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The relative strengths of rapid and delayed density dependence acting on a terrestrial herbivore change along a pollution gradient

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Statement of Authorship:

MVK designed the study and conducted the fieldwork. MDH conducted the data analysis and interpretation. MVK and MDH co-wrote the manuscript.

30   **Short Running Title:** Pollution affects density dependence

31

32

33   **Abstract**

34

35   1. Animal populations vary in response to a combination of density dependent and density

36   independent forces, which interact to drive their population dynamics. Understanding how

37   abiotic forces mediate the form and strength of density dependent processes remains a central

38   goal of ecology, and is of increasing urgency in a rapidly changing world.

39

40   2. Here, we report for the first time that industrial pollution determines the relative strength of

41   rapid and delayed density dependence operating on an animal population. We explored the

42   impacts of pollution and climate on the population dynamics of an eruptive leafmining moth,

43   *Phyllonorycter strigulatella*, around a coal fired power plant near Apatity, northwestern Russia.

44   Populations were monitored at 14 sites over 26 years.

45

46   3. The relative strengths of rapid and delayed density dependence varied with distance from the

47   power plant. Specifically, the strength of rapid density dependence increased while the strength

48   of delayed density dependence decreased with increasing distance from the pollution source.

49   Paralleling the increasing strength of rapid density dependence, we observed declines in the

50   densities of *P. strigulatella*, increases in predation pressure from birds and ants, and declines in

51   an unknown source of mortality (perhaps plant antibiosis) with increasing distance from the

52   power plant.

53

54   4. In contrast to the associations with pollution, associations between climate change and

55   leafminer population densities were negligible.

56

57   5. Our results may help to explain the outbreaks of insect herbivores that are frequently observed

58   in polluted environments. We show that they can result from the weakening of rapid (stabilizing)

59   density dependence relative to the effects of destabilizing delayed density dependence.

60   Moreover, our results may explain some of the variation reported in published studies of animal

61 populations in polluted habitats. Variable results may emerge in part because of the location of

62 the study sites on different parts of pollution gradients. Finally, in a rapidly changing world,

63 effects of anthropogenic pollution may be as, or more, important than are effects of climate

64 change on the future dynamics of animal populations.

65

66

67 **Keywords**: Climate warming; Density dependence; Emission decline; Kola Peninsula; Pollution;

68 Population cycles; Population dynamics; Insect-plant relationships

69

70

71 **1. Introduction**

72 The dynamics of animal populations are driven by a combination of density dependent

73 (Nicholson & Bailey 1935; Lack 1954) and density independent processes (Andrewartha &

74 Birch 1954), with interactions between them responsible for the fluctuations in animal numbers

75 that we observe in nature (Varley *et al.* 1973; Royama 1992; Stenseth *et al.* 1999). For example,

76 water availability, a density independent process, can determine the relative importance of

77 resource limitation and predation pressure operating on animal populations (Price & Hunter

78 2005; 2015). Likewise, spring temperatures (density independent) can dictate the strength of

79 competition between animal species (Hunter 1998). Because density dependent processes

80 regulate animal populations, and set limits on their population growth (Turchin 1990),

81 understanding how density independent processes interact with density dependent processes is

82 important for the management of both beneficial and pest species (Berryman 1981; Berryman *et*

83 *al*. 1987). In the current period of rapid environmental change, predicting the impacts of abiotic

84 forces on population regulation is of increasing urgency (Walther *et al.* 2002; Parmesan & Yohe

85 2003). For example, if environment change alters the time lag in the operation of density

86 dependent forces, it could have important implications for population dynamics. Typically, rapid

87 density dependence enhances the stability of populations, whereas delayed density dependence is

88 destabilizing (Varley *et al.* 1973; Turchin 1990). Abiotic factors that increase the relative

89 importance of delayed density dependent processes should therefore increase population

90 fluctuations (Hunter *et al*. 1997; Turchin & Hanski 1997; Stenseth et al. 2003).

91

92 The strength and form of density dependence operating on animal populations can vary

93 substantially in space. For example, the relative strengths of rapid and delayed density

94 dependence vary among populations of small mammals (Turchin & Hanski 1997; Bjornstad et al.

95 1999b; Stenseth et al. 2003) and among populations of forest insects (Klemola et al. 2002;

96 Liebhold et al. 2006). Such spatial variation in negative feedback processes is often associated

97 with latitudinal (seasonal) differences among populations, whereby delayed density dependence

98 dominates at higher latitudes, inducing cyclic population dynamics (Klemola et al. 2002;

99 Stenseth et al. 2003). However, differences in habitat type, such as stand composition, may also

100 impact the form and strength of negative feedback operating on herbivores (Liebhold et al.

101 2006). Here, we ask whether pollution may act as an additional force generating spatial variation

102 in density dependent processes.

103

104 Anthropogenic effects of climate change on population dynamics continue to receive well-

105 deserved attention in the literature (Altizer *et al.* 2013; Valtonen *et al.* 2014; Jamieson *et al.*

106 2015). However, industrial pollution is a near-ubiquitous additional driver of environmental

107 change in most ecosystems on Earth, with profound impacts on animal populations in aquatic

108 and terrestrial ecosystems (Hart & Fuller 1979; Wulff *et al*. 2001; Coleman *et al*. 2004; Mirsal

109 2008). Recent analyses suggest that effects of pollution on animal populations can exceed those

110 of climate change (Zvereva *et al.* 2016). Although it is well established that the impacts of

111 pollution on animal populations may operate through biological forces such as competition and

112 predation (Butler & Trumble 2008), the effects of variation in pollution load on the relative

113 strengths of density dependent processes remain poorly understood.

114

115 Accepted opinion is that pollution favors outbreaks of many herbivores, in particular forest pests

116 (Baltensweiler 1985; Führer 1985). Meta-analysis (Zvereva & Kozlov 2010) has supported a

117 pattern of consistent increases in herbivore abundance near point polluters, although this effect

118 may be overestimated due to various biases in published data (Kozlov et al. 2009). The positive

119 association between industrial pollution and herbivore outbreaks was supported recently by the

120 analysis of long-term data on population densities of the willow-feeding leaf beetle, *Chrysomela*

121 *lapponica*. Outbreaks of *C. lapponica* near a large non-ferrous smelter between 1990–2000s

122 attenuated as pollution levels declined, associated with the re-establishment of top-down control

123 by predators and parasitoids (Zvereva et al. 2016). However, over the same period, average

124 densities of birch-feeding insects around the same smelter did not covary with pollution load

125 either in space or in time (Kozlov et al. 2017).

126

127 Contrasting effects of pollution on the population dynamics of herbivores may be reconciled if

128 we understand the effects of pollution on density dependent processes. Most studies to date have

129 focused on single biotic or abiotic drivers of population density (Alstad et al. 1982; Selikhovkin

130 1988; Riemer & Whittaker 1989; Butler & Trumble 2008; Zvereva & Kozlov 2010), while

131 studies that explore the effects of pollution on multiple negative feedback processes

132 simultaneously (Zvereva et al. 2016) remain rare. Our limited understanding of how pollution

133 interacts with sources of negative feedback is at least partly explained by the shortage of data

134 suitable for the analysis of density dependence. Time series of at least 30–40 steps are ideal for

135 analyzing ecological factors that influence populations (Royama 1992). Notably, the maximum

136 length of population time series of herbivorous insects collected from pollution gradients,

137 reported in studies published by 2009, was only 12 years (Zvereva & Kozlov 2010). Since 2009,

138 longer (19–26 years) time-series from multiple sites around a copper-nickel smelter in

139 Monchegorsk, northwestern Russia, have been published (Zvereva et al. 2016; Kozlov et al.

140 2017). However, the vast majority of herbivorous insects monitored at theses sites did not show

141 clear population cycles during the observation period, and signals of delayed density dependence

142 were only found in populations of two leaf beetle species, *C. lapponica* and *Phratora vitellinae*,

143 around this smelter (Zvereva et al. 2016).

144

145 In 1991, M.V.K. started to monitor population densities of the leafmining moth *Phyllonorycter*

146 *strigulatella* (Lienig et Zeller) (Lepidoptera, Gracillariidae) around a coal fired power plant

147 (which at that time emitted 20,000–29,000 metric tons of sulphur dioxide annually) near Apatity,

148 northwestern Russia. After ten years of data collection, it appeared that densities of this

149 leafminer varied nearly 200-fold during the course of its population cycle, with peak population

150 densities much higher near the power plant (Kozlov 2003). Because of the apparent interaction

151 between population cycles and pollution load, monitoring was continued until 2016. Here, we

152 report the outcomes of time-series analyses of this unique data set (23–26 years at 14 study

153 sites), asking whether the strength of rapid and/or delayed density dependence operating on

154 populations of the leafmining moth *P. strigulatella* varies along the pollution gradient.

155 Additionally, we ask whether declines in pollution and climate warming, which have occurred

156 simultaneously during the observation period, have affected the population dynamics of *P.*

157 *strigulatella*.

158

159 **2. Materials and methods**

160 2.1. Study area, insects and host plants

161 The study was conducted in the central part of the Murmansk region of Russia, in an area

162 covered predominantly by secondary birch-dominated forests scattered among the remnants of

163 primary coniferous forests. Daily values of temperature and precipitation in Apatity are freely

164 available (at www.rp5.ru) only from 2012, and therefore we used climate data from

165 Monchegorsk (Table S1; described in detail by Kozlov et al. 2017), which is located 43 km

166 NNW from Apatity.

167

168 Speckled alder, *Alnus incana* (L.) Moench, is common over the entire study area, where it grows

169 mainly in disturbed habitats along roads. Very small (wing expanse about 7 mm) moths of *P.*

170 *strigulatella* fly in mid-June. Caterpillars make blotch epidermal mines (one larva in each) on the

171 lower side of alder leaves from the end of June up to pupation in the end of July–beginning of

172 August. Mine size at pupation is 1.2–1.8 cm^2, and 5–15 larvae may successfully complete their

173 development in a single alder leaf.

