Year: 2016

Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters

Concepción, Elena D ; Obrist, Martin K ; Moretti, Marco ; Altermatt, Florian ; Baur, Bruno ; Nobis, Michael P

Abstract: Urban growth is a major factor of global environmental change and has important impacts on biodiversity, such as changes in species composition and biotic homogenization. Most previous studies have focused on effects of urban area as a general measure of urbanization, and on few or single taxa. Here, we analyzed the impacts of the different components of urban sprawl (i.e., scattered and widespread urban growth) on species richness of a variety of taxonomic groups covering mosses, vascular plants, gastropods, butterflies, and birds at the habitat and landscape scales. Besides urban area, we considered the average age, imperviousness, and dispersion degree of urban area, along with human population density, to disentangle the effects of the different components of urban sprawl on biodiversity. The study was carried out in the Swiss Plateau that has undergone substantial urban sprawl in recent decades. Vascular plants and birds showed the strongest responses to urban sprawl, especially at the landscape scale, with non-native and ruderal plants proliferating and common generalist birds increasing at the expense of specialist birds as urban sprawl grew. Overall, urban area had the greatest contribution on such impacts, but additional effects of urban dispersion (i.e., increase of non-native plants) and human population density (i.e., increases of ruderal plants and common generalist birds) were found. Our findings support the hypothesis that negative impacts of urban sprawl on biodiversity can be reduced by compacting urban growth while still avoiding the formation of very densely populated areas.

1 **Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds:**

2 **not only built-up area matters**

3

4 Elena D. Concepción[1,*], Martin K. Obrist[1], Marco Moretti[1], Florian Altermatt[2,3], Bruno Baur[4],

5 Michael P. Nobis[1]

6

7 [1]WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111,

8 CH-8903 Birmensdorf, Switzerland, elena.concepcion@wsl.ch, martin.obrist@wsl.ch,

9 marco.moretti@wsl.ch, michael.nobis@wsl.ch

10 [2]Eawag: Swiss Federal Institute of Aquatic Science and Technology, Überlandstrasse

11 133,CH-8600 Dübendorf, Switzerland, florian.altermatt@eawag.ch

12 [3]Institute of Evolutionary Biology and Environmental Studies, University of Zurich

13 Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

14 [4]Section of Conservation Biology, Department of Environmental Sciences, University of

15 Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland, bruno.baur@unibas.ch

16 *Corresponding author:

17 Phone: +34 666 75 52 30. E-mail address: elenadconcepcion@gmail.com (E.D. Concepción).

18

19   **Abstract**

20   Urban growth is a major factor of global environmental change and has important impacts on

21   biodiversity, such as changes in species composition and biotic homogenization. Most

22   previous studies have focused on effects of urban area as a general measure of urbanization,

23   and on few or single taxa. Here, we analyzed the impacts of the different components of urban

24   sprawl (i.e., scattered and widespread urban growth) on species richness of a variety of

25   taxonomic groups covering mosses, vascular plants, gastropods, butterflies, and birds at the

26   habitat and landscape scales. Besides urban area, we considered the average age,

27   imperviousness, and dispersion degree of urban area, along with human population density, to

28   disentangle the effects of the different components of urban sprawl on biodiversity. The study

29   was carried out in the Swiss Plateau that has undergone substantial urban sprawl in recent

30   decades.

31   Vascular plants and birds showed the strongest responses to urban sprawl, especially at the

32   landscape scale, with non-native and ruderal plants proliferating and common generalist birds

33   increasing at the expense of specialist birds as urban sprawl grew. Overall, urban area had the

34   greatest contribution on such impacts, but additional effects of urban dispersion (i.e., increase

35   of non-native plants) and human population density (i.e., increases of ruderal plants and

36   common generalist birds) were found. Our findings support the hypothesis that negative

37   impacts of urban sprawl on biodiversity can be reduced by compacting urban growth while

38   still avoiding the formation of very densely populated areas.

39   **Key words:**

40   Built-up area; biotic homogenization; imperviousness; human population density; time-lagged

41   effects; urban dispersion.

42

Introduction

Land-use change is a central component of global change and a major threat to biodiversity (Sala et al. 2000). Urban growth is in turn an important driver of such land-use changes (Grimm et al. 2008; Elmqvist et al. 2013). The growth of urban areas worldwide was especially pronounced during the second half of the 20th century, but rapid urban expansion still continues and is expected to persist in the next decades as the world's population grows and more people live in cities (Grimm et al. 2008; Mcdonald et al. 2008; Elmqvist et al. 2013).

Species richness has frequently been found to peak at moderate levels of urban development (Rebele 1994; Niemelä 1999; Blair 1999; Crooks et al. 2004). However, not all organisms are equally affected, and the impact of urban growth may noticeably vary depending on species characteristics, such as dispersal ability, habitat specialization, or use of resources (Wood and Pullin 2002; Devictor et al. 2007). The peak in species richness at moderate urbanization levels usually results from an increase in common species adaptable to urban environments, such as early successional plants (Deutschewitz et al. 2003) or generalist animals that take advantage of high habitat heterogeneity and resource availability, as well as low competition or predation rates in urban areas (Savard et al. 2000; Crooks et al. 2004; McKinney 2008). At the same time, some species from the original communities that are sensitive to urban conditions may still survive in the remaining natural or semi-natural habitats, adding to the overall species richness (McKinney 2002, 2006, 2008).

Advanced stages of urbanization, however, usually cause a loss of native specialist in favor of a few urban exploiters, such as ruderal and non-native plants, which tolerate high levels of disturbance (Deutschewitz et al. 2003; Kühn and Klotz 2006; Nobis et al. 2009), or synanthropic animals that depend on human-subsidized resources (Crooks et al. 2004; Devictor et al. 2007). As a result, at high levels of urbanization species richness generally

68 decreases and urban biotas tend to become more and more similar – also called biotic

69 homogenization – dominated by a few common native species and some ubiquitous non-

70 native species (McKinney 2002, 2006; Clergeau et al. 2006; Lososová et al. 2012a, b; Le Viol

71 et al. 2012; Aronson et al. 2014; La Sorte et al. 2014).

72 The spatial scale at which effects of urbanization on biodiversity are analyzed has also been

73 found to be relevant, with impacts like biotic homogenization being more evident at larger

74 spatial scales, both in terms of the extent of the study area and in terms of grain size

75 (Deutschewitz et al. 2003; Kühn and Klotz 2006; La Sorte et al. 2014). However, studies have

76 traditionally focused on particular urban areas, and although some of them have compared

77 urban impacts in different cities across regions, countries, or even continents (see e.g. Pyšek

78 1993; Pyšek 1998; Aronson et al. 2014; La Sorte et al. 2014), large-scale analyses along broad

79 urbanization gradients are still scarce (Devictor et al. 2007; Lososová et al.2012a, b; Le Viol

80 et al. 2012).

81 Most previous studies analyzing urban impacts on biodiversity focused on responses of

82 organisms along urbanization gradients that typically consider increasing proportion of urban

83 area or other urban parameters, such as the degree of imperviousness (i.e., soil sealing) or

84 human population density (see McDonnell and Hahs 2008 for a review). However, most

85 studies lacked reliable measures of other components of the so-called urban sprawl (i.e.,

86 scattered and widespread urban growth; Jaeger et al. 2010). Specifically, the degree of urban

87 sprawl can be estimated with a combined measure of total urban area, intensity of urban land

88 use (e.g., population density), and degree of urban dispersion (Jaeger and Schwick 2014).

89 Besides built-up area (hereinafter referred to as 'urban area') and other characteristics of

90 urban environments, the spatial configuration of urban area, as well as natural or semi-natural

91 areas at the landscape level, may also affect biodiversity (Marzluff and Ewing 2001; Croci et

92 al. 2008; Sattler et al. 2010; Fontana et al. 2011; Latta et al. 2013). Furthermore, time lags

4

93   may occur before impacts of urban sprawl on biodiversity are apparent (Ramalho and Hobbs

94   2012). However, such delayed effects of urban development have rarely been explored (but

95   see Soga and Koike 2013).

