Ecole de biologie

Improving forest management practices for amphibians:

the relative effect of local and landscape-scale parameters

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par

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1 \Résumé

2

3   Les menaces résultantes des activités humaines sur les milieux forestiers vont toujours

4 croissantes, et cela en dépit de la valeur inestimable de ces écosystèmes en terme de services

5 socio-économiques et de diversité biologique. A l'heure actuelle, la compréhension des

6 mécanismes à travers lesquels l'urbanisation et l'exploitation forestière affectent la

7 biodiversité forestière apparaît donc comme un enjeu crucial pour concevoir des plans de

8 gestion. Dans ce contexte, l'étude des populations d'amphibiens, du fait de la grande

9 sensibilité de ces espèces face aux changements intervenant dans leur milieu de vie, peut

10 s'avérer être un outil précieux pour mieux cerner les relations existantes entre espèces et

11 environnement. C'est pourquoi nous avons investigué les effets de 16 variables

12 environnementales, allant des caractéristiques des plans d'eau jusqu'aux facteurs paysagers en

13 passant par des paramètres propres à la gestion forestière, sur l'abondance et la richesse

14 spécifique d'une communauté de batraciens. La présente étude a été réalisée sur 46 sites de

15 reproduction à amphibiens localisés dans une forêt périurbaine du Plateau Suisse, chacun

16 d'entre eux ayant été visités à trois reprises au cours de la saison de reproduction. En premier

17 lieu, nous avons utilisé la technique des modèles de distribution d'espèces en réalisant une

18 analyse classique de type GLMs afin d'identifier les principaux paramètres affectant la

19 distribution spatiale des amphibiens. Dans un second temps, nous avons appliqué aux espèces

20 menacées et qui sont par ailleurs souvent caractérisées par une faible probabilité de détection

21 une analyse qui, basée sur le principe sélection de modèles, nous a permis de tenir compte du

22 risque de fausses-absences. L'analyse au moyen des GLMs a révélé que les populations

23 d'amphibiens étudiées étaient principalement influencées par la taille des sites de

24 reproduction ainsi que la présence d'une arrivée d'eau d'une part, et par la connectivité,

25 l'altitude, la proportion d'aire forestière et l'âge du peuplement d'autre part. Ces points ont

26 été corroborés par l'analyse prenant en compte la détectabilité qui a en outre permis de les

27 affiner en identifiant certains prédicteurs additionnels influençant plus spécifiquement la

28 distribution des espèces auxquelles cette analyse à été appliquée. Ce résultat met donc en

29 évidence la contribution complémentaire des analyses de détectabilité par rapport aux

30 méthodes classiques de distribution d'espèces. Cela constitue une information de grande

31 valeur dans le contexte actuel de déclin de la biodiversité et nous ne pouvons donc

32 qu'encourager l'utilisation de cette méthode afin de cibler plus efficacement les mesures de

33 conservation en faveur des espèces cryptiques ou menacées. Finalement, nous avons

34 démontré que les principaux paramètres affectant la distribution des amphibiens proviennent

35 pour certains des caractéristiques propres aux plans d'eau, pour d'autres de celles propres à la

36 gestion sylvicole et pour d'autres enfin de celles propres au paysage. Cela souligne donc

37 l'importance de considérer ces trois différentes échelles dans le cadre des plans de gestion

38 forestiers. En conséquence, nous encourageons donc les gestionnaires forestiers premièrement

39 à protéger et restaurer les sites de reproduction à batraciens présentant une surface suffisante,

40 une alimentation en eau courante ainsi qu'une bonne interconnectivité, et deuxièmement à

41 favoriser les peuplements forestiers montrant une succession naturelle. En effet, nous avons

42 pu démontrer au cours de cette étude que la prise en compte de ces paramètres devrait

43 grandement bénéficier aux communautés d'amphibiens.

44

45 \Mots-clés

46

47 Habitats terrestres, sites de reproduction à amphibiens, modèles de distribution d'espèces,

48 modèles d'occupation de sites, *Lissotriton helveticus*, *Salamandra salamandra*.

49

50   Improving forest management practices for amphibians: the relative effect of local and

51   landscape-scale parameters

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64   \Running title

65

66   Amphibian distribution in forested landscape

67 \Abstract

68

69   Forested areas are increasingly threatened by human activities despite their

70 inestimable value in terms of socio-economic functions and above all biological diversity.

71 Understanding how urbanisation and forestry practices affect biodiversity spatial patterns in

72 forest ecosystem is therefore crucial to devise valuable conservation plans. In this context,

73 amphibians provide a useful tool to study species-environment relationships, as a result of

74 their high sensitivity to environmental changes. Therefore, we investigated the effect of 16

75 environmental variables ranging from within-pond characteristics to landscape scale factors as

76 well as forest management parameters on the abundance and species richness of pond

77 breeding amphibians. Monitoring survey, which included three visits per site during one

78 breeding season, was realised on 46 ponds located in a suburban forested landscape of Central

79 Plateau in Western Switzerland. First, we used classical GLM techniques (i.e. species

80 distribution modelling) in order to identify the main drivers of amphibian distribution. And

81 subsequently, we realised a model selection based analysis accounting for risk of false-

82 absence (i.e. site-occupancy modelling) for threatened species which moreover are often

83 characterised by a low detectability. Species distribution models reveal that amphibian

84 populations were mostly influenced by the pond size and the presence of a water supply,

85 along with connectivity, elevation, forest cover and stand age. These results are corroborated

86 by the site-occupancy analysis which highlights in a more species-specific way some

87 additional environmental predictors. Hence, our findings underscore the complementary

88 contribution provided by site-occupancy modelling to classical species distribution models in

89 the case of rare species. This information if of great concern in the current context of

90 biodiversity crisis and we thus strongly encourage the use of site-occupancy models in order

91 to powerfully target conservation measures for cryptic and endangered species. In conclusion,

92 we provide evidence that different environmental variables acting at all pond, landscape and

93 forest management levels affect amphibian distribution, which emphasize the importance of

94 considering all those different aspects in forest management programs. Finally, we encourage

95 forest managers first to protect and restore well connected ponds presenting sufficient surface

96 areas as well as running water supplies, and second to favor uneven-aged stands with natural

97 dynamic as we demonstrated that considering these parameters will greatly benefit to

98 amphibian communities.

99

100

101   \Keywords

102

103   Terrestrial habitats, breeding ponds, species distribution modelling, site-occupancy modelling,

104   *Lissotriton helveticus*, *Salamandra salamandra*.