174

175 2.2. Emission source and pollution load

176 The coal fired power plant, situated some 1.5 km N of the city of Apatity (67° 35′ 51″ N, 33

177 ° 25′ 08″ E), is the only local point source of sulphur dioxide and some metals, such as Fe,

178 Zn, Cr, Cd and Pb. The station mainly uses coal from Inta, Northern Ural (sulphur content 1.5–

179 1.9%), and sometimes from Spitsbergen or Khakassia (sulphur content 0.7–1.0%). The height of

180 the smokestack is 100 m; for more details, consult Kozlov et al. (2009). During the observation

181 period, emissions of sulphur dioxide and dust from the station decreased nearly five-fold,

182 whereas emission of nitrogen oxides did not change (Table S2). Concentrations of pollutants

183 decline to regional background levels at a distance of approximately 5 km from the power plant

184 (Kozlov 2003).

185

186   2.3. Leafminer densities

187 In total, fourteen sites were studied over the 26-year period. Sites were located along roads

188 leading either SE or NW from the power plant, and ranged in distance from 0.3–7.2 km from the

189 power plant (Table S3); the two directions from the power plant provided spatial replications of

190 pollution load. Of the 14 sites sampled during the course of the study, 10 were sampled in 1991

191 while 13 were sampled in 1992 and 1994. All 14 sites were sampled in all remaining years

192 (Table S3). Raw count data are available from the Dryad Digital Repository (Hunter & Kozlov

193 2018: https://doi.org/10.5061/dryad.sn0cn43).

194

195 Densities of *P. strigulatella* were monitored once per growth season, during the first week of

196 August in 1991–2016. Ten trees of speckled alder 2–5 m high were chosen at each site on a "first

197 found, first sampled" basis. The trees were not tagged, so observations in different years were

198 conducted on different sets of trees. One branch in the lower part of the crown (at about breast

199 height) was haphazardly selected in each tree, and the total number of mines was counted in a

200 sample of 25 leaves, starting from the tip of the branch. Care was taken to count even the

201 smallest mines, which were 2–3 mm^2 size. Leaf size of speckled alder did not change

202 systematically along the pollution gradient (Kozlov 2003), thus this method returned the number

203 of mines per constant unit of host plant resource.

204

205   2.4. Leafminer mortality

206 On 19 August 2017 we collected ca. 50 mines (range 49 to 71) haphazardly from each of the 14

207 sites. At this point during the season, over 90% of surviving leafminers have reached their final

208 size (Kozlov 2003). In each sample, we calculated the number of mines that had died during

209 early stages of their development (reaching not more than one-third of the final size), and mines

210 that had been opened by predators (wood ants and birds). All remaining mines were kept

211 outdoors in large Petri dishes until 4 November 2017. On this date, we counted the numbers of

212 mines that contained live pupae, those from which parasitoids had emerged, and any remaining

213 miners that had died from unknown causes. On the basis of this information, each collected larva

214 was assigned to one of four categories: pupated (alive), killed by predators, killed by parasitoids,

215 or death from unknown causes.

216

217   2.5. Data analysis

218   2.5.1. General patterns

219   Leafminer distributions were clumped on individual trees, such that around 40% of trees

220   examined had counts of zero. Consequently, in our initial analysis, we used a negative binomial

221   distribution and log link function (Proc GENMOD, SAS Institute 2009) to quantify the extent to

222   which leafminer densities varied among sites and years. Counts from individual trees were the

223   dependent variable, while year, site, and their interaction were independent variables.

224   Because we observed what appeared to be synchronous peaks in leafminer abundance among

225   study sites, we tested for synchronous dynamics (Bjornstad et al. 1999a) using the

226   community.sync function in the synchrony package in R (Loreau & de Mazancourt 2008;

227   Gouhier 2018). We compared among-site synchrony against 1,000 Monte Carlo randomized

228   permutations of population data, with Kendall's coefficient as our measure of synchrony. We ran

229   the synchrony analysis twice. First, we assessed synchrony among all 14 sites from 1995 to 2016

230   (years in which all 14 sites were sampled). Second we assessed synchrony among the 10 sites for

231   which we had leafminer counts for all 26 years (1991 to 2016).

232   Having established that leafminer densities varied significantly among sites and years, and that

233   their dynamics were synchronous among sites (Results), we then used averages of the 10 trees

234   per site to explore temporal and spatial variation in more detail (below).

235   2.5.2. Temporal patterns

236   First, we explored simple patterns of temporal change in leafminer densities using average

237   densities of leafminers for each sample year; averaging across sites yielded 26 density estimates,

238   one for each sample year. To assess effects of pollution load and climate on temporal patterns of

239   leafminer density, we used principal component analysis (PCA) to combine 16 climate variables

240   (Table S1: four variables for each of four seasons) into PCA axes w1–w4. Each of these axes had

241   an eigenvalue exceeding 1 and they combined to explain 79.3% variation in the climate data.

242   However, only w1 correlated with year ($r = 0.64$, $n = 26$ years, $P = 0.0004$, Fig. S1), so w1 is the

243   only PCA axis that represents systematic climate change. Similarly, we combined pollution data

244   (Table S2: annual emissions of sulphur dioxide, dust and nitrogen oxides) into a single PCA axis

245 (p1). This axis had an eigenvalue greater than 1 and explained 72.8% of the variance in pollution

246 emissions during the study period. This pollution axis correlates very strongly with year ($r = -$

247 0.88, $n = 26$ years, $P < 0.0001$) and so represents the combined declines in all three pollutants

248 over time (Table S2). We used Proc GLM (SAS Institute 2009) to correlate average leafminer

249 densities among years (dependent variable, log transformed) with PCA axes w1 and p1 in a

250 multiple regression model. PCA p1 was log-transformed prior to analysis to linearize the

251 exponential relationship.

252

253 Because we observed evidence of periodic fluctuations in leafminer density over time that might

254 obscure effects of pollution or climate, we also used time-series analysis (Box & Jenkins 1970;

255 Royama 1992) to account for any systematic variation in leafminer densities. Following

256 previously published procedures (Turchin 1990; Forchhammer et al. 1998; Price & Hunter

257 2005), we regressed leafminer per capita rates of change (r = natural log of lambda), calculated

258 between each pair of years in the time series, with their population densities at time t-1 and t-2

259 (natural log transformed). With those factors held in the model, we then asked whether pollution

260 (PCA axis p1) or climate change (PCA axis w1) could explain any additional variation in

261 leafminer per capita rates of change. Models were built using Proc GENMOD (SAS Institute

262 2009).

263

264 2.5.3. Spatial patterns

265 Second, we explored some simple spatial patterns in the data. Here, we averaged across years to

266 generate average leafminer densities for each site (14 sites total). Unlike the temporal data

267 available on annual emissions from the power plant (Table S2), we do not have spatial data on

268 pollution loads at each study site over the entire study period. Therefore, in our spatial analyses,

269 we followed previous studies (Kozlov et al. 2009; Zvereva et al. 2016), and used distance from

270 the polluter as a proxy for pollution load. The validity of this assumption has been confirmed

271 previously for these sites by a significant negative correlation between distance and iron

272 concentration in the leaves of speckled alder (Kozlov 2003). Here, we used Proc GLM (SAS

273 Institute 2009) to correlate (a) leafminer counts for each site (log transformed) and (b) the

274 temporal stability of leafminer populations (calculated as the inverse of the coefficient of among-

275 year variation) with distance from the polluter.

276

277   2.5.4. Spatio-temporal patterns

278   We then explored how temporal patterns of leafminer density varied in space. Separately for

279   each site, we conducted time-series analysis (Royama 1992; Redfern & Hunter 2005; Hunter et

280   al. 2014) to estimate the strength (slope) of any rapid and/or delayed density dependence acting

281   on leafminer population dynamics. First, we fitted multiple regression models to the relationships

282   between per capita rates of change and densities at time t-1 and t-2 (Proc GENMOD; SAS

283   Institute 2009) to generate maximum likelihood parameter values of the regression slopes. There

284   is inherent autocorrelation in time-series analysis; per capita rates of change are not independent

285   of population densities at time t-1, inflating the probability of detecting statistically significant

286   regression slopes (Royama 1992; Dennis & Taper 1994). However, we are interested here in the

287   magnitude of the slopes and how they vary with distance from the polluter, rather than in the P-

288   values associated with those slopes. Next, because observation and sampling error can cause

289   significant bias in the estimates of density dependence (Freckleton et al. 2006; Dennis et al.