96   Here, we present a comprehensive analysis of the effects of different components of urban

97   sprawl on species richness of various species groups in the Swiss Plateau, which represents

98   the largest biogeographic region of Switzerland (ca. 11,200 km^2) and is affected by severe

99   past and current urban sprawl (Schwick et al. 2012). Overall, we aimed to contribute to a

100   better understanding of the impacts driven by the distinct urban sprawl components on species

101   richness and to generate guidelines for biodiversity monitoring and conservation under future

102   urban development. We addressed the following specific questions: (1) Which types of

103   organisms benefit and which suffer most under urban sprawl? (2) Which attributes or

104   components of urban sprawl have the strongest impacts on species richness? And lastly, (3) at

105   which spatial scales are effects of urban sprawl on biodiversity more evident?

106   We considered five taxonomic groups (i.e., birds, butterflies, terrestrial gastropods, vascular

107   plants, and mosses) that were covered in Swiss biodiversity monitoring programs at varying

108   spatial scales from 10 m^2 (habitat level) to 1 km^2 (landscape level). We evaluated effects of

109   urban sprawl on the species richness of each taxonomic group and of distinct ecological

110   groups defined according to species characteristics that were expected to be sensitive to urban

111   development (e.g., habitat and resource specialization, commonness, dispersal ability). We

112   investigated urban effects along with other environmental variables (climate, topography, and

113   land use) that are known to affect biodiversity. In addition, we used a wide set of urban

114   predictors to disentangle relationships between different components of urban sprawl and

115   species richness. Besides urban area, which was expected to strongly affect species richness,

116   we analyzed the impact of additional urban attributes of likely influence, such as the degree of

117   imperviousness, human population density, urban dispersion, and average age of urban area.

Methods

1) Study area, species richness, and ecological groups

Our study focused on the Swiss Plateau (Fig. 1), the central part of Switzerland between the Alps and the Jura Mountains delimited according to the definition of Swiss biogeographic regions (Gonseth et al. 2001). This region has a mean altitude of 540 m a.s.l. (range: 300–940 m a.s.l.), a mean annual temperature of 8.5 °C (6.5–9.5°C), and a mean annual precipitation of 1140 mm (730–2000 mm). In the Swiss Plateau, agricultural land use predominates (around 50% area), followed by forests (24%) and urban areas (15%). Total urban area has tripled since the beginning of the 20th century, especially between 1960 and 1980 when an increase of around 50% occurred, and is still expected to grow in the future, though at lower rates (Schwick et al. 2012). We analyzed data on species richness of five taxonomic groups (mosses, vascular plants, terrestrial gastropods, butterflies, and birds) regularly collected using a systematic sampling design in the biodiversity monitoring programs of Switzerland (BDM – Biodiversity Monitoring in Switzerland Coordination Office 2009) and of the Canton of Aargau (LANAG; Kanton Aargau 1996). From the BDM program, we used species lists of all available plots in the Swiss Plateau, that is, 109 plots at the landscape level (each 1 km^2 in area; including vascular plants, butterflies, and birds; BDM Z7 indicator) and 473 circular plots at the habitat level (each 10 m^2 in area; including mosses, vascular plants, and gastropods; BDM Z9 indicator; Table 1, Fig. 1). From the LANAG program, we analyzed 436 plots at the habitat level located within the Swiss Plateau (10 m^2 plots for vascular plants and gastropods, 100 m radius-plots for birds, and 250 m transects for butterflies). From both programs, we used data of surveys performed between 2007 and 2011 (see Table A.1 for further details about sampling designs of the different biodiversity monitoring programs).

142   For each taxonomic group and monitoring program, we calculated overall species richness per

143   plot as well as species richness of a variety of ecological groups classified according to

144   species-specific characteristics that we expected to influence species' responses to urban

145   sprawl. Species characteristics were morphological, physiological, or phenological features

146   (functional traits sensu Violle et al. 2007), such as dispersal ability, growth form, and resource

147   use (e.g., diet, habitat use and specialization). Species were additionally classified according

148   to their commonness or rarity (calculated as frequency of occurrence in the dataset), and in

149   the case of vascular plants as native and non-native species. We further classified non-native

150   vascular plant species according to time of introduction (archeophytes and neophytes, i.e.,

151   species introduced in Switzerland by humans before or after 1500 A.D.). Resource range and

152   habitat requirements were used to classify species as specialists or generalists (for a detailed

153   description of species characteristics and classification see Table A.2). To explicitly test for a

154   qualitative shift in species composition along the urbanization gradient, we calculated ratios

155   of generalist to specialist species, very common to rare species, and native to non-native plant

156   species. Threatened species according to Swiss Red Lists were also considered.

157

158   2) <u>Urban sprawl data</u>

159   To describe urban sprawl, we calculated a set of explanatory variables at the different plot

160   scales of the distinct biodiversity monitoring programs (see Table 1 for details). As urban

161   variables, we used urban area (defined as built-up area, i.e., houses, industries, roads, and

162   other infrastructures, but also gardens, parks, and other recreational areas), degree of

163   imperviousness (i.e., soil-sealing), average age of urban area (considered over a period of 125

164   years, i.e. 1885–2010), human population density (number of inhabitants per area), and the

165   spatial dispersion of urban areas. This last variable was quantified using the mean proximity

166   index of urban areas (MPI, with low MPI values meaning high urban dispersion) for larger

167　plot sizes, or the nearest distance to urban areas in the case of the small plots at the habitat

168　level. Overall, we investigated urban sprawl impacts along a broad urbanization gradient,

169　which covers a range from 0% up to 66% of urban area at the landscape scale (see Table 2 for

170　a detailed description of urban sprawl variables).

171　We also used other environmental predictors known to affect biodiversity, like climatic,

172　topographic, and additional land use variables (see e.g. Blair 1999; Wood and Pullin 2002;

173　Nobis et al. 2009; Lososová et al. 2012a), which were calculated at the same spatial scale as

174　species richness data to control for possible confounding effects (see Tables 1 and 2 for

175　details).

176　3)　Data analyses

177　We followed a hierarchical approach to analyze the relationships between urban sprawl and

178　species richness. In a first step, we compared the overall importance of all urban versus all

179　non-urban predictors to explain the variability in species richness for the different taxonomic

180　and ecological groups. Second, for those groups for which urban predictors explained a

181　substantial amount of variability, independently from non-urban predictors, we looked at the

182　effects of individual urban predictors.

183　For the first step, we performed generalized linear models (GLMs) with species richness of

184　the different taxonomic and ecological groups as response and a Poisson error distribution for

185　count data. For the ratios of generalist to specialist species, very common to rare species, and

186　non-native to native plant species, we applied GLMs with a normal distribution of errors. We

187　used two sets of predictors: (1) all urban variables and (2) all environmental variables other

188　than urban ones (Tables 1 and 2). Pearson's product-moment correlations between single

189　predictors were all below 0.8. To control for possible bias caused by collinearity, we

190　compared results of models both excluding and including human population density, the only

8

191   predictor that showed noticeable correlations with other urban predictors ($0.8 \geq r \geq 0.7$;

192   Dormann et al. 2013). Linear and quadratic terms of urban predictors were included in models

193   to account for possible non-linear effects. For every response variable, we then calculated the

194   percentage of null deviance explained by full models (i.e., including the whole set of urban

195   and non-urban predictors; D^2_{full}), the percentage of null deviance (D^2) explained by the two

196   sets of environmental predictors independently ($D^2_{I.Urban}$ and $D^2_{I.Non-urban}$), as well as their joint

197   contribution to deviance explanation (D^2_J).