105 \Introduction

106

107   Forested areas currently cover about 27% of land surface around the Earth (Larsson,

108 2011) and are of crucial importance for biodiversity in hosting more than 80% of world

109 terrestrial species (Achard et al., 2009). Furthermore, forests perform a wide range of socio-

110 economic and ecosystem functions: they provide natural resource products, play a protective

111 role against destructive natural events, serve for population recreational purposes and above

112 all are essential to biogeochemical cycles achievement, climate regulation and atmosphere

113 quality control (Führer, 2000). In Europe, despite this state of knowledge, threats to forest

114 biodiversity are continuously increasing, largely due to human activity (Bengtsson et al.,

115 2000). Indeed, urbanisation (Hamer and McDonnell, 2008) and forestry practices (Hansen et

116 al., 1991) have been identified as key threatening processes for this rich ecosystem, mainly

117 through the disturbances, the loss of suitable habitats and the landscape fragmentation they

118 provoke (Herrmann et al., 2005). Hence, because strictly protected forests won't be sufficient

119 to conserve biological richness (Demaynadier and Hunter, 1995), the most relevant challenge

120 at the moment consist in finding a right balance between human induced pressure on forested

121 areas and forest biodiversity preservation (McNeely, 1994).

122   In this respect, forest amphibians constitute a privileged taxon to obtain a better

123 understanding of the mechanisms through which human activity negatively impact forest

124 ecosystems. Indeed, amphibians are highly sensitive to most environmental changes occurring

125 in their natural habitats, essentially as a result of their limited dispersal ability, their reduced

126 home range, their dependence to both aquatic and terrestrial habitats and their high

127 vulnerability to road traffic, pathogens, invasive species, pollutions and climate changes

128 (Cushman, 2006). Moreover, in forest as well as wetland ecosystems amphibian populations

129 frequently represent a considerable proportion of vertebrate biomass and are in addition a key

130 component of food webs in being important prey and predator species (Demaynadier and

131 Hunter, 1995; Hamer and McDonnell, 2008). These considerations make amphibian species

132 valuable bioindicators in forested landscape (Semlitsch et al., 2009) and highlight the benefit

133 derived by a large guild of species from attention paid to this taxon.

134   Thus, and even if amphibians have received less interest in the past than some other

135 groups such as birds or mammals (Russell et al., 2004), numerous studies already investigated

136 the main drivers of forest amphibian distribution patterns (for a review: Demaynadier and

137 Hunter, 1995). To date, these researches investigated the influence of environmental variables

138 on forest amphibian populations mainly in relation to three different axes: pond scale, forest

139   management scale and landscape scale. At the pond level, factors known to affect amphibian

140   species richness and abundance include: (1) the canopy closure, which can induce pond

141   hypoxia both in increasing leaf litter decomposition (McCormick and Laing, 2003) and in

142   reducing in situ photosynthesis through limitation of incoming light (Colburn, 2004), (2) the

143   aquatic vegetation, which provides oviposition sites, shelters for larvae and adults and

144   contributes to tadpole diet (Hamer and McDonnell, 2008; Smallbone et al., 2011), and (3) the

145   pond morphology, which is related to microhabitat diversity and invertebrate-prey availability

146   (Hamer and McDonnell, 2008; Smallbone et al., 2011). At forest management scale,

147   important variables for amphibian distribution comprise: (1) the amount of coarse woody

148   debris, which favour a high humidity level (Moseley et al., 2004) and provide overwintering

149   refuges as well as feeding substrates (Demaynadier and Hunter, 1998; Waldick et al., 1999;

150   Owens et al., 2008), (2) the coniferous rate, which affects soil microclimate (Bury, 1983) and

151   acidity (Augusto et al., 2002) along with leaf litter quality (Waldick et al., 1999) and coarse

152   woody debris quantity (Fleming and Freedman, 1998), (3) the stand age, which is related to

153   quality and quantity of microhabitat elements such as canopy cover, soil moisture and litter

154   type and depth (Spies and Cline, 1988; Hansen et al., 1991; Demaynadier and Hunter, 1995),

155   and (4) the exploitation intensity, which decreases soil arthropods diversity and abundance as

156   well as microhabitat and coarse woody debris availability. Finally, at landscape scale,

157   parameters shown to impact amphibian populations include: (1) the pond connectivity, which

158   is expected to be of crucial importance for species such as amphibians whose dynamic

159   resembles metapopulation models (Marsh and Trenham, 2001), (2) the stream density, which

160   participates to pond connectivity and is in addition associated with soil humidity (Wyman,

161   1988), and (3) the forest cover, which enhances pond connectivity and favours moisture as

162   well as shade at ground level (Cushman, 2006).

163   But despite this abundant literature, there is lack of studies investigating the

164   conjugated effects of within-pond variables, forest management parameters and landscape

165   factors at the same time (but see Hamer and McDonnell, 2008; Lemckert and Mahony, 2010;

166   Hamer and Parris, 2011). Therefore, with the present survey we aim at improving our

167   understanding of issues related to amphibian conservation in forested landscape. We thus

168   investigated how 16 different environmental variables resulting from either pond, forest

169   management, or landscape scales affect both species richness and abundance of forest

170   amphibians. Additionally, we integrated a detectability aspect into our analysis as it was

171   demonstrated by several studies (Moilanen, 2002; Gu and Swihart, 2004; Mazerolle et al.,

172   2005) that not accounting for probability of detection can lead to erroneous conclusions

173 concerning relationships linking species distribution to environmental factors. Consequently,

174 in studying amphibian species-environment relationships in forested landscape, we intend to

175 better target conservation measures favourable to amphibian communities, and to provide

176 clear guidance to forest managers and stakeholders.

177

178 \Methods

179

180 Study area

181 The study area is located in the Western Switzerland on the Central Plateau to the

182 North of Lausanne (46.58°N/6.68°E), an area with moraine soil and semi-continental climate

183 (Bouët, 1985; Steinlin et al., 1993). It covers about 20 km^2 separated into three patches of

184 dense mixed forest with elevation ranging from 570 to 930 m.a.s.l. (Figure 1). This forested

185 area is mainly composed of two different landscape types: *Galio-Fagenion* at the lowest

186 elevations and *Lonicero-Fagenion* at higher altitudes (for phytosociological cartography of

187 the study area: Clot et al. 1994, for landscape typology: Delarze and Gonseth 2008). Human

188 influence has been for long important in the whole part of the study area through forestry due

189 to high wood needs for heating, construction, transport and industry. The 19th century as well

190 as the first part of the 20th century were particularly marked by the conversion of natural

191 forests into conifer plantations (principally *Picea abies*) as well as clear-cutting resulting in

192 the formation of even-aged stands dominated by a very low number of different tree species.