290   2006), we used a simulation extrapolation (SIMEX) procedure (Cook & Stefanski 1994) to help

291   mitigate effects of census error on our estimates of density dependence. Specifically, we used the

292   standard error associated with our mean counts from 10 sample trees per year at each site to

293   simulate the effects of census error on our estimates (See Table S4 for details). While our

294   estimates of density dependence were generally robust to the effects of simulated error (Table

295   S4), we have used the SIMEX-corrected estimates in subsequent analyses. Specifically, we

296   correlated (using Proc GLM) the estimated slopes of rapid and delayed density dependence at

297   each site with distance from the polluter. Finally, to investigate any systematic variation in the

298   periodicity in leafminer fluctuations among sites, we conducted spectral analyses (Bloomfield

299   2000) on the log transformed counts of leafminers from each site, using the spectrum function in

300   R.

301

302   2.5.5. Mortality patterns

303   Given that we observed differences in patterns of negative feedback with distance from the

304   polluter (see Results), we investigated whether sources of leafminer mortality might also vary

305   with pollution load. Using the sources of mortality that we had measured from mines collected in

306   2017, we assessed whether the proportion of leafminers dying from each mortality factor varied

307   with distance from the power plant. We analysed the proportions using binomial models with

308   logit link functions in the GENMOD procedure in SAS (Littell et al. 2002), with mortality

309   factors as dependent variables and distance from the power plant as the independent variable.

310

311   **3. Results**

312   3.1. Overall patterns

313   Densities of *P. strigulatella* varied 235-fold among years and 20-fold among sites, with the

314   magnitude of difference among sites much more pronounced during population peaks (Fig 1a.).

315   Fluctuations in leafminer populations were synchronous among sites, whether we compared all

316   14 sites from 1995 to 2016 (Synchrony = 0.758, P = 0.001), or the 10 sites for which had counts

317   from 1991 to 2016 (Synchrony = 0.701, P = 0.001).

318

319   3.2. Temporal patterns

320   Pollution emissions declined over the period of the study (Fig. 2a), with a six-fold decline in SO_2

321   emissions, a halving of dust emissions, and more modest declines in NOx emissions. These

322   simultaneous declines in pollution are reflected in declines in the scores of PCA axis p1 (Year

323     $F_{1,24}$ = 110.45, P < 0.0001, Fig. 2a insert). In turn, low pollution emissions were correlated with

324   low leafminer densities among years (p1 $F_{1,23}$ = 5.11, P = 0.033, Fig. 2b). Our estimate of

325   climate change (PCA w1) was not a significant predictor of leafminer density (w1 $F_{1,23}$ = 0.16, P

326   = 0.89) in the simple multiple regression model. Despite declines in pollution emissions over

327   time, we observed no clear reductions in leafminer densities between 1991 and 2016 (Year $F_{1,24}$

328   = 2.77, P = 0.1037, Fig. 2c).

329

330   To further investigate any impacts of climate change or pollution on moth dynamics, we first

331   accounted for the effects of leafminer densities at time t-1 and t-2 on leafminer per capita rates of

332   change (see Methods). With densities included in the time series models, we then assessed

333   whether any of the residual variance in per capita rates of change was associated with climate or

334   pollution data. After accounting for variation in leafminer densities, there was still no effect of

335   our climate change estimate on leafminer per capita rates of change (w1 $F_{1,20}$ = 0.29, P = 0.595).

336   As with their impact on density (above), pollution emissions were associated positively with

337   leafminer per capita rates of change (PCA p1 $F_{1,20}$ = 4.38, P = 0.0494).

338

339 3.2. Spatial patterns

340 When averaged across years, leafminer densities declined by 45% over the 7.2 km from the site

341 closest to the power plant to the most distant site ($F_{1,12}$ = 19.76, P = 0.0008, Fig. 3). The

342 temporal stability of leafminer populations (i.e., inverse of the coefficient of among-year

343 variation) was unrelated to distance from the power plant ($F_{1,12}$ = 0.64, P = 0.438).

344

345 3.3. Spatio-temporal patterns

346 The strength of rapid density dependence increased ($F_{1,12}$ = 19.81, P = 0.0008), while the

347 strength of delayed density dependence decreased ($F_{1,12}$ = 9.95, P = 0.0083), with increasing

348 distance from the power plant (Fig. 4a). At distances greater than 3km from the power plant,

349 rapid and delayed density dependence became equally powerful forces acting on *P. strigulatella*

350 per capita rates of change (Fig. 4a). Because delayed density dependence remained pervasive

351 among sites (Table S4), the combined values of rapid and delayed density dependence across all

352 sites (Figure 4a) remained within ranges that should favour population cycles (see "Royama's

353 Triangle"; Royama 1992), explaining the apparent presence of cycles in the leafminer time series

354 at all sites (Fig. 1). However, while the periodic fluctuations were similar among sites, average

355 population sizes and the magnitude of outbreaks declined with increasing distance from the

356 power plant (Figs. 1B-O, Fig. 3). The periodograms from spectral analyses (Fig. S2) illustrated

357 pervasive high spectral densities at a frequency of 0.11–0.12, consistent with apparent 8–9 year

358 cycles in the time series data (Fig. 1), and consistent with the action of delayed density

359 dependence. While there were additional higher frequencies typical of more rapid cycles

360 observed at some of the sites more distant from the power plant, there was no unequivocal

361 evidence for a systematic change in outbreak periodicity with distance from the power plant (Fig.

362 S2).

363

364 3.4. Mortality patterns

365 Across all sites, only 6.2% of *P. strigulatella* larvae survived until pupation in 2017 (Table S5).

366 Most larvae (69.3%) died of unknown causes, either when their mines were small, or just prior to

367 pupation. Parasitoids (several species of Braconidae and Ichneumonidae, some of which may

368 have been super-parasitoids) emerged from 16.5% mines, while 8.0% of mines were opened by

369 predators (birds and ants).

370

371 The proportion of leafminers killed by predators increased nearly five-fold with increasing

372 distance from the power plant (Chi-square = 12.62, d.f. = 1, P = 0.0004, Fig. 4b). In contrast,

373 mortality caused by unknown factors declined by about 10% with increasing distance from the

374 power plant (Chi-square = 4.44, d.f. = 1, P = 0.0353, Fig. 4b), driven primarily by failed

375 development early in life (Chi-square = 2.95, d.f. = 1, P = 0.0860). No other mortality factors

376 that we measured were related to the distance from the power plant.

377

378 **4. Discussion**

379 Based on time-series analyses of long-term data, we report for the first time that the order of the

380 negative feedback processes operating on an animal population varies predictably with distance

381 from a pollution source. Population dynamics of the leafmining moth, *P. strigulatella*, are

382 dominated by delayed density dependent processes close to a coal-fired power plant. With

383 increasing distance from the pollution source, the impact of delayed density dependence declines

384 while the impact of rapid density dependence increases, so that they become equally powerful

385 forces acting on leafminer dynamics at distances greater than 3km from the power plant (Fig.

386 4a). From a single year of mortality data, we note that the change in the relative strengths of

387 negative feedback is associated with increases in predation pressure, and declines in an unknown

388 mortality factor, with increasing distance from the power plant (Fig. 4b).

389

390 Density dependent processes impose negative feedback, thereby maintaining a limit on

391 population growth (Varley *et al.* 1973; Berryman 1991). However, it is the interaction between

392 density dependent and density independent forces that determines the temporal dynamics of

393 animal populations (Turchin & Hanksi 1997; Forchhammer *et al.* 1998; Stenseth *et al.* 1999;

394 Hunter 2016). While previous studies have focused on the impacts of climatic factors on the

395 form and strength of density dependence (Hunter *et al.* 1997; Stenseth *et al.* 1999; Price &

396 Hunter 2015), our results add another abiotic driver, pollution, to the list of factors that can

397 mediate the relative strengths of density dependent processes.

398

399 Moreover, our results may explain some of the variation that has been reported previously in the

400 effects of pollution on animal population dynamics. For example, studies have differed in their

401 conclusions on the relative importance of direct pollutant toxicity, changes in plant quality, and

402 changes in predation pressure in determining herbivore population dynamics under pollution

403 stress (Butler & Trumble 2008; Kozlov et al. 2009; Zvereva & Kozlov 2010). Our data suggest

404 that the relative importance of ecological factors varies with distance from the pollution source,

405 and may generate different lags in the action of density dependence. It is therefore possible that

406 apparent differences in dynamics among studies partly reflect differences in the distance from

407 the polluter at which the study was conducted, rather than intrinsic differences based on the study

408 system.

409

410 What density dependent factors varied in response to changing pollution loads? Unfortunately,

411 we do not have the long-term data on predation pressure or plant quality that would be necessary

412 to determine if and how they impose density-dependence on leaf miner populations. The

413 suggestions that follow are therefore speculative. However, in the current study, generalist

414 predators that tear open leaf mines (wood ants and birds) imposed higher rates of mortality at

415 sites far from the power plant (Fig. 4b). High levels of pollution can influence the morphology,

416 physiology, density, and behavior of ants (Grześ 2010; Eeva et al. 2012; Grześ et al. 2015),

417 including reducing the aggressiveness of wood ants (Sorvari & Eeva 2010). Likewise, high

418 pollution levels can compromise the physiology (Geens et al. 2010) and abundance (Eeva et al.

419 2012; Morelli et al. 2018) of birds. Because both ants and birds can show rapid behavioral and

420 numerical responses to variation in prey density (Perrins 1979; Holldobler & Wilson 1990), they

421 may be responsible for the increasing importance of rapid density dependence with increasing

422 distance from the power plant (Fig. 4a). Previous studies of both insects and small mammals

423 have illustrated that increases in the relative strength of rapid density dependence can emerge

424 from increasing predation by generalist predators (Turchin & Hanski 1997; Klemola et al. 2002;

425 Stenseth et al. 2003). Our studies of *P. strigulatella* populations are therefore consistent with the

426 suggestion that increases in the abundance of generalist predators impose strong rapid density

427 dependence on herbivores. Moreover, our results suggest that a weakening of rapid density

428 dependent mortality may explain the frequently reported (Zvereva & Kozlov 2010) increase in

429 abundance of plant-feeding insects in polluted habitats. Critically, delayed density dependence is

430   destabilizing relative to rapid density dependence (Turchin 1990; Royama 1992), and a

431   dominance of delayed density dependence near sources of pollution may facilitate insect

432   outbreaks.