198   In a second step, we examined the individual effects of urban predictors on species richness

199   for those taxonomic and ecological groups that were substantially affected by urban

200   predictors, independent from non-urban predictors ($D^2_{I.Urban} \geq 15\%$). We selected this

201   threshold because it coincided with significant effects ($p \leq 0.05$) of single urban predictors

202   included in full models. We used multi-model inference based on model averaging in order to

203   calculate more robust estimates of the coefficients of urban predictors (Burnham and

204   Anderson 2002). For each response variable, we performed GLMs with all possible

205   combinations of predictors (including both urban and other environmental variables) and

206   ranked them according to the second-order Akaike's information criterion (AICc), or its

207   quasi-likelihood counterpart (QAICc) in cases where over-dispersion occurred. We then

208   selected the most plausible models according to these criteria (delta AICc or QAICc ≤ 4) and

209   calculated averaged parameter estimates using Akaike's weights. To assess the relative

210   contribution of each urban predictor to the overall effects of urban sprawl on species richness,

211   we calculated the relative variable importance (RVI), that is, the sum of Akaike weights that

212   measures the overall likelihood of the selected models in which the parameter of interest

213   appears. RVI values range from 0 (for predictors excluded in all selected models) to 1 (for

214   predictors included in all selected models; Burnham and Anderson 2002). Finally, we used

215   partial residual plots of best-fit models (AIC-based) to graphically illustrate and explore the

216   direction of significant relationships between distinct urban predictors and species richness.

217   Partial residuals plots of models represent relationships between response variables and an

218   explanatory variable of interest once the effects of all the other predictors have been

219   accounted for.

220   All statistical analyses were done in R 3.0.2 (R Core Team 2014), using the package MuMIn

221   (Bartón 2013) for model averaging. Urban and non-urban predictors were calculated using the

222   R package raster (Hijmans 2015), as well as ArcGIS and its extension Patch Analyst (ESRI

223   2011).

224

225   **Results**

226   Urban predictors explained together and independently of other environmental predictors a

227   substantial proportion of the variability ($D^2_{I.Urban} \geq 15\%$) in species richness of distinct

228   ecological groups of vascular plants and birds. For these groups urban predictors were slightly

229   more relevant than the other environmental variables (23% $D^2_{I.Urban}$ and 20% $D^2_{I.Non-urban}$ on

230   average; see Table 3 for details). These responses were found almost exclusively at the

231   landscape level (BDM Z7; with 16 responding groups out of 80), with only a few groups of

232   bird species being affected also at the habitat level (LANAG; 3 responding groups out of 82).

233   All these species groups showed significant responses to specific urban predictors (Table 3;

234   for additional details see Tables A.3 and A.4).

235   Urban area had on average the highest relative variable importance (RVI), followed by human

236   population density, degree of urban dispersion (i.e., mean proximity index of urban areas

237   [MPI] or nearest distance to urban areas), degree of imperviousness, and average age of urban

238   areas (Table 3, Fig. 2). Models excluding human population density as a predictor to control

239 for slight collinearity with other predictors showed consistent results for the remaining urban

240 variables, and therefore we only present the models including the complete set of predictors.

241 For vascular plants, partial regression plots showed along the gradient of increasing urban

242 area a considerable increase in species richness of non-natives, in particular neophytes (Table

243 3, Fig. 3a), specific growth forms (phanerophytes and chamaephytes), and human-dispersed

244 (anthropochorous) plants. In addition, species richness of plants inhabiting eutrophic habitats

245 (Fig. 3b), non-native, habitat specialist, and annual (therophytes) plants increased together

246 with human population density. The degree of urban dispersion had additional positive effects

247 on the ratio between non-native and native plant species and on the species richness of

248 neophytes, phanerophytes, and chamaephytes (i.e., negative effects of MPI; Table 3 and Fig.

249 3c). Last, the degree of imperviousness of urban areas mostly increased species richness of

250 highly dispersive and wind-dispersed (anemochorous) plants (Table 3 and Fig. 3d).

251 Among birds, species groups showing responses relevant to urban sprawl variables were

252 urban, zoophagous, ground breeding, and breeding generalist birds as well as the ratio of

253 breeding generalist to specialist birds. All these groups showed positive responses to urban

254 area and human population density, except ground breeding birds whose species richness

255 significantly decreased with the amount of urban area (see Fig. 4 for examples of the most

256 relevant effects of these variables on birds). When considered at the habitat level, species

257 richness of zoophagous and urban birds and the ratio of breeding generalist to specialist birds

258 significantly decreased as the nearest distance to urban areas increased, whereas the ratio of

259 breeding generalists to specialists increased with the average age of urban areas (Table 3).

260 Species richness of all other ecological and taxonomic groups (i.e., mosses, gastropods and

261 butterflies), including endangered species of the different taxa, showed only weak ($D^2_{I.Urban}$ <

262 15 %) or non-significant responses to urban sprawl variables, and were more strongly affected

263   by non-urban variables (7% $D^2_{I.Urban}$ and 15% $D^2_{I.Non-urban}$ on average; see Tables A.3 and A.4

264   for details).

265

266   **Discussion**

267   Overall, our study showed important impacts of urban sprawl on species richness of distinct

268   taxonomic and ecological groups. As we hypothesized, these impacts considerably varied

269   depending on the species groups, urban sprawl components and spatial scales considered.

270   1) <u>Taxonomic and ecological groups</u>

271   Time of introduction, dispersal mode, growth form and habitat specialization were the species

272   characteristics that mainly affected the responses of plant species richness to urban sprawl.

273   Non-native species, especially neophytes, benefitted most from urban sprawl, which confirms

274   results of previous studies for our study area (Kühn and Klotz 2006; Nobis et al. 2009;

275   Lososová et al. 2012a).

276   Species richness of plants inhabiting eutrophic places, as well as annual, highly dispersive,

277   wind- and human dispersed plants, also benefitted from urban sprawl (see e.g. Knapp et al.

278   2009). These results are in line with previous findings revealing that native common

279   generalists still predominate in most urban areas (Lososová et al. 2012a, b; Schmidt et al.

280   2013; Aronson et al. 2014).

281   Habitat specialist plants also benefitted from intermediate levels of urbanization covered in

282   our study, probably because of the wide variety of habitats and more extreme environmental

283   conditions in urban areas (Rebele 1994; Niemelä 1999). According to our definition (Table

284   A.2), this group of plants consists of species with narrow ranges of habitat preferences, that is,

285   preferring habitat extremes with respect to temperature, continentality, light, or moisture, pH,

286   nutrients, humus, or aeration of soils. Valued species like native specialist or endangered

12

287   species are still known to inhabit less-disturbed urban sites (e.g. Kühn and Klotz 2006; Sattler

288   et al. 2010; Fontana et al. 2011; Lososová et al. 2012a; Schmidt et al. 2013). However, we did

289   not find significant responses of these valued species to urban sprawl, likely because they are

290   affected by factors related to local habitat characteristics that were not included in our set of

291   predictors. Likewise, specialist species from rare natural habitats are hardly covered in the

292   distinct biodiversity monitoring programs used in this study, given the broad extension they

293   cover and their regular sampling designs. In addition, whereas colonization by highly

294   dispersive species may more directly track environmental change caused by urban sprawl,

295   species that are negatively affected by urban sprawl may show less clear or direct responses

296   due to the delay in the manifestation of such effects in species richness (i.e., extinction debt;

297   Ramalho and Hobbs 2012; Soga and Koike 2013). Therefore, the positive response of habitat

298   specialists in our study was most probably driven by species occurring in disturbed eutrophic

299   or dry habitats, such as early successional plants, rather than specialist species from rare

300   natural habitats (Knapp et al. 2009). Most habitat specialist plants in our study actually were

301   common species inhabiting eutrophic places (around 70% of species occurrences), and both

302   groups of plants in fact showed similar responses to urban sprawl, being affected most by

303   population density (i.e., intensity of urban land use).

304   Habitat specialization, together with foraging and breeding traits, also had a large influence

305   on birds' responses to urban sprawl. As expected, birds pre-defined as urban benefitted most,

306   confirming the classification developed by the Swiss Ornithological Institute

307   (http://www.vogelwarte.ch/). More interestingly, our results indicate a shift towards breeding

308   generalists, while species richness of ground breeding birds decreased as urban sprawl grew.

309   Breeding specialists, especially ground-nesting birds, tend to be highly sensitive to urban

310   development (McKinney 2002, 2006; Clergeau et al. 2006), whereas birds able to nest in

311 buildings and on other artificial substrates such as cavity and cliff nesters (e.g., swifts, doves,

312 or falcons) benefit from urban areas (Blair 1996; Savard et al. 2000; Chace and Walsh 2006).