193 In addition, swamps and marshy grasslands were drained and devoted to afforestation

194 (Steinlin et al., 1993). However, since 1950, forest management is oriented in a more

195 ecological way, favouring natural regeneration, thus leading progressively to the

196 establishment of uneven-aged and varied stands. In the late eighties, Forest services have

197 likewise launched a program of conservation and restoration of forest wetlands which

198 represent to date about 5% of forested landscape in the study area (Induni-Gaffiot and Moret,

199 2000).

200

201 Amphibian survey

202 Except two ponds with surface superior to 5000 m^2 and which were stocked with fish,

203 all amphibian breeding ponds of the study area known by the Forest Services were surveyed

204 (n=46). Each of them was visited three times between the 14th March and the 15th June 2011.

205 Visits occurred during the first part of the night and consisted in call and light survey looking

206 for adults, larvae and clutches. Moreover, the first and third visits included the overnight

207 utilization of 6 funnel traps per site. For each site, we thus computed its species richness (i.e.

208 the total number of different species observed during the survey) and its total abundance in

209 amphibians (i.e. the sum of the maximal number of adults, and eventually larvae – only for

210 Caudata – or clutches – only for Anura, observed for each species). We excluded from the

211 analysis *T. carnifex* and *P. ridibundus* which are invasive species in the study area.

212

213 Environmental predictors

214 We selected a set of 16 different environmental variables classified into 3 categories

215 (Table 1) related to amphibian ecology in order to investigate amphibian species richness and

216 abundance patterns in the study area:

217 • Amphibian aquatic habitat has to fulfil different ecological characteristics with regard for

218 example to water quality (Sacerdote and King, 2009), feeding resources availability (Babbitt

219 et al., 2003) or microhabitats diversity (Hamer and McDonnell, 2008; Smallbone et al.,

220 2011). And such decisive qualities are tightly linked to pond properties. Therefore, we

221 considered the four following variables associated with pond characteristics: (1) the pond

222 surface area (abbreviated Size), (2) the percentage of emergent aquatic vegetation cover

223 (Aqua-Veg), (3) the canopy density above the pond (Canopy) and (4) the existence of a

224 running water supply (Water), each of them estimated on the field.

225 • Relative to terrestrial habitat, amphibian distribution is also constrained by different

226 criteria such as soil humidity and temperature (Wyman, 1988; Waldick et al., 1999), leaf

227 litter quality (Demaynadier and Hunter, 1998), soil invertebrate abundance (Vonesh, 2001)

228 and availability of shelters and overwintering refuges (Mitchell et al., 1997). Landscape type

229 and forest management both influence these criteria. Hence, we measured four variables

230 peculiar to landscape properties: (1) the proportion of forested area (Forest), (2) the stream

231 density (Hydro), (3) the pond elevation (Elev) and (4) the pond connectivity (Connect). All

232 of them were obtained aid of ArcGIS v9.3 (Esri, 2008). In particular, we simplified the

233 distance-weighted area of occupied habitat (incidence function model) presented by Prugh

234 (2009) in order to calculate pond connectivity, which resulted in the following formula

$$S_i = \sum_{j \neq i} exp(-\alpha\, d_{ij}),$$

235

236 where S_i is the connectivity measure for patch i, d_{ij} is the distance between focal patch i and

237 patch j, and α equals 1/the average migration distance of the species. In this calculation, we

238 set the average migration distance to 1 km given that Smith and Green (2005) and Kovar et

239   al. (2009) demonstrated that amphibians, especially juvenile specimens, are often capable of

240   migrating for hundred meters or even several kilometres.

241   •   And we finally considered the following aspects of forest management: (1) the

242   coniferous rate (Conifer-A and Conifer-B), (2) the exploitation intensity (Exploit), (3) the

243   stand age (Age, Diam and Sd-Diam), (4) the amount of coarse woody debris (CWD) and (5)

244   the herbaceous vegetation cover (Veg). Coniferous rate represents the proportion of

245   coniferous stems against the total number of stems, and was measured within a small

246   (Conifer-A) and a large (Conifer-B) radius in order to investigate the effect of conifer on

247   both aquatic and terrestrial habitats. Exploitation intensity corresponds to the proportion of

248   forested landscape that wasn't logged or harvested during the past decade. Stand age was

249   measured in three different ways. Firstly, we described if the zone close to the pond was

250   already a forested area before the 20th century or if natural reforestation occurred during the

251   last century (Age). Secondly, stand age was indirectly measured through the mean diameter

252   at breast height of the forest stand (Diam). And thirdly, we account for the heterogeneity of

253   forest seral stage in calculating the standard deviation of this mean diameter (Sd-Diam).

254   Those variables regarding coniferous rate and stand age were obtained aid of ArcGIS.

255   Finally, we estimated visually the herbaceous (height < 50 cm) vegetation cover (Veg), and

256   we measured the volume of large dead wood (length > 130 cm and diameter > 12 cm) at

257   ground level (CWD) in accordance with Kaufmann (2001), both of these variables were

258   collected on the field. The amount of coarse woody debris at ground level as well as the

259   pond surface area were transformed using natural logarithm function in order to achieve

260   normality.

261   Previous studies (Cushman, 2006; Kovar et al., 2009) demonstrated that after they

262   reach sexual maturity, migration of amphibians with biphasic lifecycle are restricted to a

263   small area surrounding their breeding pond to which they show considerable fidelity.

264   Therefore, whenever it was possible, we measured landscape and forest management

265   predictors within a 500 m radius around the pond (Forest, Hydro, Exploit, Diam, Sd-Diam

266   and Conif-B). But field data collecting constrained us to reduce this buffer to a 100 m radius

267   for several predictors (Age, CWD, Veg and Conif-A, see Table 1).

268

269   Modelling approaches

270   First of all, we examined possible correlations between variables to ensure their

271   independency. We then employed classical macroecological approaches as referred in Dubuis

272   et al. (2011) using GLM modelling techniques (McCullagh and Nelder, 1989) in order to test

273   the link between each of our environmental variables and the amphibian distribution. We used

274   Gaussian distribution in the case of species richness and quasi-Poisson distribution for the

275   total abundance in amphibians. According to the method developed by Johnson and Omland,

276   (2004) we conducted minimum AIC procedure aiming at the selection of most parsimonious

277   model. We then evaluated the reliability of these GLMs by calculating their adjusted deviance

278   (i.e. the explanatory power of the model, referred as R^2 thereafter). Results of this analysis

279   were then used to project the expected amphibian abundance on the whole study area

280   following Guisan and Zimmermann (2000).