433

434   The results presented here support previous work, in which we reported the re-establishment of

435   predation pressure on an insect herbivore following temporal declines in pollution load (Zvereva

436   et al. 2016). Specifically, populations of the willow-feeding leaf beetle, *C. lapponica*, near a

437   nickel-copper smelter declined over time as the combined impacts of predation and parasitism

438   increased. Our current results are similar, but occur over space rather than over time. Because we

439   measured sources of mortality on *P. strigulatella* only in a single year, we are unable to assess

440   any temporal changes in natural enemy impacts in the current study. However, we note that any

441   temporal declines in the densities of *P. strigulatella*, are much weaker (Fig. 2c) than were the

442   dramatic temporal declines we reported for *C. lapponica* (Zvereva et al. 2016). For *P.*

443   *strigulatella*, the effects of spatial variation in pollution load appear much stronger than the

444   effects of temporal variation. In support of that premise, we found no significant correlation

445   between distance from the pollution source and the magnitude of density fluctuations (coefficient

446   of variation) in *P. strigulatella* populations. This contrasts with the pattern that was observed

447   around the copper-nickel smelter in Monchegorsk, where the magnitude of density fluctuations

448   of birch-feeding insects correlated positively with pollution load (Kozlov et al. 2017). This

449   difference may be explained by the lower environmental impact of the Apatity power plant

450   relative to the Monchegorsk smelter, which emitted ten times more sulphur dioxide than the

451   power plant (Kozlov et al. 2009).

452

453   In addition to changes in rapid density dependence, we observed increases in the strength of

454   delayed density dependence under higher pollution loads. However, delayed density dependence

455   was still apparent across a majority of our study sites (Table S4), occurring at levels that should

456   promote cyclic dynamics (Royama 1992), irrespective of distance to the power plant.

457   Accordingly, such forces may have been responsible for the synchronous population fluctuations

458   that we observed at our sites (Fig. 1). While we cannot rule out the possibility that density

459   independent processes generated the apparent cycles in leafminer populations (as described by

460 Williams & Liebhold 1995; Hunter & Price 1998; Louca & Doebeli 2014), there is no evidence

461 of periodicity in climatic factors over the study period (Fig. S1).

462

463 Why did our populations of *P. strigulatella* remain synchronous, despite systematic variation in

464 the relative strengths of rapid and delayed density dependence? Previous work with spatially

465 disjunct gypsy moth, *Lymantria dispar*, populations may help to answer this question. Like *P.*

466 *strigulatella*, gypsy moth populations exhibit substantial spatial variation in the relative

467 importance of rapid and delayed density dependence operating on their dynamics, likely due to

468 variation in forest composition (Liebhold et al. 2006). Importantly, the authors developed a

469 stochastic population model that included both rapid and delayed density dependence to explore

470 how variation in the form and strength of density dependence influenced synchrony among

471 disjunct populations. The authors concluded that variation in the strengths of negative feedback

472 had minimal impact on population synchrony that was generated by dispersal among

473 populations; variation in the strength of rapid density dependence could diminish synchrony that

474 was generated primarily by stochastic forcing (Liebhold et al. 2006). This suggests that our

475 populations of *P. strigulatella* may retain synchrony across space primarily through dispersal

476 mechanisms rather than stochastic forcing. It has also been suggested that the dispersal of

477 predators can maintain synchrony among sites (Bjornstad et al. 1999b); unfortunately, we lack

478 data to compare the potential importance of dispersal by *P. strigulatella* or its enemies on

479 population synchrony.

480

481 Although the spatial variation in negative feedback processes among our *P. strigulatella*

482 populations was insufficient to influence gross dynamics (i.e. all populations were cyclic),

483 effects are much stronger in some other systems. For example, populations of gray-sided voles,

484 *Clethrionomys rufocanus*, in Japan suffer increases in the strength of delayed density dependence

485 in northern sites where winters are long, which causes those populations to exhibit cyclic

486 dynamics (Stenseth et al. 2003). In that example, spatial variation in the strength of predation

487 during winter months drives differential dynamics among sites, and we suggest that similar

488 patterns may occur near some larger polluters.

489

490   Although delayed density dependence operated at most of our study sites, its relative importance

491   for population dynamics declined with distance from the power plant (Fig. 4a) in concert with

492   declines in leafminer mortality from unknown causes (Fig. 4b). When insects that feed within

493   their host plants die from unknown causes prior to completing their development, authors often

494   invoke the operation of plant antibiosis (induced plant defence, poor nutritional quality) as a

495   contributing factor (Haukioja 1974; Connor et al. 1994; Price & Hunter 2005. We therefore

496   suggest that the delayed density dependent force that declined with distance from the polluter

497   could have been plant-mediated. However, the possibility remains that other hidden sources of

498   mortality, such pathogen attack, may have generated the delayed density dependence that we

499   observed. For example, in some small mammal and insect populations, the switch from stable to

500   cyclic dynamics with increasing latitude is associated with a relative increase in the role of

501   specialist predators at higher latitudes, which induce delayed density dependence (Turchin &

502   Hanski 1997; Klemola et al. 2002; Stenseth et al. 2003).

503

504   The climate of our study region has changed rapidly over the past decades. The annual surface

505   air temperature in the Kola Peninsula has increased by 2.3°C over the past 50 years, due to

506   warming in spring and fall. Furthermore, springs are wetter and falls are drier than before

507   (Marshall et al. 2016). Predictions suggest that increasing temperatures will cause larger

508   increases in herbivory than in plant productivity (Ayres & Lombardero 2000; O'Connor et al.

509   2009; DeLucia et al. 2012), thereby increasing overall plant damage by insects. Studies

510   conducted along latitudinal climatic gradients predict that increases in herbivory will be greater

511   at high latitudes than at low latitudes (Kozlov et al. 2015a,b). However, contrary to expectations,

512   rising temperatures in our study region have not caused significant increases in the population

513   density of *P. strigulatella* (Fig. 1) and we observed no correlation between leafminer density and

514   the PCA w1 axis for climate change. This result is consistent with the absence of positive effects

515   of climate warming on willow- and birch-feeding insects in the Kola Peninsula (Zvereva et al.

516   2016; Kozlov et al. 2017). It is also consistent with the general absence of changes in foliar

517   losses of temperate woody plants to insects in natural ecosystems between 1952 and 2013

518   (Kozlov & Zvereva 2015).

519

520   Pollution imposes substantial environmental stress on organisms including birds (Radhouani et al.

521   2012; Morelli et al. 2018), insects (Butler & Trumble 2008; Bonisoli-Alquati et al. 2018), and

522   mammals (Fritsch et al. 2010; Drouhot et al. 2014). Our data confirm that effects of pollution on

523   animal population dynamics can be stronger than those of climate change (Zvereva *et al.* 2016),

524   and highlight the importance of studying pollution as an integral component of global change

525   research (Sun & Zhou 2002; Batty & Hallberg 2010). By understanding how different density

526   dependent processes respond to pollution load, we may be better able to predict population

527   change, and manage species of economic and cultural importance. Finally, we note that pollution

528   research can provide fundamental insights of general importance to population dynamics theory,

529   by explaining temporal variation (Zvereva *et al.* 2016) and spatial variation (data presented here)

530   in the relative strengths of negative feedback processes.

531

532   **Data Accessibility**

533   Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sn0cn43

534   (Hunter & Kozlov 2018).

535

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546

547   **References**

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745

746

747   **Figure Legends**

748   Figure 1. (A) Synchronous population dynamics of the leafmining moth, *Phyllonorycter*

749   *strigulatella*, over 26 years at 14 study sites around a coal fired power plant near Apatity,

750   northwestern Russia. Densities are the average number of leafmines per 25 leaves (N = 10 trees

751   per site). (B-O) Average leafminer densities (natural log scale) at each of the 14 study sites,

752   ordered by increasing distance from the power plant. E and W refer to sites east and west of the

753   power plant, while horizontal lines represent mean densities at each site.

754

755   Figure 2. (A) Temporal declines in pollution emissions from a coal fired power plant near

756   Apatity, northwestern Russia (the insert illustrates the PCA-axis that combines all three

757   pollutants). Data were log-transformed prior to analysis, but are shown here in raw form. (B) The

758   relationship between pollution load (PCA-axis) and the density of the leafmining moth,

759   *Phyllonorycter strigulatella*, averaged across 14 study sites. Each point represents a single year.

760   (C) Average leafminer densities (log scale) did not decline systematically over the course of the

761   study.

762

763   Figure 3. Densities of the leafmining moth, *Phyllonorycter strigulatella*, decline with increasing

764   distance from a coal fired power plant near Apatity, northwestern Russia. Each point represents a

765   single study site, with densities averaged across 23 to 26 years of sampling. Grey symbols refer

766   to sites east of the power plant while black symbols refer to sites west of the power plant.

767

768   Figure 4. (A) Systematic changes in the strengths of rapid (diamonds) and delayed (squares)

769   density dependence operating on populations of the leafmining moth, *Phyllonorycter*

770   *strigulatella*, at 14 study sites around a coal fired power plant near Apatity, northwestern Russia.