313 Species richness of zoophagous birds was also positively affected by urban sprawl, probably

314 driven by ground foragers and aerial insectivores that benefit from the high food availability

315 and the variety of open spaces at the still moderate levels of urbanization gathered in our

316 study (Beissinger 1982; Clergeau et al. 1998; McKinney 2002, 2006; Chace and Walsh 2006).

317 According to additional data from the Swiss Ornithological Institute, the groups of birds that

318 benefitted from urban sprawl hold larger population sizes in Switzerland than those that were

319 negatively affected. Breeding generalist species have on average ca. 122,000 (± 32,000 [SE])

320 breeding pairs, whereas breeding specialists and especially ground breeding specialists in our

321 study have on average only ca. 34,000 (± 7,000) breeding pairs. Birds pre-defined as urban

322 (ca. 90,000 ± 43,000 breeding pairs) or zoophagous (ca. 64,000 ± 12,000 pairs) also exceed

323 the mean population size of the overall set of bird species in our study (ca. 62,000 ± 12,000

324 pairs). Consequently, urban sprawl clearly favored more common generalist birds at the

325 expense of less-abundant specialist species and thus tended to homogenize bird communities

326 (see e.g. Savard et al. 2000; Devictor et al. 2007).

327 Surprisingly, all species groups of mosses, gastropods, and butterflies showed only marginal

328 responses to urban sprawl in our analyses. Lack of response of these groups is probably due to

329 either spatial or temporal constraints in our study that are discussed in depth in the last section

330 of the discussion, and therefore cannot directly be interpreted as a signal of insensitivity to

331 urbanization of these species groups.

332 2) Components of urban sprawl

333　As expected, urban area had the largest effects, but the other components of urban sprawl also

334　had a great influence. Besides urban area, relevant changes in species richness were also

335　driven by human population density and the degree of urban dispersion.

336　Human population density in urban areas can be related to the intensity of urban land use and

337　was positively related to groups of birds that are more tolerant of human disturbances. These

338　groups include common generalists with respect to both breeding and foraging requirements,

339　in contrast to more sensitive and specialist species (Blair 1996; Clergeau et al. 1998; Savard et

340　al. 2000; McKinney 2002, 2006). For plants, increased human population density mostly

341　favored species associated with eutrophic habitats. Likewise, degree of imperviousness,

342　which is related to the extent of modification of the previous habitats, favored highly

343　dispersive and wind-dispersed plant species. These species thus tend to occur in intensively

344　used (i.e., human-populated) or altered (i.e., impervious) urban sites and take advantage of

345　modified urban habitats that are maintained at early successional stages by recurrent urban

346　disturbances (Deutschewitz et al. 2003; Kühn and Klotz 2006; Nobis et al. 2009; Lososová et

347　al. 2012a, b).

348　The spatial configuration of urban areas also had relevant effects on species richness.

349　Increased urban dispersion (measured as mean proximity index [MPI] of urban area) mostly

350　favored the proliferation of non-native plant species, in particular neophytes. Neophytes tend

351　to proliferate in highly dispersed urban areas probably because these regions offer more

352　opportunities for species spread, with the consequent risk of dispersal into rural or semi-

353　natural areas.

354　With respect to the temporal component of urban sprawl, increased age of urban areas

355　augmented the ratio of breeding generalist to specialist birds at the habitat level. Despite

356　possible effects of building typology and structure related to the age of urban areas, this result

357　might indicate a time lag in the shift from breeding specialists to generalists related to urban

358   sprawl. Longer (i.e., more delayed) time-lagged effects of urbanization are usually expected

359   for organisms with lower turnover rates, such as birds or perennial plants, compared to short-

360   lived organisms like annual plants (Ramalho and Hobbs 2012; Soga and Koike 2013). Our

361   results partially support this postulate since birds behaved as expected, but we only found

362   marginally significant age-related effects for perennial plants.

363   3) <u>Spatial scales and constraints</u>

364   Most effects of urban sprawl on species richness were found at the landscape scale, and only a

365   few groups of birds significantly responded at the habitat scale, demonstrating that larger

366   spatial scales are more appropriate for monitoring impacts of urban sprawl on biodiversity.

367   This is probably due to the small size of plots at the habitat level, especially the 10 m^2 plots,

368   where factors related to local habitat characteristics or land-use intensity and history might be

369   more important than our set of urban predictors, which describe a process occurring at the

370   landscape level. Species groups that showed strong responses at the landscape level, like

371   vascular plants, exhibited no clear responses at the habitat level at all. Hence, the lack of

372   responses of those taxonomic groups that were exclusively surveyed at the habitat level (i.e.,

373   mosses and gastropods) may be partly due to the unsuitability of this spatial scale to explore

374   impacts of urban sprawl. This is supported by the fact that birds that were surveyed at a larger

375   habitat scale (3.14 ha plots) in the Canton of Aargau (LANAG) responded similarly to those

376   sampled at the landscape scale (BDM Z7). Together with the typically large home ranges of

377   birds, this finding suggests that responses of birds at the habitat level also reflect what occurs

378   in the surrounding landscape (see e.g. Chace and Walsh 2006).

379   The absence of a significant impact of urban sprawl for some groups of organisms (mosses,

380   gastropods, butterflies, or endangered species), however, might also be due to strong declines

381   in species richness of these groups between 1950 to 1980 due to large-scale changes and

382   intensification of land uses in our study region (Lachat et al. 2010). Hence, past large-scale

declines of these taxonomic groups are likely to be masking potential urbanization signals in the present. Specifically in the case of butterflies, we did not find clear responses to urban variables at the landscape or at the habitat level. These results contradict previous studies that have found this taxon to be highly sensitive to the loss of natural and semi-natural habitats due to the expansion of urban areas and intensive agriculture (e.g. Blair 1999; Wood and Pullin 2002; Stefanescu et al. 2004; Altermatt 2012; Casner et al. 2014). However, contemporary levels of butterfly species richness in our study region are likely so low that no further urbanization impacts are detectable. Mean species richness of butterflies per plot in our dataset (22.4 species in landscape plots) was indeed lower than for those groups that markedly responded to urban sprawl (i.e., plants and birds, with 248.4 and 40.2 species per plot, respectively).

Meta-community dynamics of butterflies that move across dispersed patches of suitable habitat in the landscape are probably influencing their responses to urban sprawl as well, so that urban impacts may only be evident at even larger spatial scales than those considered in our study (1 km^2). Most studies showing urban impacts on butterfly diversity actually measured urbanization levels in large areas around the sites where diversity data were gathered (e.g., 5–10 km radius buffers; Stefanescu et al. 2004; Casner et al. 2014).

Lastly, due to the fact that our study did not cover a whole urban gradient our survey, reaching only maxima of 66% urban area at the landscape scale (see Table A.5 for details), impacts of urban sprawl on species richness at the end of the urban gradient (i.e., completely urbanized areas) were not explored and may have been unnoticed. Nevertheless, our approach allowed us to investigate the impacts of urban sprawl in the transition from rural to urban landscapes, where most relevant impacts on biodiversity are expected to occur (Miller and Hobbs 2002; Mcdonald et al. 2008). The absence of response of some groups of organism, probably because of either spatial (i.e., unsuitable scale of analysis) or temporal (i.e.,

408   remarkable impacts happened in the past) constraints, also suggests that some impacts of

409   urbanization may have gone undetected. These facts compel us to be cautious in the

410   interpretation of our results, even more so if we consider possible time-lagged effects. A

411   broader spatio-temporal perspective might thus be required to find relevant impacts of urban

412   sprawl for groups that seemed to be unaffected in our analyses.