281   In most monitoring surveys, species detection is imperfect, thus leading to an

282   underestimation of the true distribution of the focal species (Yoccoz et al., 2001) and

283   consequently to erroneous interpretation of species-environment relationships (Gómez-

284   Rodríguez et al., 2011). Subsequently, we derived detection histories from our repeated visits

285   and ran species-specific analysis aid of the free software program PRESENCE v3.1 (Hines,

286   2006) with the intention of accounting for detection probabilities and true site-occupancy

287   rates (MacKenzie et al., 2002, 2003). Based on the latter and according to Pellet and Schmidt

288   (2005), we calculated the probability of not detecting a species after the three visits per site

289   we carried out. For species with this estimator being different from zero, we realised a model

290   selection based analysis accounting for potential false-absence. For this, we used the single-

291   season analysis option implemented in program PRESENCE, introducing the 16 previously

292   mentioned environmental predictors as site-occupancy covariables and assuming a constant

293   detection probability over sites and sampling occasions. We then defined 11 models we

294   believed might explain species site-occupancy, each of them combining a different set of

295   covariables (Table 2). Finally, we used the parametric bootstrap procedure described by

296   Mackenzie and Bailey (2004) for assessing the fit of these site-occupancy models (bootstrap

297   value was set to 3000).

298

299   \Results

300

301   Amphibian survey

302   Excluding observations of invasive species (*Triturus carnifex* and *Pelophylax*

303   *ridibundus*), we detected during our field survey on 46 breeding ponds the presence of more

304   than 12'000 amphibian individuals belonging to six different species: *Bufo bufo*, *Rana*

305   *temporaria*, *Pelophylax lessonae*, *Mesotriton alpestris*, *Lissotriton helveticus*, and

306   *Salamandra salamandra*. Three of them (*B. bufo*, *L. helveticus* and *S. salamandra*) are

307 included in the Swiss Red List of endangered species with vulnerable (VU) conservation

308 status (Schmidt and Zumbach, 2005). Amphibian species distribution varied between one and

309 five for species richness (mean = 3.28 ± 0.88) and between five and 1016 for total abundance

310 (mean = 279.85 ± 258.9). Site-occupancy and abundance were high for *B. bufo* (site-

311 occupancy rate: 83%, total occurrences proportion: 27%), *R. temporaria* (100%, 56%) and *M.*

312 *alpestris* (96%, 16%), whereas *L. helveticus* (17%, <1%), *S. salamandra* (26%, <1%) and *P.*

313 *lessonae* (7%, <1%) were much rare.

314

315 Generalized linear model analysis and community projection

316   The analysis of the data using GLM techniques showed that several pond, landscape

317 and forest management variables affect amphibian distribution at the same time (Table 3).

318 The best model obtained relative to species richness ($R^2 = 0.49$) emphasises significant effects

319 (significance threshold: $P < 0.05$) of the pond surface area, the presence of a running water

320 supply, the presence of a recent forest stand close to the pond(positive correlations) and the

321 pond elevation (negative correlation). In a similar way, the best model in relation to

322 amphibian total abundance ($R^2 = 0.73$) identifies the pond size, the connectivity, the stand age

323 heterogeneity and forest cover as having a positive significant influence. Moreover, even if

324 not presenting significant effect, the following variables were kept in these final models: the

325 aquatic vegetation cover, the canopy closure and the stand age heterogeneity in the species

326 richness model, and the aquatic vegetation cover, the streams density, the coniferous rate

327 around the pond, the exploitation intensity, the volume of large dead wood at ground level

328 and the pond elevation in the total abundance model.

329   Landscape and forest management predictors highlighted by the previous GLM

330 procedure were then used to build a projection for the whole study area of the expected total

331 abundance in amphibians on breeding ponds (Figure 1). By locating the most suitable areas

332 for new ponds creation in the centre of the forested landscape and at locations characterized

333 by a high proximity with existing breeding ponds, this projection emphasizes the importance

334 of connectivity and forest cover for the determination of amphibian total abundance. Given

335 the dominance of pond variables compared with landscape and forest management variables

336 shown to influence species richness, repeating this projection for the latter wasn't relevant.

337

338 Site-occupancy statistics and model selection analysis

339   Given the very low number of occurrences observed for *P. lessonae* (n = 3), we

340 excluded this species from this part of the analysis. Concerning the five remaining species, we

341 found that the three of them belonging to the Swiss Red List of endangered species, namely *B.*
342 *bufo*, *S. salamandra* and *L. helveticus*, present a considerable risk of false absence after the
343 three visits per site we carried out (respectively 0.04, 0.14 and 0.16), whereas this estimator is
344 equal to zero in the case of *R. temporaria* and *M. alpestris* (Figure 2). Therefore, we
345 submitted only the three Red List species to the model selection based analysis accounting for
346 potential false-absence. This analysis reveals that models related to pond management and to
347 metapopulation survival in the case of *L. helveticus*, and those related to larvae survival and to
348 pond management in the case of *S. salamandra* perform best than the others (Table 4).
349 Indeed, the cumulative sum of Akaike weights of each of these pairs of "best models" is
350 greater than 0.7. In addition, each of them comes before the full model in the AIC ranking.
351 Furthermore, this ranking is supported by the high p-value (0.48 and 0.5 in the case of *L.*
352 *helveticus*, and 0.69 and 0.59 in the case of *S. salamandra*) obtained by the top models via the
353 bootstrap procedure, which indicates that they predict in a consistent way with what was
354 observed on the field. Consequently, these results suggest that environmental covariables that
355 are shared in common by these two pairs of "best models", which means the pond
356 connectivity and the streams density in the case of *L. helveticus*, and the pond surface area,
357 the aquatic vegetation cover and the presence of a running water supply in the case of *S.*
358 *salamandra*, are of crucial importance for the focal species. Concerning *B. bufo*, the null
359 model performs best than all the others, thus indicating that this analysis didn't provide any
360 trustworthy results for this species (we therefore chose not to show the resulting table).

361

362 \Discussion

363

364   Understanding ecological requirements of biphasic lifecycle amphibians is hard due to
365 their dependence to both aquatic and terrestrial habitats. Consequently, research efforts
366 concerning amphibian distribution generally focused on one aspect of amphibian ecology
367 (Trenham and Shaffer, 2005). Relatively to forest amphibian species, numerous studies thus
368 investigated either the effect of forest management (Hansen et al., 1991; Demaynadier and
369 Hunter, 1995), or the effect of pond characteristics (Egan and Paton, 2004) or else the
370 influence of landscape parameters (Herrmann et al., 2005; Werner et al., 2007). Whereas
371 canopy closure, aquatic vegetational cover and pond morphology have been identified as the
372 main factors influencing amphibian species richness and abundance at pond scale (Burne and
373 Griffin, 2005; Skidds et al., 2007), pond connectivity, stream density and forest cover
374 appeared to be the key predictors at landscape scale (Cushman, 2006; Ficetola et al., 2009;

375 Ribeiro et al., 2011). Finally, studies investigating effects of forest management parameters

376 highlighted the importance of dead wood, coniferous rate and stand age for forest amphibian

377 distribution (Petranka, 1994; Bull, 2002; Loehle et al., 2005). But very few studies try to

378 investigate those different axes simultaneously (Hamer and McDonnell, 2008; Lemckert and

379 Mahony, 2010; Hamer and Parris, 2011). Here by examining the influence of 16

380 environmental variables, we show that pond, landscape and forest management characteristics

381 affect amphibian species richness and abundance at the same time.