771   In (A), the strengths of density dependence are SIMEX estimates of the slopes of regressions

772   between leafminer per capita rates of change and population densities at time t-1 (rapid) and t-2

773   (delayed), with more negative numbers representing stronger effects. (B) The effects of distance

774   from the power plant on predation (diamonds) and an unknown mortality source (squares)

775   operating on populations of *P. strigulatella*. Each point represents mortality at a single site from

776   a sample of 49 to 71 leafminers per site. Statistics refer to binomial models of proportional

777   mortality against distance. In both (A) and (B), grey symbols refer to sites east of the power plant

778   while black symbols refer to sites west of the power plant.

779

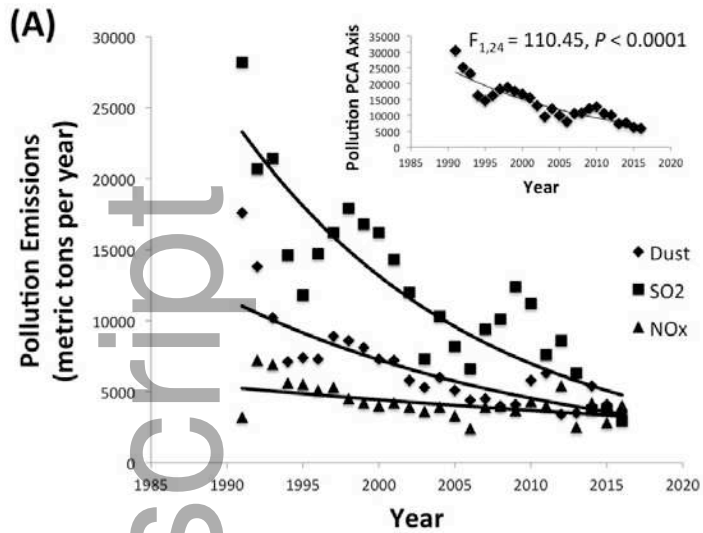780   **Figures**

781

782   Figure 1.

783

Figure 2.

(A)

(B) $F_{1,23} = 5.11$, $P = 0.033$

(C) $F_{1,24} = 2.77$, $P = 0.1037$
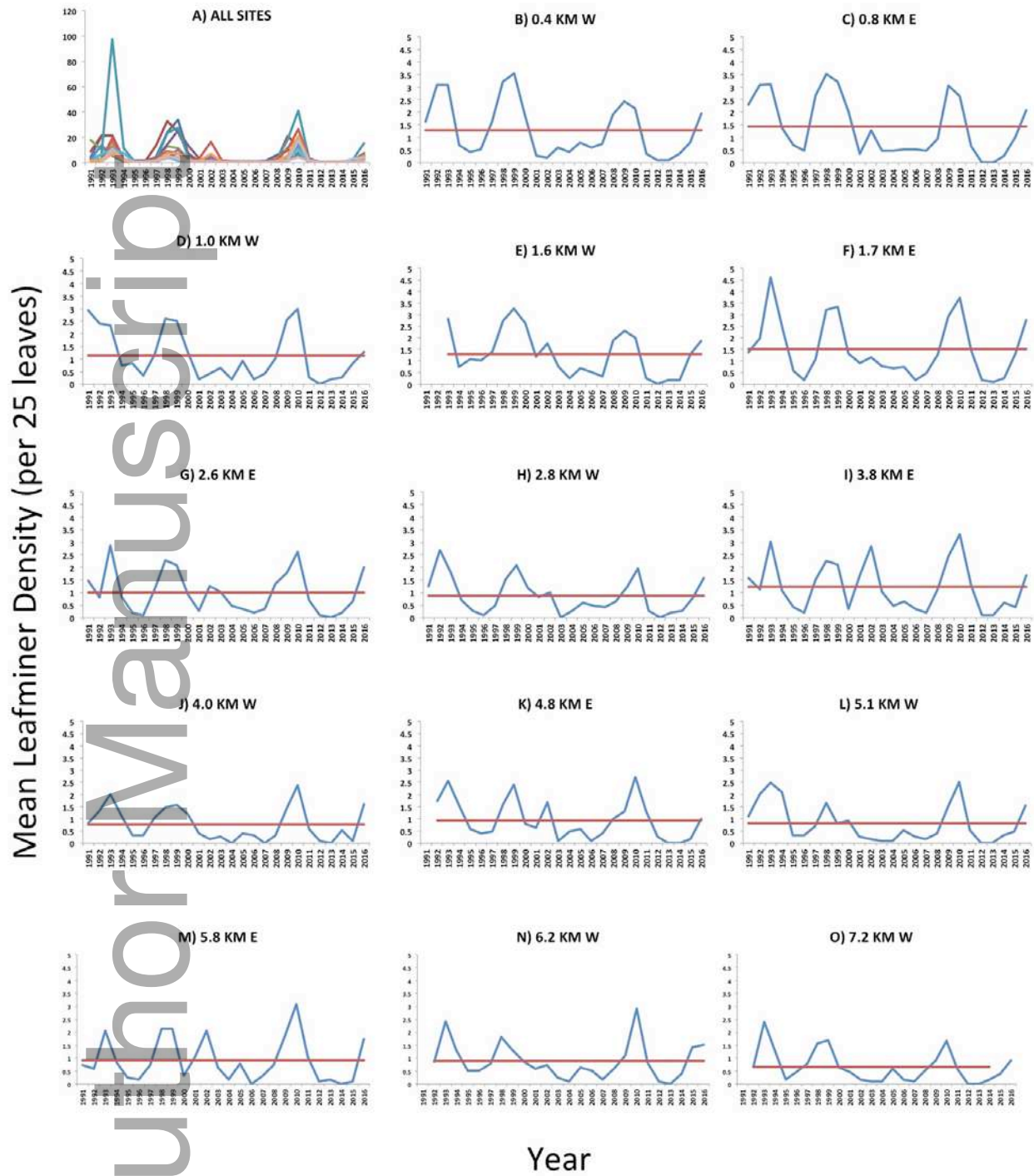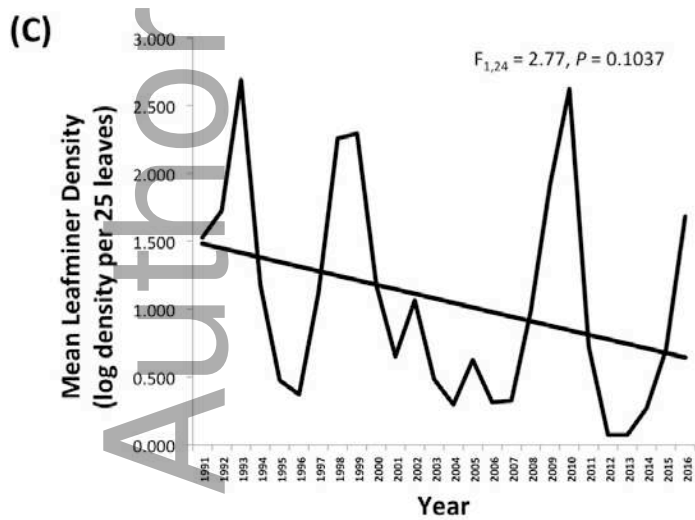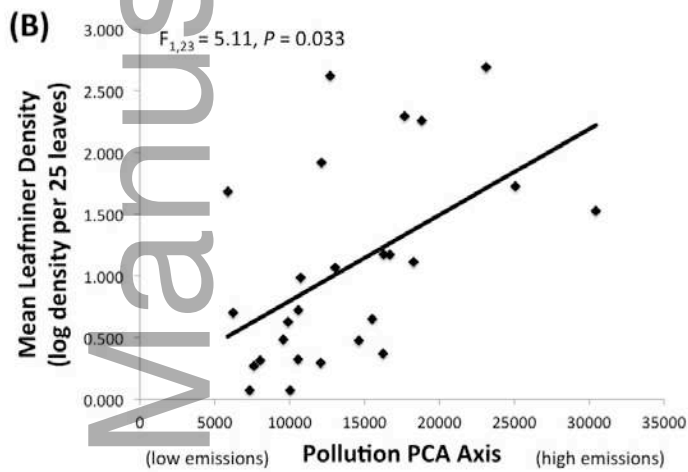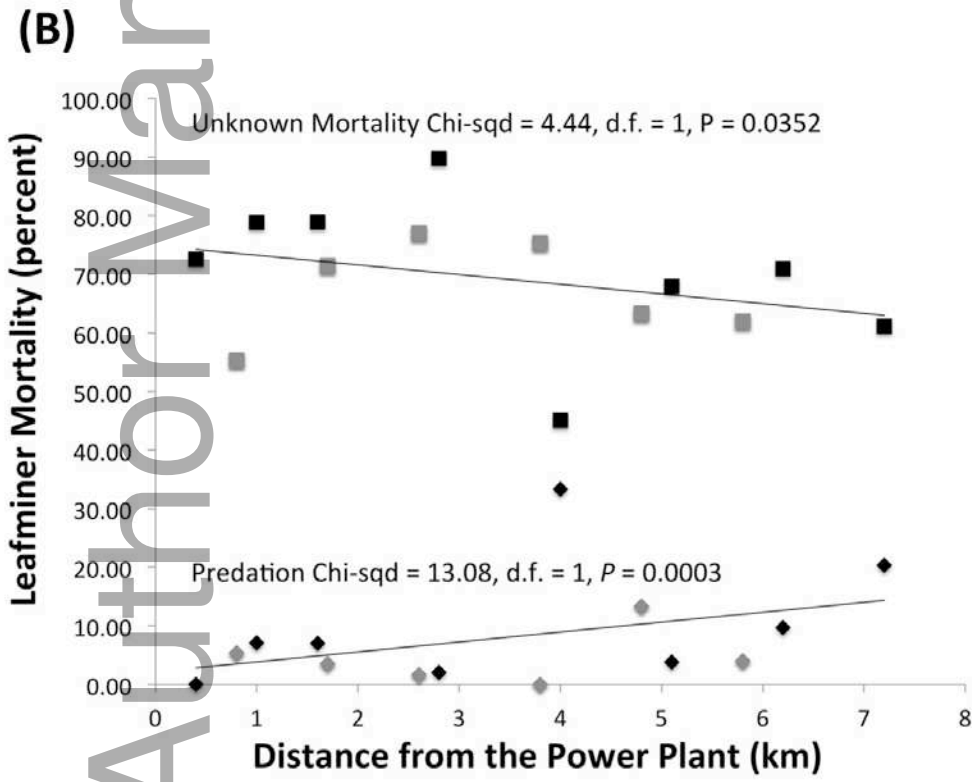
790
791
792