413

Conclusions

415   Urban sprawl was a strong predictor of species richness for distinct groups of plants and birds

416   in the Swiss Plateau. It mostly related to the proliferation of non-native, especially neophyte,

417   and ruderal plant species, as well as to the replacement of specialist birds with more common

418   and generalist species, and thus to the homogenization of species assemblages. Moreover, we

419   found that most impacts of urban sprawl were driven by the increase in urban area, but

420   interestingly other components of this process greatly contributed to these impacts as well. In

421   particular, the increases of ruderal plants and common generalist birds were highly related to

422   the intensity of urban land use, whereas the spread of non-native plants was strongly related to

423   urban dispersion. These results pointed out the negative impacts of urban spreading into

424   natural or semi-natural areas on biodiversity. In the context of the current discussion on urban

425   dispersion versus densification, the latter seems preferable (see also Soga et al. 2014). Hence,

426   new urban areas should be developed close to already urbanized areas rather than dispersed

427   into rural landscapes. However, such new developments should also provide enough high-

428   quality open spaces (i.e., parks, gardens and other green areas) that soften urban land use

429   intensity in order to support biodiversity and concurrently foster residents' welfare (e.g.,

430   Miller and Hobbs 2002; Sattler et al. 2010; Fontana et al. 2011). Even though dense urban

431   development may reduce opportunities for people to live close to nature, it facilitates public

432   access (Sushinsky et al. 2013). Finally, if we consider present rates of land consumption by

urban development, both worldwide (Grimm et al. 2008; Mcdonald et al. 2008) and

particularly in our study region (Schwick et al. 2012), and the likely time lag in the

manifestation of some impacts of urban sprawl on biodiversity (Ramalho and Hobbs 2012),

the balance inclines towards an urban densification. Upper limits of urban densification have

however to be carefully investigated taking together into account biodiversity conservation

and human quality of life.

Acknowledgements

References

Altermatt F (2012) Temperature-related shifts in butterfly phenology depend on the habitat.
Glob Chang Biol 18:2429–2438.

Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, Warren PS,
Williams NSG, Cilliers S, Clarkson B, Dobbs C, Dolan R, Hedblom M, Klotz S,
Kooijmans JL, Kühn I, MacGregor-Fors I, McDonnell M, Mörtberg U, Pysek P,
Siebert S, Sushinsky J, Werner P, Winter M (2014) A global analysis of the impacts of

456   urbanization on bird and plant diversity reveals key anthropogenic drivers A global

457   analysis of the impacts of urbanization on bird and plant diversity reveals key

458   anthropogenic drivers. Proc R Biol Sci 281:20133330.

459   Bartón K (2013) MuMIn: multi-model inference. R package version 1.9.13.

460   BDM - Biodiversity Monitoring in Switzerland Coordination Office (2009) The state of

461   biodiversity in Switzerland. Overview of the findings of Biodiversity Monitoring

462   Switzerland (BDM) as of May 2009. Abridged version. State of the environment no.

463   0911. Federal Office for the Environment, Bern.

464   Beissinger SR (1982) Effects of urbanization on avian community organization. Condor

465   84:75–83.

466   Blair RB (1996) Land use and avian species diversity along an urban gradient. Ecol Appl

467   6:506–519.

468   Blair RB (1999) Birds and butterflies along an urban gradient: surrogate taxa for assessing

469   biodiversity? Ecol Appl 9:164–170.

470   Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical

471   information-theoretic approach, 2nd edn. 488 p. Springer-Verlag, New York.

472   Casner KL, Forister ML, O'Brien JM, Thorne J, Waetjen D, Shapiro AM (2014) Contribution

473   of urban expansion and a changing climate to decline of a butterfly fauna. Conserv

474   Biol 28:773–782.

475   Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plann

476   74:46–69.

477   Clergeau P, Croci S, Jokimäki J, Kaisanlahti-Jokimäki M-L, Dinetti M (2006) Avifauna

478   homogenisation by urbanisation: Analysis at different European latitudes. Biol

479   Conserv 127:336–344.

480   Clergeau P, Savard JL, Mennechez G, Falardeau G (1998) Bird abundance and diversity

481   along an urban-rural gradient: a comparative study between two cities on different

482   continents. Condor 100:413–425.

483   Croci S, Butet A, Georges A, Aguejdad R, Clergeau P (2008) Small urban woodlands as

484   biodiversity conservation hot-spot: a multi-taxon approach. Landsc Ecol 23:1171–1186.

485   Crooks KR, Suarez A V, Bolger DT (2004) Avian assemblages along a gradient of

486   urbanization in a highly fragmented landscape. Biol Conserv 115:451–462.

487   Deutschewitz K, Lausch A, Kühn I, Klotz S (2003) Native and alien plant species richness in

488   relation to spatial heterogeneity on a regional scale in Germany. Glob Ecol Biogeogr

489   12:299–311.

490   Devictor V, Julliard R, Couvet D, Lee A, Jiguet F (2007) Functional homogenization effect of

491   urbanization on bird communities. Conserv Biol 21:741–751.

492   Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marquéz JR, Gruber

493   B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B,

494   Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of

495   methods to deal with it and a simulation study evaluating their performance.

496   Ecography 36:27–46.

497   Elmqvist T, Fragkias M, Goodness J, Güneralp B, Marcotullio PJ, Mcdonald RI, Parnell S,

498   Schewenius M, Sendstad M, Seto KC, Wilkinson C (2013) Urbanization, Biodiversity

499   and Ecosystem Services: Challenges and Opportunities. 755 p. Springer, New York.

500   ESRI (2011) ArcGIS Desktop: Release 10. Redlands, California: Environmental Systems

501   Research Institute.

502   Fontana S, Sattler T, Bontadina F, Moretti M (2011) How to manage the urban green to

503   improve bird diversity and community structure. Landsc Urban Plann 101:278–285.

504   Gonseth Y, Wohlgemuth T, Sansonnens B, Buttler A (2001) Die biogeographischen Regionen

505   der Schweiz. Erläuterungen und Einteilungsstandard. 48 p. Umwelt Materialien Nr.

506   137 Bundesamt für Umwelt, Wald und Landschaft, Bern.

507   Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global

508   change and the ecology of cities. Science 319:756–760.

509   Hijmans RJ (2015) raster: Geographic data analysis and modeling. R package version 2.3-24.

510   http://CRAN.R-project.org/package=raster.

511   Jaeger JAG, Bertiller R, Schwick C, Cavens D, Kienast F (2010) Urban permeation of

512   landscapes and sprawl per capita: New measures of urban sprawl. Ecol Indic 10:427–

513   441.

514   Jaeger JAG, Schwick C (2014) Improving the measurement of urban sprawl: Weighted Urban

515   Proliferation (WUP) and its application to Switzerland. Ecol Indic 38:294–308.

516   Kanton Aargau (1996) Das Projekt Langfristbeobachtung der Artenvielfalt in der

517   Normallandschaft des Kantons Aargau (LANAG). 3 p.

518   Knapp S, Kühn I, Bakker JP, Kleyer M, Klotz S, Ozinga W, Poschlod P, Thompson K,

519   Thuiller W, Römermann C (2009) How species traits and affinity to urban land use

520   control large-scale species frequency. Divers Distrib 15:533–546.

521   Kühn I, Klotz S (2006) Urbanization and homogenization – Comparing the floras of urban

522   and rural areas in Germany. Biol Conserv 127:292–300.

523   Lachat T, Pauli D, Gonseth Y, Klaus G, Scheidegger C, Vittoz P, Walter T (2010) Wandel der

524   Biodiversität in der Schweiz seit 1900: Ist die Talsohle erreicht? 435 p. Bristol-

525   Stiftung, Zürich.

526   La Sorte FA, Aronson MFJ, Williams NSG, Celesti-Grapow L, Cilliers S, Clarkson BD,

527   Dolan RW, Hipp A, Klotz S, Kühn I, Pyšek P, Siebert S, Winter M (2014) Beta diversity

528   of urban floras among European and non-European cities. Glob Ecol Biogeogr 23: 769–

529   779.

530   Latta SC, Musher LJ, Latta KN, Katzner TE (2013) Influence of human population size and

531   the built environment on avian assemblages in urban green spaces. Urban Ecosyst

532   16:463–479.

533   Le Viol I, Jiguet F, Brotons L, Herrando S, Lindström A, Pearce-Higgins JW, Reif J, Van

534   Turnhout C, Devictor V (2012) More and more generalists: two decades of changes in

535   the European avifauna. Biol Lett 8:780–782.