382   At pond scale and according to numerous previous studies (Waldick et al., 1999;

383 Burne and Griffin, 2005; Skidds et al., 2007), we found that pond size positively affect both

384 amphibian species richness and abundance. This finding may result from an increase in

385 aquatic microhabitat diversity and above all in feeding resources availability with pond size.

386 One can nevertheless expects that this relation follows a curvilinear relationship, as bigger

387 ponds are more likely to contain predatory fish (Hecnar, 1997; Hecnar and M'Closkey, 1998).

388 Our predictor range was probably insufficient to detect such a pattern. A second valuable

389 result with conservation implications concerns the significant increase in species richness

390 observed in the presence of a running water supply. This can be explained by the fact that

391 individuals of *S. salamandra*, and to a lesser extent *L. helveticus*, were almost exclusively

392 monitored in ponds presenting a permanent water supply. This observation fits perfectly the

393 ecological requirements of those species which are known to be mainly restricted to cool and

394 oligotrophic water (Günther, 1996; Meyer et al., 2009).

395   In managed forest, many studies revealed a clear effect of stand age on amphibian

396 species, older forests being richer than young ones (Raphael, 1988; Welsh, 1990; Petranka,

397 1994; Petranka et al., 1994; Dupuis et al., 1995; Russell et al., 2002). But in many cases, this

398 outcome simply reflect the obvious detrimental effect of clear-cutting on amphibian

399 populations (Demaynadier and Hunter, 1995), young forests being often mingle with recently

400 clearcut stands (Loehle et al., 2005). In our study area, clear-cutting practice was abandoned

401 for a few decades which certainly explains the positive relation we observed between forest

402 seral stage heterogeneity and amphibian abundance. Indeed, stand age heterogeneity is related

403 to forest structural complexity and diversity (Hansen et al., 1991) which in turn underlies

404 important habitat factors for amphibians such as the amount of coarse woody debris, the litter

405 quality and the soil moisture (Spies and Cline, 1988; Demaynadier and Hunter, 1995). The

406 positive effect of recent (20th century) forest stands on amphibian species richness should be

407 interpreted in the same way, those areas promoting the establishment of an uneven-aged

408   stand. At forest management level, our study thus emphasizes the importance of maintaining a

409   seral succession that gets as close as possible to natural forest dynamic.

410   At the landscape scale, we obtained a decline of amphibian species richness along

411   increasing elevation gradient, which is consistent with the general findings of Rahbek (1995).

412   Actually in our survey, this pattern mainly results from the almost complete absence of *L.*

413   *helveticus* and especially *S. salamandra* above 800 m.a.s.l., both these species preferentially

414   occurring at around 400 to 500 m.a.s.l. in Western Europe (Günther, 1996; Meyer et al.,

415   2009). According to numerous studies reviewed by Cushman (2006), we observed a positive

416   relationship between amphibian abundance and the proportion of forested areas in the

417   surroundings. Forested zones are known to be of crucial importance for pond breeding

418   amphibians in providing shade, favouring moisture at ground level and contributing to the

419   availability of diversified habitats (Corn and Bury, 1989; Waldick, 1997; Naughton et al.,

420   2000; Herrmann et al., 2005). Furthermore, this result has to be related to the observed

421   positive effect of pond connectivity on amphibian abundance, which in addition supports the

422   previous studies by Ribeiro et al. (2011), Hamer and McDonnell (2008) and Sjogren (1991).

423   Indeed, taken together these observations make a strong case for the assumption that pond

424   breeding amphibian dynamic often resemble metapopulation models (Marsh and Trenham,

425   2001) and thus underscore the vulnerability of local amphibian populations to habitat loss and

426   fragmentation (Cushman, 2006).

427   Despite the abundant literature highlighting and describing the mechanisms through

428   which the amount of coarse woody debris positively impacts amphibian populations (Harmon

429   et al., 1986; Hansen et al., 1991; Demaynadier and Hunter, 1995; Whiles and Grubaugh,

430   1996), we found no evidence of such a relationship in our survey. This failure can probably be

431   attributed to the insufficiently proximal way we measured the amount of dead wood at ground

432   level. Actually, our measurements didn't considered neither the spatial distribution of coarse

433   woody debris (e.g. rather in piles or rather scattered), nor its decomposition stage although

434   these parameters were shown to influence the dead wood quality for amphibians species

435   (decomposition stage: Waldick et al., 1999; spatial distribution: Indermaur and Schmidt,

436   2011). Interestingly and contrary to the findings of numerous studies (Demaynadier and

437   Hunter, 1995; Waldick et al., 1999; Loehle et al., 2005), coniferous rate didn't appeared as a

438   main driver of amphibian populations. But this can be related to the fact that the vast majority

439   of the study area is located above 700 m.a.s.l. and is thus naturally dominated for a long time

440   by mixed forests (Steinlin et al., 1993).

441   A recurrent problem with species distribution models relying on correlation analysis

442   between environmental factors and species richness or abundance of a taxon arises when there

443   are significant differences in species detection frequencies, the majority of them being very

444   common while a few are much rarer or cryptic. In such case, models identify with reliability

445   parameters influencing distribution of abundant species, but results are less trustworthy for

446   species with scarce distribution or that often go undetected (Gotelli and Colwell, 2001; Engler

447   et al., 2004). And this constitutes a great conservation issue knowing that rare species are

448   generally classified as endangered. In order to avoid such a problem, we ran a model selection

449   based analysis accounting for potential false-absence for the three Red List species of our

450   survey, namely *B. bufo*, *L. helveticus* and *S. salamandra*. With the exception of *B. bufo* for

451   which we obtained no valuable result, this analysis indeed reveals that environmental

452   variables influencing distribution of *L. helveticus* and *S. salamandra* partially differ from the

453   ones identified by the classical macroecological method as affecting the whole amphibian

454   community.

455   Thus, results of this model selection based analysis indicate that distribution of *S.*

456   *salamandra* is firstly related to within-pond variables (i.e. pond size, emergent aquatic

457   vegetation cover and presence of a running water supply), whereas *L. helveticus* occurrence is

458   mainly affected by landscape scale parameters (i.e. pond connectivity and streams density).