793   Figure 3.

794

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797

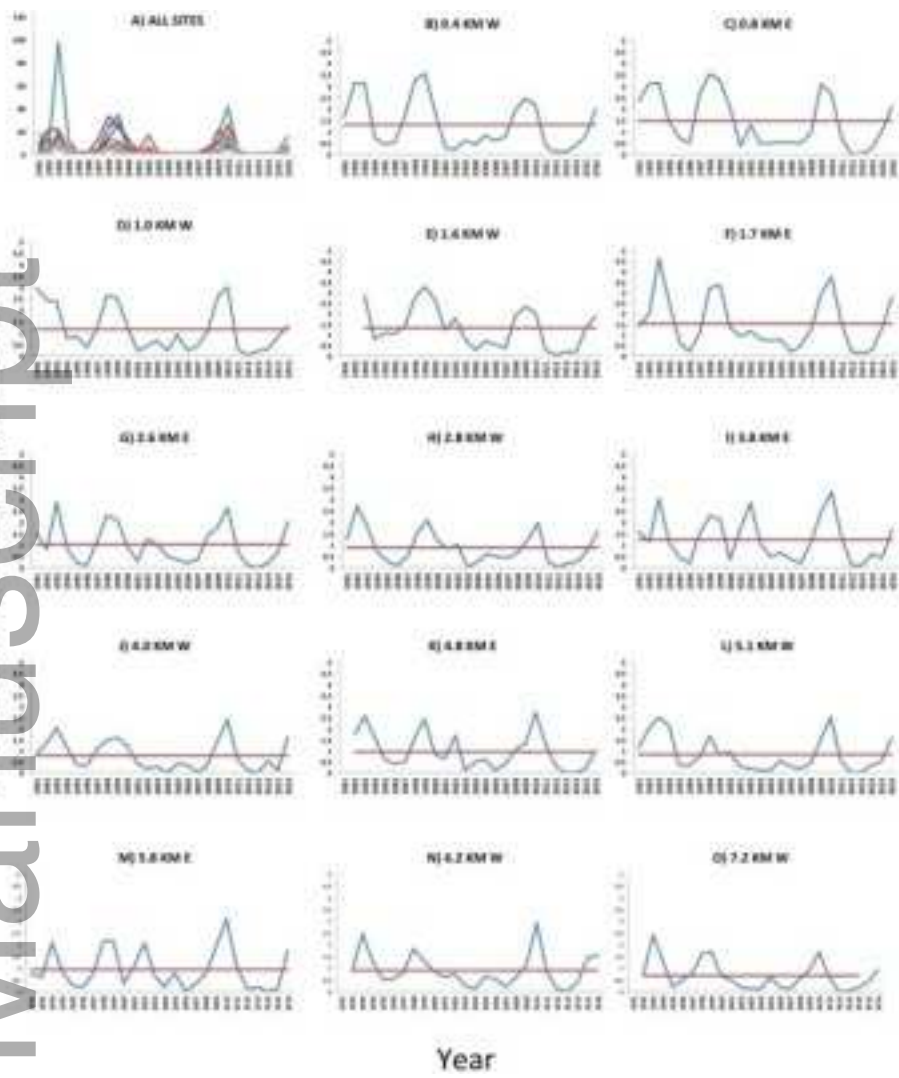$F_{1,12} = 19.76$, $P = 0.0008$
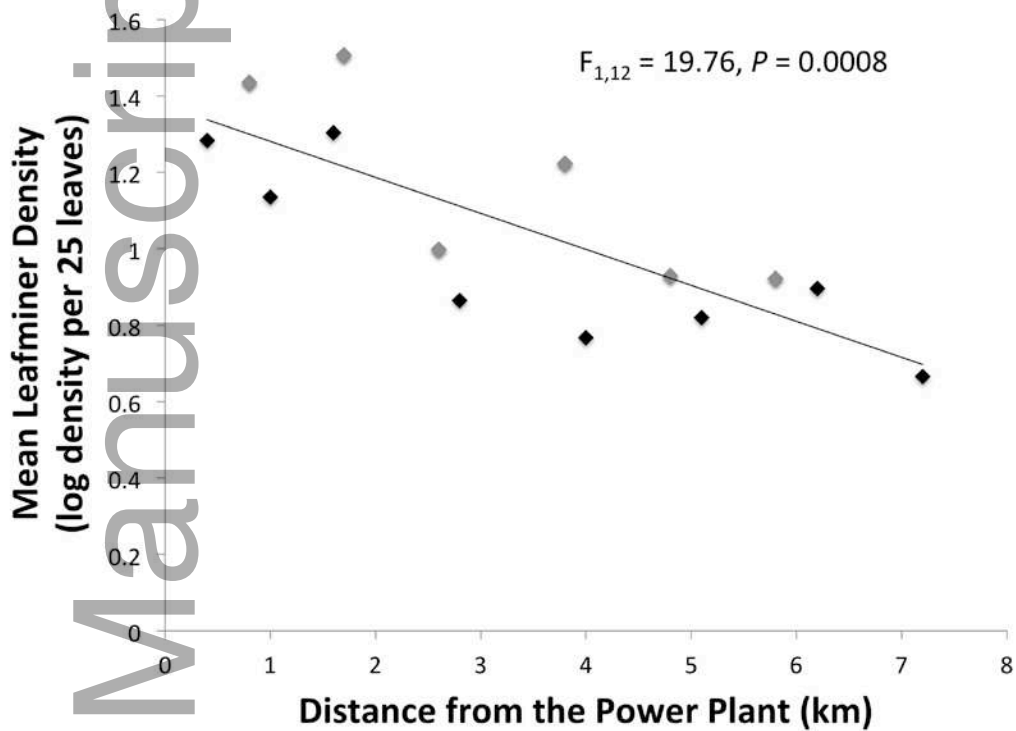
798

799

800

801   Figure 4.

802

(A) Distance from the Power Plant (km)

(B)

Unknown Mortality Chi-sqd = 4.44, d.f. = 1, P = 0.0352

Predation Chi-sqd = 13.08, d.f. = 1, P = 0.0003

803

Year
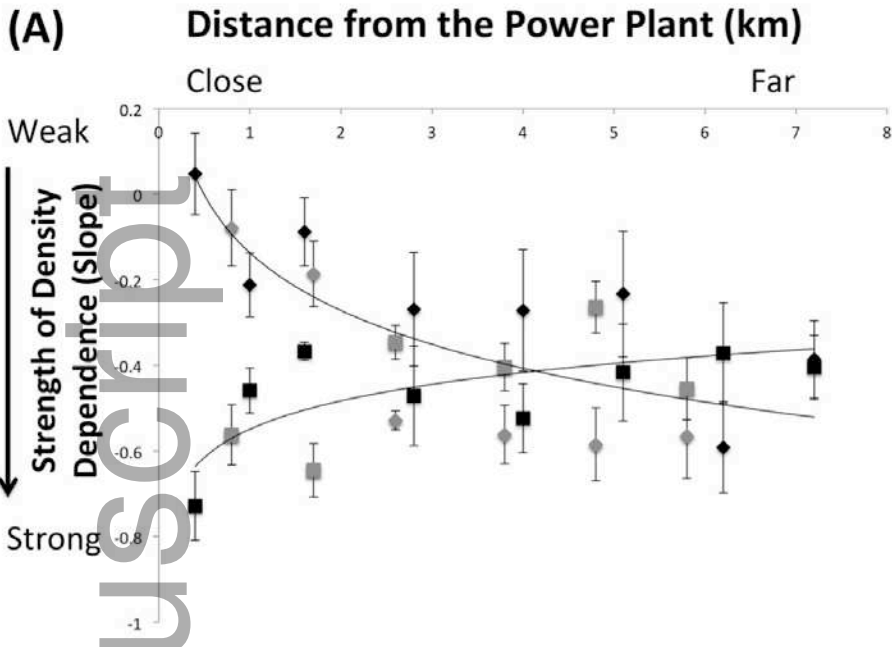
jane_12930_f1.jpeg

(A)

jane_12930_f2a.jpg

(B)

$F_{1,23} = 5.11$, $P = 0.033$

Mean Leafminer Density (log density per 25 leaves)

Pollution PCA Axis

(low emissions)