536   Lososová Z, Chytrý M, Tichý L, Danihelka J, Fajmon K, Hájek O, Kintrová K, Láníková D,

537   Otýpková Z, Řehořek V (2012a) Native and alien floras in urban habitats: a

538   comparison across 32 cities of central Europe. Glob Ecol Biogeogr 21:545–555.

539   Lososová Z, Chytrý M, Tichý L, Danihelka J, Fajmon K, Hájek O, Kintrová K, Kühn I,

540   Láníková D, Otýpková Z, Řehořek V (2012b) Biotic homogenization of Central

541   European urban floras depends on residence time of alien species and habitat types.

542   Biol Conserv 145:179–184.

543   Marzluff JM, Ewing K (2001) Restoration of fragmented fandscapes for the conservation of

544   birds: A general framework and specific recommendations for urbanizing landscapes.

545   Restor Ecol 9:280–292.

546   Mcdonald RI, Kareiva P, Forman RTT (2008) The implications of current and future

547   urbanization for global protected areas and biodiversity conservation. Biol Conserv

548   141:1695–1703.

549   McDonnell MJ, Hahs AK (2008) The use of gradient analysis studies in advancing our

550   understanding of the ecology of urbanizing landscapes: current status and future

551   directions. Landsc Ecol 23:1143–1155.

552   McKinney ML (2002) Urbanization, biodiversity, and conservation. BioScience 52:883–890.

553   McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv

554   127:247–260.

555   McKinney ML (2008) Effects of urbanization on species richness: A review of plants and

556   animals. Urban Ecosyst 11:161–176.

557   Miller JR, Hobbs RJ (2002) Conservation where people live and work. Conserv Biol 16:330–

558   337.

559   Niemelä J (1999) Ecology and urban planning. Biodivers Conserv 119–131.

560   Nobis MP, Jaeger JAG, Zimmermann NE (2009) Neophyte species richness at the landscape

561   scale under urban sprawl and climate warming. Divers Distrib 15:928–939.

562   Pyšek P (1993) Factors affecting the diversity of flora and vegetation in central European

563   settlements. Vegetatio 106:89–100.

564   Pyšek P (1998) Alien and native species in Central European urban floras: a quantitative

565   comparison. J Biogeogr 25:155–163.

566   R Core Team (2014). R: A language and environment for statistical computing. R Foundation

567   for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

568   Ramalho CE, Hobbs RJ (2012) Time for a change: dynamic urban ecology. Trends Ecol Evol

569   27:179–188.

570   Rebele F (1994) Urban ecology and special features of urban ecosystem. Glob Ecol Biogeogr

571   Lett 4:173–187.

572   Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E,

573   Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA,

574   Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global

575   Biodiversity Scenarios for the Year 2100. Science 287:1770–1774.

576   Sattler T, Duelli P, Obrist MK, Arlettaz R, Moretti M (2010) Response of arthropod species

577   richness and functional groups to urban habitat structure and management. Landscape

578   Ecol 25:941–954.

579   Savard J-PL, Clergeau P, Mennechez G (2000) Biodiversity concepts and urban ecosystems.

580   Landsc Urban Plann 48:131–142.

581   Schmidt KJ, Poppendieck H-H, Jensen K (2013) Effects of urban structure on plant species

582   richness in a large European city. Urban Ecosyst 17:427–444.

583   Schwick C, Jochen J, Bertiller R, Kienast F (2012) L'étalement urbain en Suisse - Impossible

584   à freiner? Analyse quantitative de 1935 à 2002 et conséquences pour l'aménagement

585   du territoire. Urban sprawl in Switzerland - Unstoppable? Quantitative analysis 1935

586   to 2002 and implications for regional planning. 216 p. Bristol-Stiftung, Zurich.

587   Soga M, Koike S (2013) Mapping the potential extinction debt of butterflies in a modern city:

588   implications for conservation priorities in urban landscapes. Anim Conserv 16:1–11.

589   Soga M, Yamaura Y, Koike S, Gaston KJ (2014) Land sharing vs. land sparing: does the

590   compact city reconcile urban development and biodiversity conservation? J Appl Ecol

591   51:1378–1386.

592   Stefanescu C, Herrando S, Páramo F (2004) Butterfly species richness in the north-west

593   Mediterranean Basin: the role of natural and human-induced factors. J Biogeogr

594   31:905–915.

595   Sushinsky JR, Rhodes JR, Possingham HP, Gill TK, Fuller RA (2013) How should we grow

596   cities to minimize their biodiversity impacts? Glob Chang Biol 19:401–410.

597   Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the

598   concept of trait be functional! Oikos 116:882–892.

599   Wood BC, Pullin AS (2002) Persistence of species in a fragmented urban landscape: the

600   importance of dispersal ability and habitat availability for grassland butterflies.

601   Biodivers Conserv 11:1451–1468.

Table 1. Details on species data from the different monitoring programs operating in the study areas at the habitat and landscape scales. The set of urban and other environmental predictors (i.e., climate, topography and land use) tested for each taxonomic group and monitoring program is provided. See also Table 2.

Spatial scale	Biodiversity monitoring program	Study area	Plot size	Taxonomic group	Urban variables	Other environmental variables
Habitat	BDM Z9	Swiss Plateau	10 m^2	Mosses Vascular plants Gastropods	Urban area Age of urban area Imperviousness	Mean annual temperature Mean annual precipitation Aspect
	LANAG	Swiss Plateau of the Canton of Aargau	10 m^2	Vascular plants Gastropods	Human population density Nearest distance to urban areas (urban dispersion)	Slope (surface roughness) Forest area
			3.14 ha (100 m-radius buffers)	Birds		
			78.54 ha (250 m-transects around plot centers within 500 m-radius buffers)	Butterflies	Urban area Age of urban area Imperviousness degree	Mean annual temperature Mean annual precipitation Aspect
Landscape	BDM Z7	Swiss Plateau	1 km^2	Vascular plants Butterflies Birds	Human population density Mean proximity index (MPI) of urban area (urban dispersion)	Standard deviation of altitude (surface roughness) Forest area

Table 2. Definitions and data sources of environmental predictors, including variables describing urban sprawl and other environmental variables for the plots of the distinct biodiversity monitoring programs at the habitat level (BDM Z9 and LANAG) and landscape level (BDM Z7). See also Table 1.

Predictor	Definition	Data source
Urban variables:		
Urban area	Proportion of plot area occupied by houses (including gardens), roads and other infrastructures, industries, parks and recreational areas, used for BDM Z7 plots and for butterflies in LANAG plots. Location in urban area, used for BDM Z9 plots and for LANAG plots (except butterflies)	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung / (2010, 15 m resolution)
Age of urban area	Average age (weighted by area) of urban areas (in years) using 2011 as reference year, calculated from data on urban areas at different time points (1885, 1935, 1960, 1980, 2002 and 2010)	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung / (time series: 1885–2010; 15 m resolution)
Imperviousness of urban area	Degree of soil-sealing of urban area (%)	Pan-European Copernicus Land Monitoring Services http://www.copernicus.eu/ (2009, 20 m resolution)
Human population density in urban area	Number of human inhabitants (residents) per ha of urban area	Swiss Federal Statistical Office http://www.statistics.admin.ch/ (2011, 100 m resolution)
Mean proximity index (MPI) of urban area	Degree of dispersion of urban area (low MPI values = high dispersion), calculated as the ratio between the mean size of urban patches and the nearest neighbor distance to other urban patches (dimensionless). Used for BDM Z7 plots and for butterflies from LANAG plots	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung / (2010, 15 m resolution)
Nearest distance to urban areas	Distance from plots to the nearest neighbor urban area (m). Used for BDM Z9 plots and for LANAG plots (except butterflies)	
Non-urban variables:		
Mean annual temperature	Average value of monthly mean temperatures (°C)	Swiss Federal Office of Meteorology and Climatology
Annual precipitation	Sum of monthly precipitation (mm)	http://www.meteoswiss.ch (Data averaged for the period 1961–1990, at 25 and100 m resolution for the habitat and landscape scales, respectively)
Northness (aspect)	Orientation or direction to which slope faces, ranges from 1 (north-	Swiss Federal Office of Topography

	facing slope) to -1 (south-facing slope)	http://www.swisstopo.ch/
		(Data at 25and100 m resolution for the habitat and landscape scales, respectively)
Surface roughness	Standard deviation (SD) of altitude (m a.s.l.), used for BDM Z7 plots and for butterflies in LANAG plots.	
	Slope (surface inclination relative to horizontal, 0–90°), used for BDM Z9 plots and for LANAG plots (except butterflies)	
Forest area	% plot area occupied by forest, used for BDM Z7 plots and for butterflies in LANAG plots.	Federal Statistical Office (FSO) Land use statistics (2004/09, 100 m resolution) http://www.bfs.admin.ch/
	Location in forest area, used for BDM Z9 plots and for LANAG plots (except butterflies)	

