature	-0.23	0.17	-0.56	0.09	2310	1.00
Water potential	-0.05	0.16	-0.37	0.26	2143	1.00
Tree size	0.08	0.12	-0.17	0.32	2321	1.00
Latitude	-0.08	0.22	-0.50	0.36	2104	1.00
Longitude	0.04	0.30	-0.55	0.62	1975	1.00
NDVI	0.01	0.17	-0.31	0.33	2270	1.00
Year	-1.19	0.12	-1.39	-0.91	711	1.00
On-road CO_2 emissions ✕ Year	0.13	0.09	-0.04	0.32	3553	1.00

814 *c. Mechanistic model including distance from nearest major highway ($R^2 = 0.83$)*

Variable	β_{avg}	SE	2.5%	97.5%	n_{eff}	Rhat
Intercept	-4.52	0.29	-5.07	-3.96	1474	1.00
Distance from highway	0.14	0.52	-0.88	1.15	2053	1.00
Illuminance	-0.11	0.17	-0.44	0.22	1935	1.00
Surface temperature	-0.17	0.19	-0.54	0.21	1922	1.00
Water potential	-0.02	0.17	-0.37	0.31	1813	1.00
Tree size	0.08	0.14	-0.20	0.35	2063	1.00
Latitude	-0.15	0.24	-0.61	0.31	2086	1.00
Longitude	-0.03	0.34	-0.71	0.64	1716	1.00
NDVI	0.01	0.18	-0.33	0.37	1854	1.00
Year	-1.18	0.15	-1.47	-0.87	1561	1.00
Distance from highway ✕ Year	0.10	0.28	-0.48	0.65	3090	1.00

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