(high emissions)
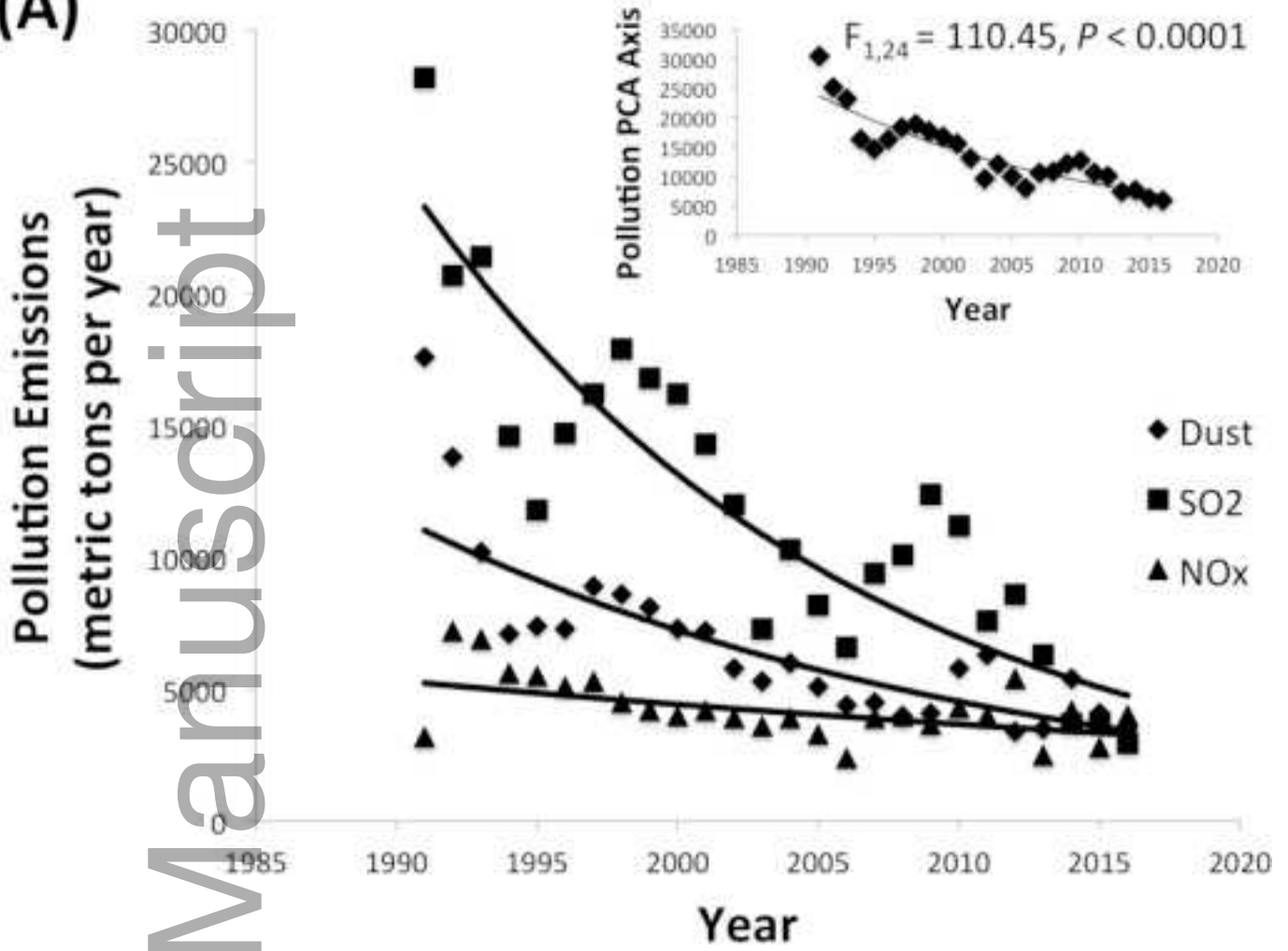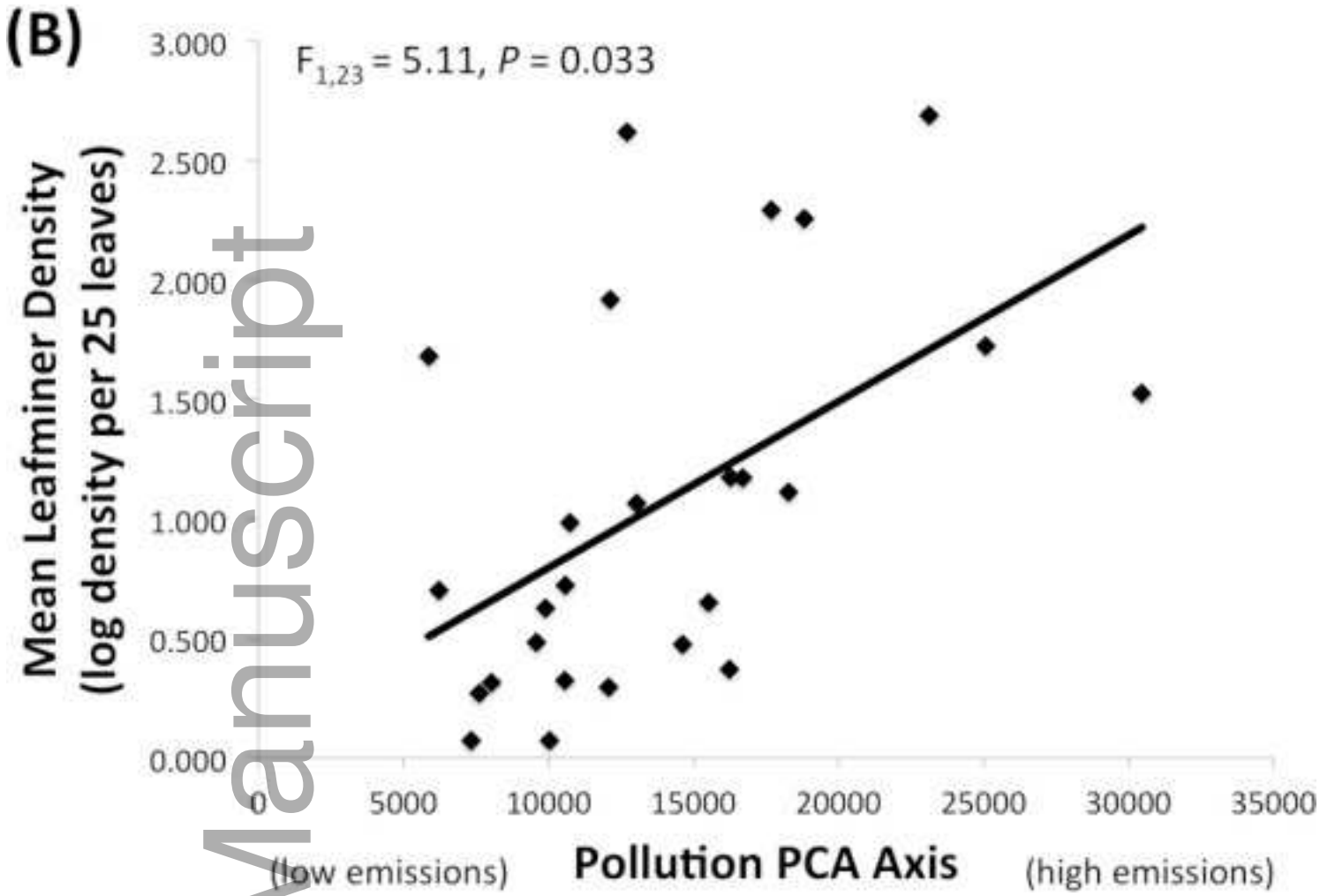
jane_12930_f2b.jpg

(C)