459   This seems consistent with what was observed on the field, that is to say that presence of *S.*

460   *salamandra* was strongly associated with ponds fitted with a water supply, and that *L.*

461   *helveticus* presents a patchy distribution over the study area. Concerning *B. bufo*, our inability

462   to obtain conclusive outcomes obviously results from the high observed site-occupancy rate

463   of this species in the study area (i.e. 83%, see Figure 2) which is incompatible with such site-

464   occupancy-modelling. Nevertheless, we can expect that management recommendations

465   provided on the basis of analysis ran for *S. salamandra* and *L. helveticus* will also benefit to

466   *B. bufo* as this species is already widely distributed in the study area.

467   Consequently, our results indicate that, when aiming at identifying main drivers of

468   amphibian distribution, considering risk of false-absence for rare and cryptic species provides

469   complementary results to those obtained with classical species distribution models. This

470   support the findings of numerous previous studies (Moilanen, 2002; Gu and Swihart, 2004;

471   Mazerolle et al., 2005) concluding that not accounting for detectability in species distribution

472   models can result in over- or under-estimating the influence of the investigated variables,

473   which can at worst lead to erroneous conclusions. Hence, this information is of great concern

474   in the current context of biodiversity loss (Wake and Vredenburg, 2008) and we thus strongly

encourage the use of site-occupancy models in order to powerfully target conservation measures for cryptic and endangered species.

Management implications

Although this study was carried out in a restricted area and only during one breeding season, the results raise several issues of general importance for the management and conservation of forest amphibians. Studies investigating amphibian distribution in forest dominated landscape generally focus on forest management variables and often ignore the contribution of within-pond parameters (Demaynadier and Hunter, 1995). Here we provide evidence that different environmental variables acting at all pond, landscape and forest management levels affect amphibian distribution. This emphasizes the importance of considering all those different aspects in forest management programs in order to first efficiently identify and protect the most suitable areas for amphibians, and second to create adequate breeding ponds surrounded by favourable terrestrial habitats. In this respect and according to our results, we strongly recommend to forest managers and stakeholders to protect and restore primarily breeding ponds characterized by sufficient surface areas and by the presence of running water supplies, as we demonstrated the beneficial effects of these parameters for amphibian species in providing ponds with varied microhabitats and microclimates. Finally at a larger scale, our findings highlight the crucial importance of considering pond connectivity, both through stream corridors and above all forest cover, as well as providing uneven-aged stands in order to guarantee habitat structure diversity and mosaic landscapes, which are highly favorable to amphibian communities.

\Acknowledgements

503   \References

504   Achard, F., Bennett, J., Beyer, D., Carle, J., Carneiro, A., Csoka, P., DelLungo, A., Durand,
505   F., Fernagut, M., Haney, L.E., Innes, J., Kaimowitz, D., Karmann, M., Kothari, A.,
506   Ladsten, I., Lambrechts, C., Lassen, B., Lebedys, A., Wilkie, M.L., Martin, C., Marr, C.,
507   Miles, L., Mutasa, M., Nellemann, C., Olsen, V., Otto, M., Parviainen, J., Ramos, A.,
508   Rekacewicz, P., Rucevska, I., Sellar, J., Olsen, C.S., Tavora-Jainchill, B., Turyatunga, F.,
509   Unterstell, N., Van Brusselen, J., Vuorinen, P., Weißschnur, M., 2009. Vital Forest
510   Graphics, Cartography. UNEP/GRIG-Adrendal.

511   Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species
512   of European temperate forests on soil fertility. Annals of Forest Science 59, 233-253.

513   Babbitt, K.J., Baber, M.J., Tarr, T.L., 2003. Patterns of larval amphibian distribution along a
514   wetland hydroperiod gradient. Revue canadienne de zoologie 81, 1539-1552.

515   Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances,
516   ecosystem function and management of European forests. Forest Ecology and
517   Management 132, 39–50.

518   Bouët, M., 1985. Climat et météorologie de la Suisse romande. Payot, Lausanne.

519   Bull, E.L., 2002. The value of coarse woody debris to vertebrates in the Pacific Northwest.

520   Burne, M.R., Griffin, C.R., 2005. Habitat associations of pool-breeding amphibians in eastern
521   Massachusetts, USA. Wetlands Ecology and Management 13, 247-259.

522   Bury, R.B., 1983. Differences in Amphibian Populations in Logged and Old Growth
523   Redwood Forest. Northwest Science 57, 167-178.

524   Clot, F., Kissling, P., Plumettaz-Clot, A.-C., 1994. Carte phyto-écologique des forêts
525   lausannoises. Notice explicative. Lausanne: Service des Forêts, Domaines et Vignobles.

526   Colburn, E.A., 2004. Vernal Pools: Natural History and Conservation. The MacDonald and
527   Woodward Publishing Company, Blacksburg, VA, USA.

528   Corn, P.S., Bury, R.B., 1989. Logging in Western Oregon - Responses of Headwater Habitats
529   and Stream Amphibians. Forest Ecology and Management 29, 39-57.

530   Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: A review and
531   prospectus. Biological Conservation 128, 231-240.

532   Delarze, R., Gonseth, Y., 2008. Guide des milieux naturels de Suisse. Rossolis, Bussigny.

533   Demaynadier, P.G., Hunter, M.L., 1995. The relationship between forest management and
534   amphibian ecology: a review of the North American literature. Environmental Reviews
535   3, 230-261.

536 Demaynadier, P.G., Hunter, M.L., 1998. Effects of silvicultural edges on the distribution and
537   abundance of amphibians in Maine. Conservation Biology 12, 340-352.

538 Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.-P., Guisan, A., 2011. Predicting
539   spatial patterns of plant species richness: a comparison of direct macroecological and
540   species stacking modelling approaches. Diversity and Distributions 17, 1122-1131.

541 Dupuis, L.A., Smith, J.N.M., Bunnell, F., 1995. Relation of Terrestrial-Breeding Amphibian
542   Abundance to Tree-Stand Age. Conservation Biology 9, 645-653.

543 Egan, R.S., Paton, P.W.C., 2004. Within-pond parameters affecting oviposition by wood
544   frogs and spotted salamanders. Wetlands 24, 1-13.

545 Engler, R., Guisan, A., Rechsteiner, L., 2004. An improved approach for predicting the
546   distribution of rare and endangered species from occurrence and pseudo-absence data.
547   Journal of Applied Ecology 41, 263-274.

548 Esri, 2008. ArcGIS 9.3.

549 Ficetola, G.F., Padoa-Schioppa, E., De Bernardi, F., 2009. Influence of Landscape Elements
550   in Riparian Buffers on the Conservation of Semiaquatic Amphibians. Conservation
551   Biology 23, 114-123.

552 Fleming, T.L., Freedman, B., 1998. Conversion of natural, mixed-species forests to conifer
553   plantations: Implications for dead organic matter and carbon storage. Ecoscience 5, 213-
554   221.