Table 3. Results of the two steps of analysis. Step 1: Model performance D^2_{full} of the full models, i.e., percentage of null deviance explained by urban and non-urban predictors, and the corresponding values $D^2_{I.Urban}$, i.e., the percentage of null deviance independently explained by urban predictors based on hierarchical partitioning. All species groups with $D^2_{I.Urban} \geq 15\%$ are shown. Step 2: Relative variable importance (RVI) of single urban predictors from multi-model averaging. Values are provided for urban predictors included in best fitted models (delta AICc or QAICc ≤ 4) for each diversity variable. Arrows indicate the direction of effects (positive ↗ and negative ↘) based on partial regression plots of the best fitted model (AIC-based) and coefficients estimates which are significantly different from zero (P<0.05; values in bold).

Species group (Monitoring program)	Step 1: Deviance partitioning		Step 2: Multi-model averaging & partial regressions				
	D^2_{full} (%)	$D^2_{I.Urban}$ (%)	Urban area	Population density	Dispersion	Imperviousness	Average age
Vascular plants							
Non-native plants (BDM Z7)	64.2	28.4	**0.45 (↗)**	**0.97 (↗)**	0.22	**0.42 (↗)**	0.03
Neophytes (BDM Z7)	61.8	41.9	**1.00 (↗)**	**0.97 (↗)**	**1.00 (↘)**	0.12	0.07
Ratio non-native *vs.* native plants (BDM Z7)	66.4	17.7	**0.67 (↗)**	**0.69 (↗)**	**0.64 (↘)**	0.07	-
Habitat-specialist plants (BDM Z7)	43.8	15.7	-	**0.67 (↗)**	0.03	**0.43 (↗)**	0.02
Phanerophytes (BDM Z7)	42.6	19.3	**0.98 (↗)**	0.07	**1.00 (↘)**	**0.13 (↗)**	0.17
Chamaephytes (BDM Z7)	29.8	24.5	**0.51 (↗)**	0.01	**0.83 (↘)**	0.03	0.07
Therophytes (BDM Z7)	61.9	16.9	**0.24 (↗)**	**0.49 (↗)**	-	**0.41 (↗)**	0.02
Eutrophic-habitat plants (BDM Z7)	52.9	24.1	-	**0.97 (↗)**	0.04	**0.41 (↗)**	**0.05 (↘)**
Anemochorous plants (BDM Z7)	42.0	17.4	-	-	0.07	**1.00 (↗)**	0.10
Anthropochorous plants (BDM Z7)	45.2	29.7	**1.00 (↗)**	-	0.05	0.18	-
Highly dispersive plants (BDM Z7)	42.0	16.1	0.05	**0.11 (↗)**	0.05	**0.95 (↗)**	0.12
Birds							
Zoophagous birds (BDM Z7)	36.2	23.4	-	**1.00 (↗)**	0.03	-	-
(LANAG)	27.3	18.5	**0.96 (↗)**	0.03	**0.96 (↘)**	0.07	0.03
Ground-breeding birds (BDM Z7)	28.6	15.0	**0.92 (↘)**	0.06	0.12	-	0.04
Urban birds (BDM Z7)	39.2	29.5	**0.76 (↗)**	**0.29 (↗)**	0.02	-	0.05
(LANAG)	37.9	31.7	**1.00 (↗)**	0.03	**1.00 (↘)**	0.05	0.04
Breeding-generalist birds (BDM Z7)	25.7	15.4	0.05	**0.54 (↗)**	0.02	0.04	0.05
Ratio breeding-generalist vs. specialist birds (BDM Z7)	31.0	24.2	**1.00 (↗)**	0.02	0.21	0.02	-
(LANAG)	41.7	28.9	0.02	**1.00 (↗)**	**0.75 (↘)**	0.14	**1.00 (↗)**

Figure 1. Delimitation of study area within Switzerland (thin boundary line), i.e. the Swiss Plateau (thick solid boundary line; Gonseth et al. 2001), and the location of plots from the different monitoring programs are shown: BDM Z7 indicator *Species Diversity in Landscapes* (large dots; 109 plots of 1 km^2); BDM Z9 indicator *Species Diversity in Habitats* (small dots; 473 circular plots of 10 m^2); and LANAG program of the canton of Aargau (denser small dots; 436 plots of different sizes at the habitat level in the Swiss Plateau). The location of the main cities within the study area are indicated in grey.

Figure 2. Average (±SE) relative variable importance (RVI) of the different urban predictors (i.e., urban area, population density, dispersion, imperviousness, and average age of urban area) to explain the variation in species richness variables for all species groups that showed relevant responses to urban sprawl ($D^2_{I.Urban} \geq 15\%$) independent from other environmental predictors (see Table 3). Averaged-values are shown for all these groups (grey) and for the subsets of groups for vascular plants (white) and birds (black).

Figure 3. Partial residual plots of significant responses of species richness to single components of urban sprawl at the landscape scale for (a) neophytes and urban area (linear term), (b) plants from eutrophic habitats and human population density of urban area (linear and quadratic terms), (c) neophytes and urban disperson (MPI) (linear term), and (d) highly dispersive plants and imperviousness (linear term). Partial residual plots represent the estimated relationships between response variables and a predictor of interest (solid lines; ±1 SE, dotted lines) once the effects of other predictors have been accounted for. Mean values of species richness per plot (avg.sr) are provided to contextualize the size of effects.

Figure 4. Partial residual plots of significant responses of birds to single components of urban sprawl at the landscape scale for (a) species richness of ground breeding birds to urban area,
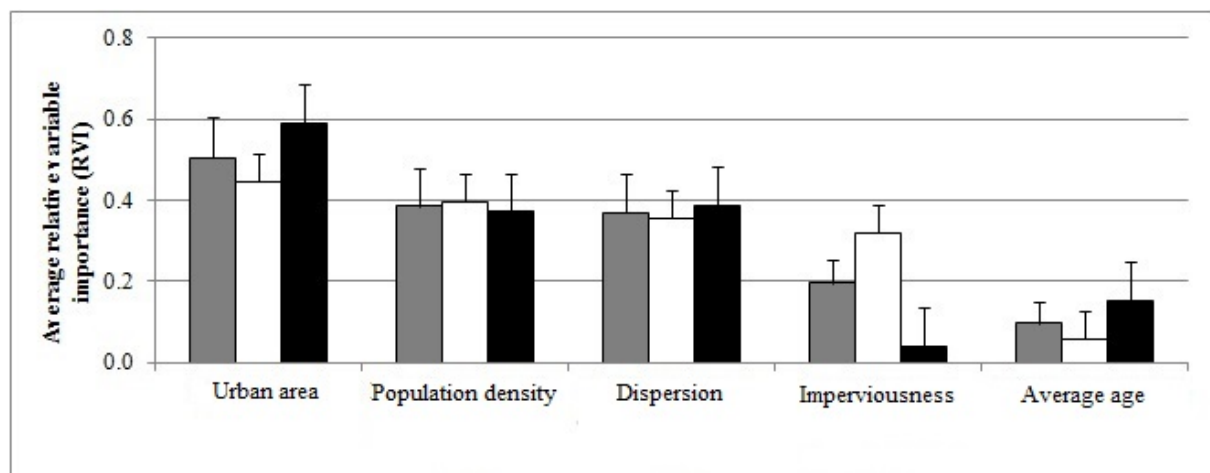
and (b) the ratio of breeding generalist to specialist bird species to urban area (linear terms).