jane_12930_f2c.jpg

$F_{1,12} = 19.76$, $P = 0.0008$
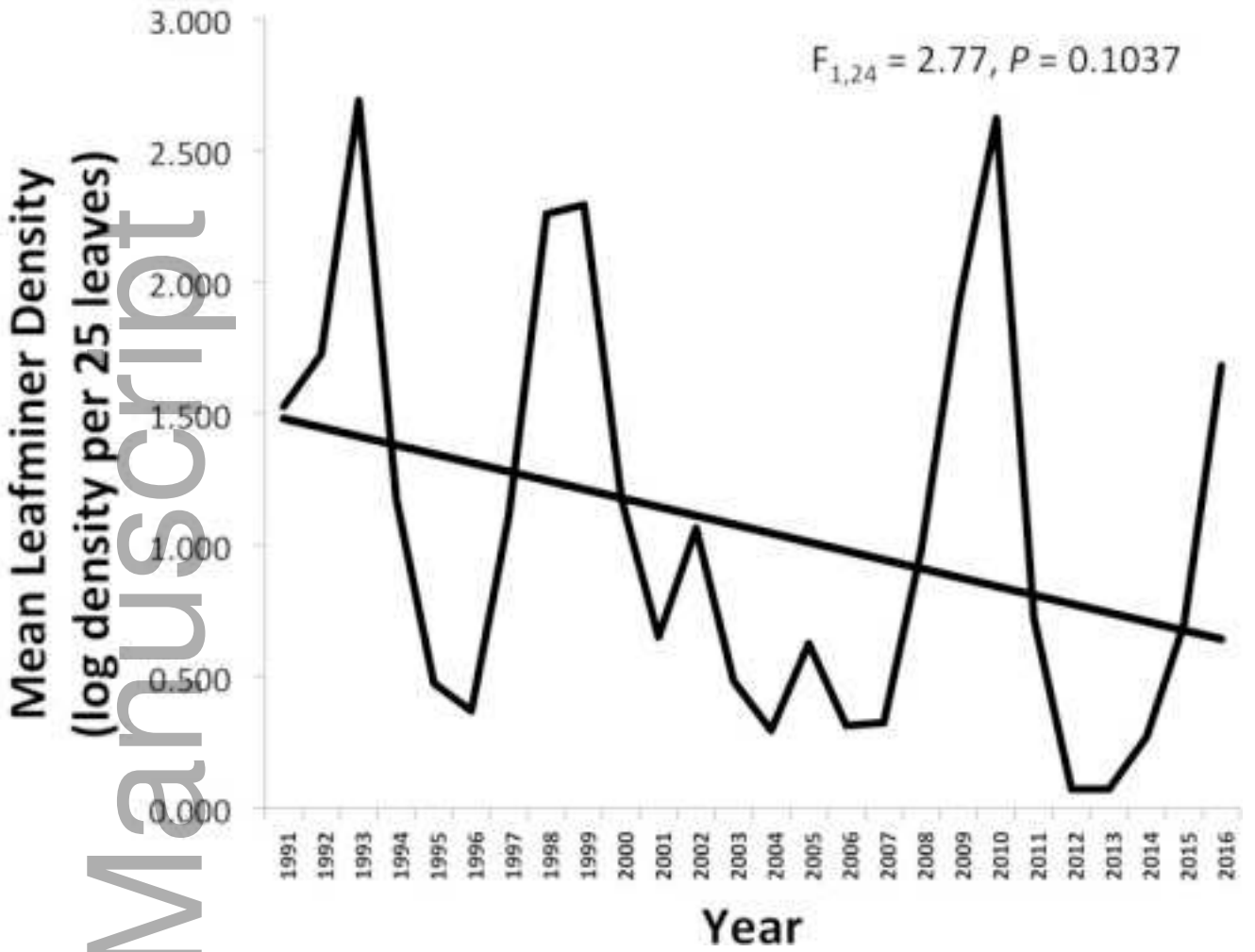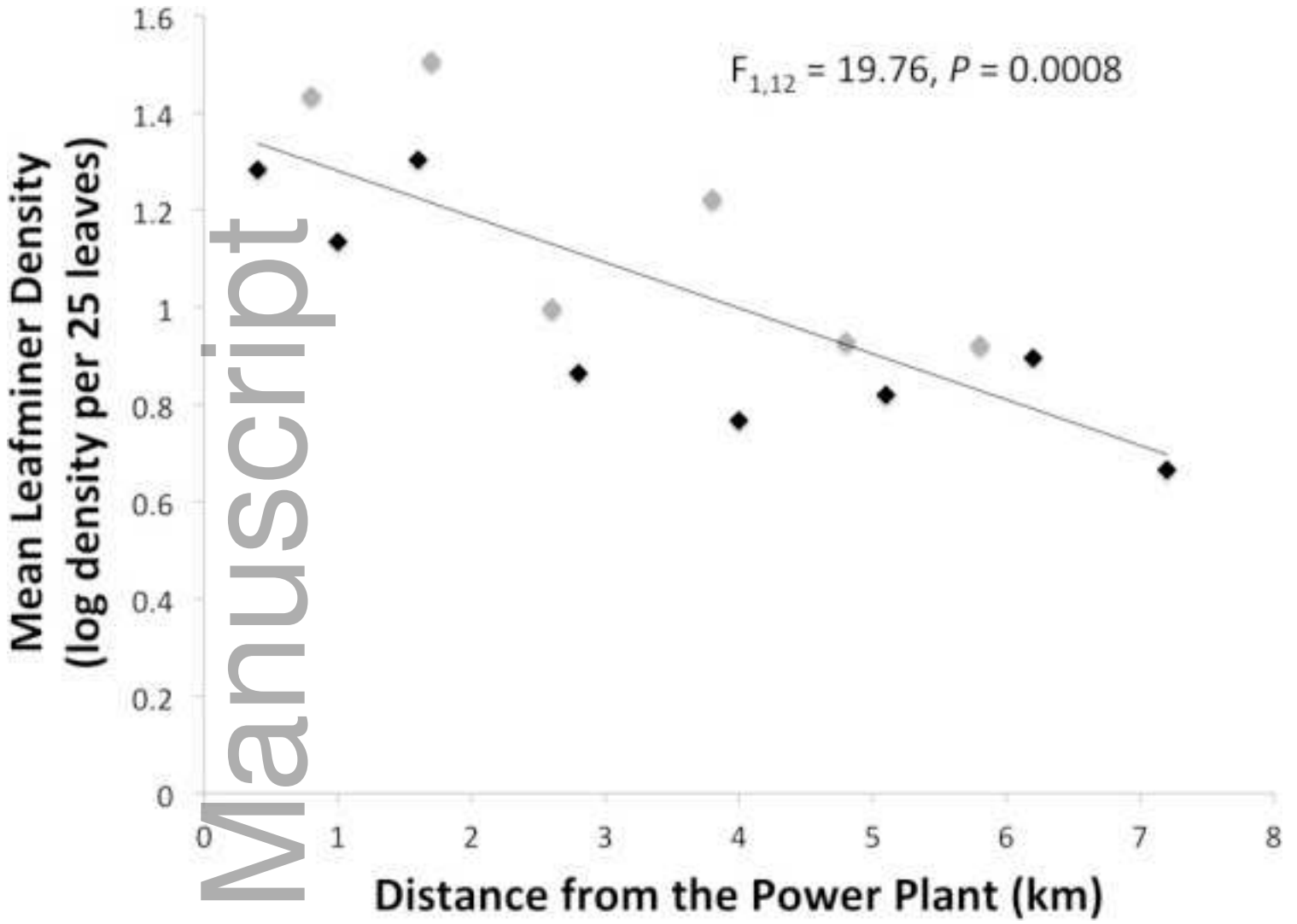
jane_12930_f3.jpg

(A) Distance from the Power Plant (km)
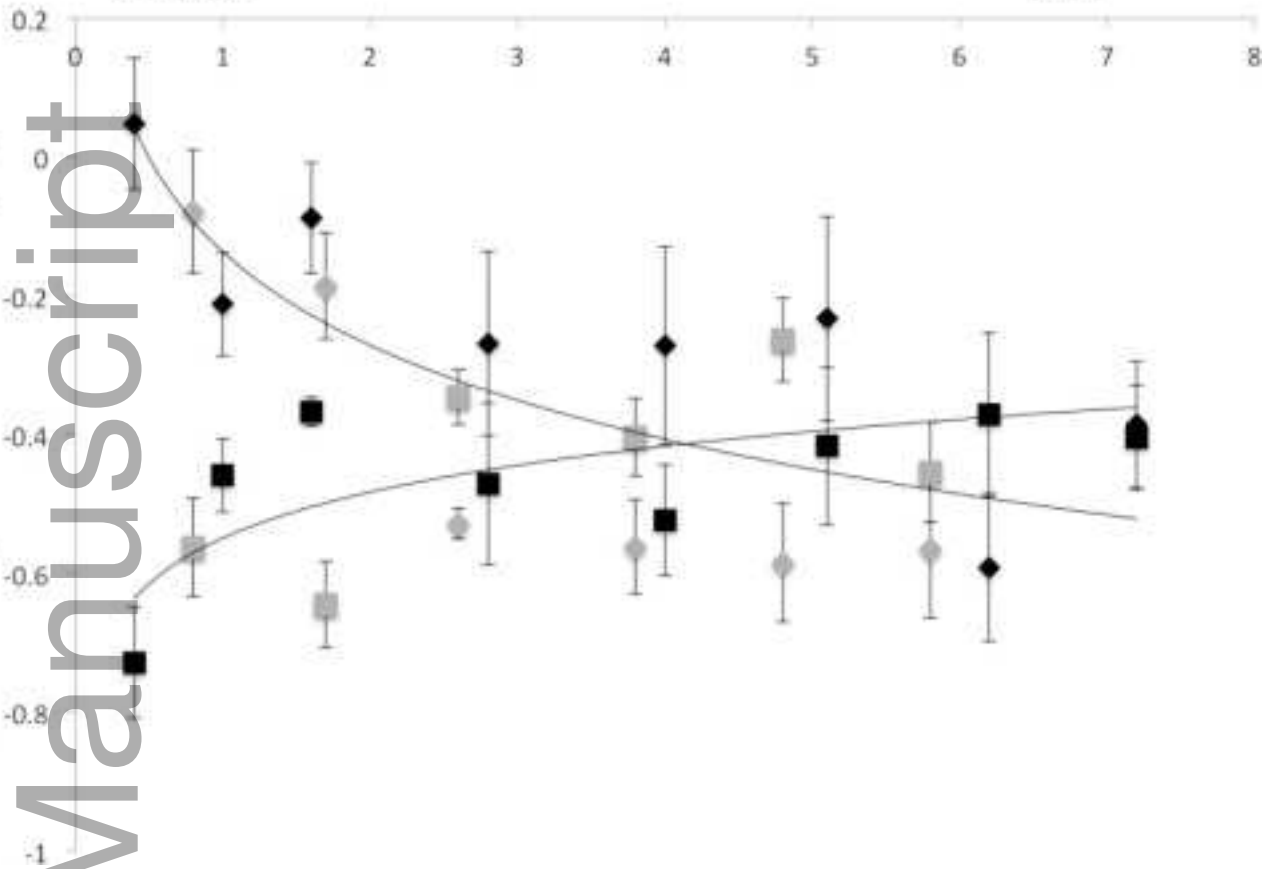
jane_12930_f4a.jpg

jane_12930_f4b.jpg