555 Führer, E., 2000. Forest functions, ecosystem stability and management. Forest Ecology and
556   Management 132, 29–38.

557 Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the
558   measurement and comparison of species richness. Ecology Letters 4, 379-391.

559 Gu, W., Swihart, R.K., 2004. Absent or undetected? Effects of non-detection of species
560   occurrence on wildlife–habitat models. Biological Conservation 116, 195-203.

561 Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology.
562   Ecological Modelling 135, 147-186.

563 Gómez-Rodríguez, C., Bustamante, J., Díaz-Paniagua, C., Guisan, A., 2011. Integrating
564   detection probabilities in species distribution models of amphibians breeding in
565   Mediterranean temporary ponds. Diversity and Distributions no-no.

566 Günther, R., 1996. Die Amphibien und Reptilien Deutschlands. Jena.

567 Hamer, A.J., McDonnell, M.J., 2008. Amphibian ecology and conservation in the urbanising
568   world: A review. Biological Conservation 141, 2432-2449.

569 Hamer, A.J., Parris, K.M., 2011. Local and landscape determinants of amphibian
570   communities in urban ponds. Ecological Applications 21, 378-390.

571 Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving Biodiversity in
572   Managed Forests - Lessons from Natural Forests. Bioscience 41, 382-392.

573 Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D.,
574   Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack,
575   K., Cummins, K.W., 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems.
576   Advances in Ecological Research 15, 133-302.

577 Hecnar, S., 1997. The effects of predatory fish on amphibian species richness and distribution.
578   Biological Conservation 79, 123-131.

579 Hecnar, S.J., M'Closkey, R.T., 1998. Species richness patterns of amphibians in southwestern
580   Ontario ponds. Journal of Biogeography 25, 763-772.

581 Herrmann, H.L., Babbitt, K.J., Baber, M.J., Congalton, R.G., 2005. Effects of landscape
582   characteristics on amphibian distribution in a forest-dominated landscape. Biological
583   Conservation 123, 139-149.

584 Hines, J.E., 2006. PRESENCE2 - Software to estimate patch occupancy and related
585   parameters.

586 Indermaur, L., Schmidt, B.R., 2011. Quantitative recommendations for amphibian terrestrial
587   habitat conservation derived from habitat selection behaviour. Ecological Applications
588   21, 2548-2554.

589 Induni-Gaffiot, C., Moret, J.-L., 2000. Mouilles et Gouilles du Jorat: Promenades botaniques
590   à travers quelques lieux humides des forêts lausannoises. Les Cahiers de la Forêt
591   Lausannoise 13, 1-80.

592 Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends in
593   Ecology & Evolution 19, 101-108.

594 Kaufmann, E., 2001. Estimation of standing timber, growth and cut, in: Brassel, P., Lischke,
595   H. (Eds.), Swiss National Forest Inventory: Methods and Models of the Second
596   Assesement. Swiss Federal Research Institute WSL, Birmensdorf, pp. 162-196.

597 Kovar, R., Brabec, M., Vita, R., Bocek, R., 2009. Spring migration distances of some Central
598   European amphibian species. Amphibia-Reptilia 30, 367-378.

599 Larsson, T.-B., 2011. Biodiversity evaluation tools for European forests. - Ecol. Bull 50.

600 Lemckert, F., Mahony, M., 2010. The Relationship among Multiple-Scale Habitat Variables
601   and Pond Use by Anurans in Northern New South Wales, Australia. Herpetological
602   Conservation and Biology 5, 537-547.

603 Loehle, C., Wigley, T.B., Shipman, P.A., Fox, S.F., Rutzmoser, S., Thill, R.E., Melchiors,
604   M.A., 2005. Herpetofaunal species richness responses to forest landscape structure in
605   Arkansas. Forest Ecology and Management 209, 293-308.

606 MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. Journal of
607   Agricultural, Biological and Environmental Statistics 9, 300-318.

608 MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating
609   site occupancy, colonization, and local extinction when a species is detected imperfectly.
610   Ecology 84, 2200-2207.

611 MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A.,
612   2002. Estimating site occupancy rates when detection probabilities are less than one.
613   Ecology 83, 2248-2255.

614 Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation.
615   Conservation Biology 15, 40-49.

616 Mazerolle, M., Desrochers, A., Rochefort, L., 2005. Landscape characteristics influence pond
617   occupancy by frogs after accounting for detectability. Ecological Applications 15, 824–
618   834.

619 McCormick, P.V., Laing, J.A., 2003. Effects of increased phosphorus loading on dissolved
620   oxygen in a subtropical wetland, the Florida Everglades. Wetlands Ecology and
621   Management 11, 199-216.

622 McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models. 2nd edition. Chapman and
623   Hall, London.

624 McNeely, J.A., 1994. Lessons from the past: forests and biodiversity. Biodiversity and
625   conservation 3, 3–20.

626 Meyer, A., Zumbach, S., Schmidt, B.R., Monney, J.-C., 2009. Les amphibiens et reptiles de
627   Suisse, Haupt. ed. Berne.

628 Mitchell, J.C., Rinehart, S.C., Pagels, J.F., Buhlmann, K.A., Pague, C.A., 1997. Factors
629   influencing amphibian and small mammal assemblages in central Appalachian forests.
630   Forest Ecology and Management 96, 65-76.

631 Moilanen, A., 2002. Implications of empirical data quality to metapopulation model
632   parameter estimation and application. Oikos 96, 516–530.

633 Moseley, K.R., Castleberry, S.B., Ford, W.M., 2004. Coarse woody debris and pine litter
634   manipulation effects on movement and microhabitat use of Ambystoma talpoideum in a
635   Pinus taeda stand. Forest Ecology and Management 191, 387-396.

636 Naughton, G.P., Henderson, C.B., Foresman, K.R., McGraw, R.L., 2000. Long-toed
637   salamanders in harvested and intact Douglas-fir forests of western Montana. Ecological
638   Applications 10, 1681-1689.

639 Owens, A.K., Moseley, K.R., Mccay, T.S., Castleberry, S.B., Kilgo, J.C., Ford, W.M., 2008.
640   Amphibian and reptile community response to coarse woody debris manipulations in
641   upland loblolly pine (Pinus taeda) forests. Forest Ecology and Management 256, 2078-
642   2083.

643 Pellet, J., Schmidt, B.R., 2005. Monitoring distributions using call surveys: estimating site
644   occupancy, detection probabilities and inferring absence. Biological Conservation 123,
645   27-35.

646 Petranka, J.W., 1994. Response to Impact of Timber Harvesting on Salamanders.
647   Conservation Biology 8, 302-304.

648 Petranka, J.W., Brannon, M.P., Hopey, M.E., Smith, C.K., 1994. Effects of Timber
649   Harvesting on Low Elevation Populations of Southern Appalachian Salamanders. Forest
650   Ecology and Management 67, 135-147.