For further details on partial residual plots see Figure 3.
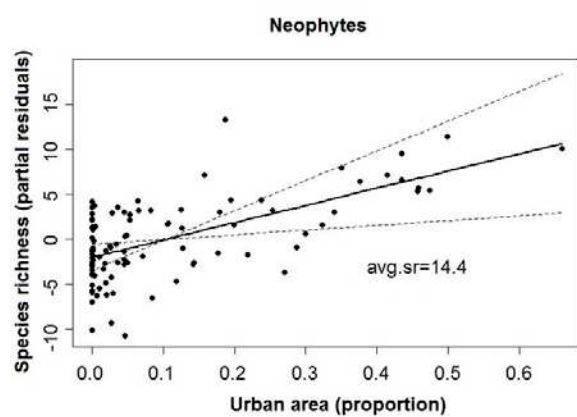
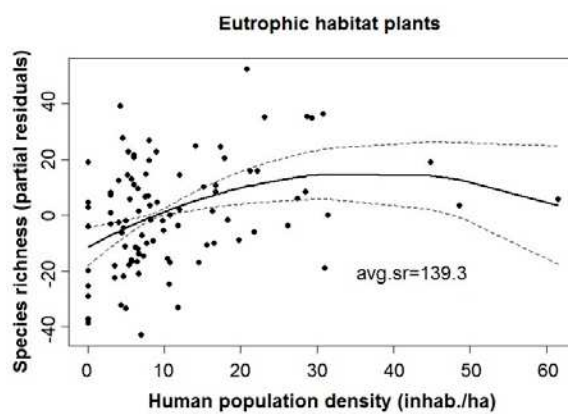**Concepción et al., Figure 1**
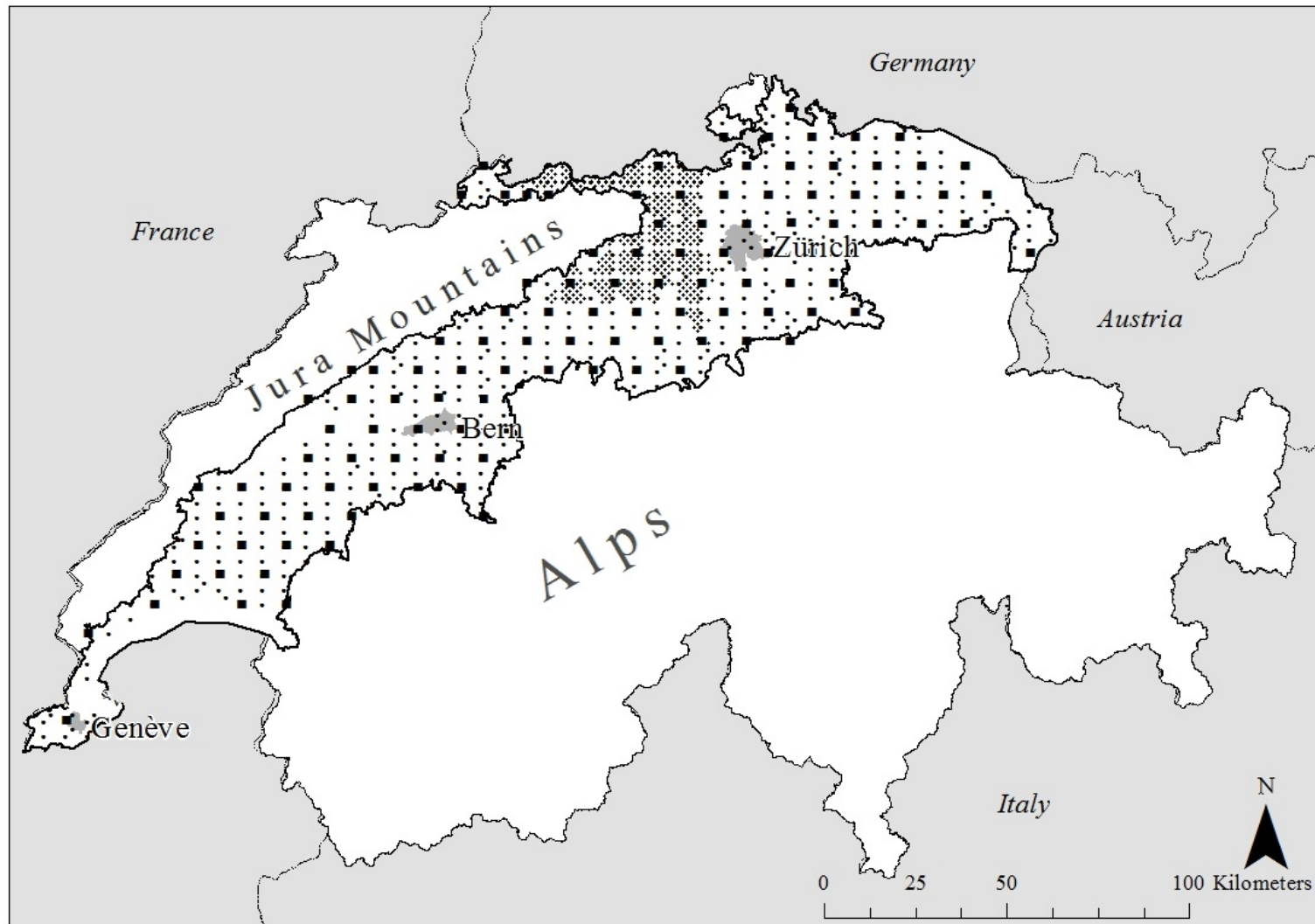
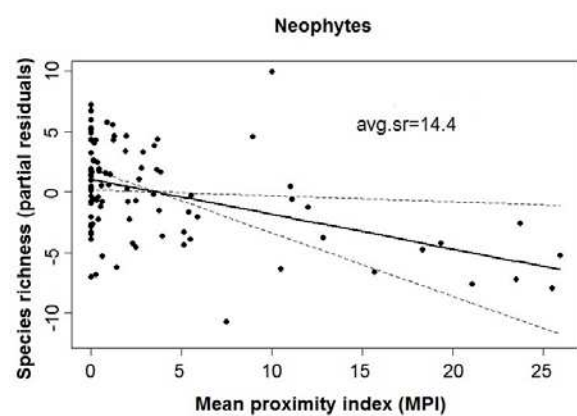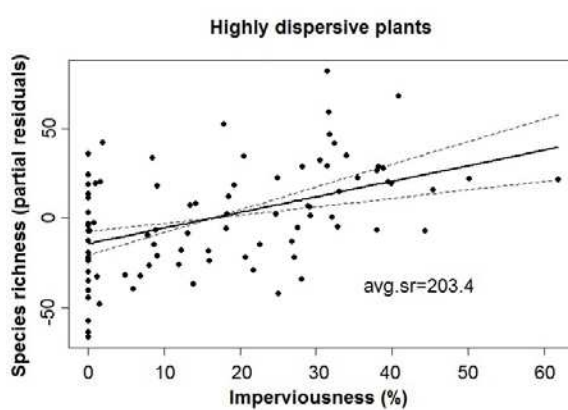**Concepción et al., Figure 2**

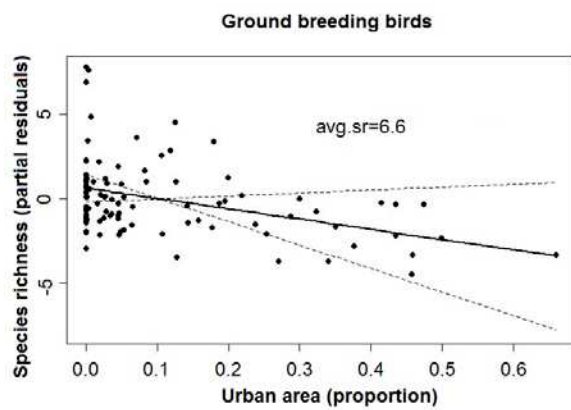**Concepción et al., Figure 3**

a)

b)

c)

d)

Concepción et al., Figure 4

a)   b)