651 Prugh, L.R., 2009. An evaluation of patch connectivity measures. Ecological applications : a
652   publication of the Ecological Society of America 19, 1300-1310.

653 Rahbek, C., 1995. The Elevational Gradient of Species Richness - a Uniform Pattern.
654   Ecography 18, 200-205.

655 Raphael, M.G., 1988. Long-term trends in abundance of amphibians, reptiles, and mammals
656   in Douglas-fir forests of northwestern California, in: Szaro, R.C., Severson, K.E., Patton,
657   D.R. (Eds.), Management of Amphibians, Reptiles and Small Mammals in North
658   America. USDA For. Serv. Gen. Tech. Rep. RM-166, pp. 23-31.

659 Ribeiro, R., Carretero, M.A., Sillero, N., Alarcos, G., Oritz-Santaliestra, M., Lizana, M.,
660   Llorente, G.A., 2011. The pond network: can structural connectivity reflect on
661   (amphibian) biodiversity patterns? Landscape Ecology published online.

662 Russell, K.R., Guynn, D.C., Hanlin, H.G., 2002. Importance of small isolated wetlands for
663   herpetofaunal diversity in managed, young growth forests in the Coastal Plain of South
664   Carolina. Forest Ecology and Management 163, 43-59.

665 Russell, K.R., Wigley, T.B., Baughman, W.M., Hanlin, H.G., Ford, W.M., 2004. Responses
666   of southeastern amphibians and reptiles to forest management: a review, Southern Forest
667   Science: Past, Present, Future, Southern Research Station General Technical Report
668   SRS-75. USDA Forest Service. Koeltz Scientific Books Koenigstein, Germany,
669   Asheville, NC: U.S.

670 Sacerdote, A.B., King, R.B., 2009. Dissolved Oxygen Requirements for Hatching Success of
671   Two Ambystomatid Salamanders in Restored Ephemeral Ponds. Wetlands 29, 1202-
672   1213.

673 Schmidt, B.R., Zumbach, S., 2005. Liste Rouge des amphibiens menacés en Suisse. Berne.

674 Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J.K., Gibbons, J.W., Gibbs, J.P.,
675   Graeter, G.J., Harper, E.B., Hocking, D.J., Hunter, M.L., Patrick, D.A., Rittenhouse,
676   T.A.G., Rothermel, B.B., 2009. Effects of Timber Harvest on Amphibian Populations:
677   Understanding Mechanisms from Forest Experiments. Bioscience 59, 853-862.

678 Sjogren, P., 1991. Extinction and Isolation Gradients in Metapopulations - the Case of the
679   Pool Frog (Rana-Lessonae). Biological Journal of the Linnean Society 42, 135-147.

680 Skidds, D.E., Golet, F.C., Paton, P.W.C., Mitchell, J.C., 2007. Habitat correlates of
681   reproductive effort in wood frogs and spotted salamanders in an urbanizing watershed.
682   Journal of Herpetology 41, 439-450.

683 Smallbone, L.T., Luck, G.W., Wassens, S., 2011. Anuran species in urban landscapes:
684   Relationships with biophysical, built environment and socio-economic factors.
685   Landscape and Urban Planning 101, 43-51.

686 Smith, A.M., Green, D.M., 2005. Dispersal and the metapopulation paradigm in amphibian
687   ecology and conservation: are all amphibian populations metapopulations? Ecography
688   28, 110–128.

689 Spies, T.A., Cline, S.P., 1988. Coarse woody debris in forests and plantations of coastal
690   Oregon, in: Maser, C., Tarrant, K.F., Trappe, J.M., Franklin, J.F. (Eds.), From the Forest
691   to the Sea: a Story of Fallen Trees. Serv. Gen. Tech. Rep. PNW-GTR-229, pp. 5-23.

692 Steinlin, H., Chevallaz, O., Weidmann, M., Calame, F., Wanders, A.-C., Matthey, G., Gratier,
693   M., Kissling, P., Plumettaz, A.-C., Richoz, I., Vollenweider, P., Cherix, D., Cuendet, G.,
694   Beaud, P., Coutaz, G., Robert, J.-F., Badan, R., Racine, A., 1993. L'environnement
695   forestier lausannois, diversité et réalité mouvante, Cahier binding. S. and K. Binding
696   Stiftung, Basel.

697 Trenham, P.C., Shaffer, H.B., 2005. Amphibian upland habitat use and its consequences for
698   population viability. Ecological Applications 15, 1158-1168.

699 Vonesh, J.R., 2001. Patterns of richness and abundance in a tropical African leaf-litter
700   herpetofauna. Biotropica 33, 502-510.

701 Wake, D.B., Vredenburg, V.T., 2008. Are we in the midst of the sixth mass extinction? A
702   view from the world of amphibians. Proceedings of the National Academy of Sciences of
703   the United States of America 105, 11466-11473.

704 Waldick, R.C., 1997. The impact of forestry practices upon amphibian populations in eastern
705   North America, in: Green, D.M. (Ed.), Amphibians in Decline: Canadian Studies of a
706   Global Problem. St. Louis, Missouri, pp. 191-205.

707 Waldick, R.C., Freeman, B., Wassersug, R.J., 1999. The consequences for amphibians of the
708   conversion of natural, mixed-species forests to conifer plantations in southern New
709   Brunswick. The Canadian Field-Naturalist 113, 408-418.

710 Welsh, H.H., 1990. Relictual Amphibians and Old-Growth Forests. Conservation Biology 4,
711   309-319.

712 Werner, E.E., Skelly, D.K., Relyea, R.A., Yurewicz, K.L., 2007. Amphibian species richness
713   across environmental gradients. Oikos 116, 1697-1712.

714 Whiles, M.R., Grubaugh, J.W., 1996. Importance of Coarse Woody Debris to Souhtern Forest
715   Herpetofauna, in: Biodiversity and Coarse Woody Debris in Southern Forests. Gen.
716   Tech. Rep. SE-94. Asheville, NC: U.S. Department of Agriculture, Forest Service,
717   Southeastern Forest Experiment Station., pp. 94-100.

718 Wyman, R.L., 1988. Soil Acidity and Moisture and the Distribution of Amphibians in 5
719   Forests of Southcentral New-York. Copeia 394-399.

720 Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space
721   and time. Trends in Ecology & Evolution 16, 446-453.

722

723   \Figure captions

724

725   Figure 1: Study area located on the Central Plateau in the Western Switzerland. Polygons with

726   black outline delimit forested areas and black dots represent the amphibian breeding ponds

727   surveyed. Red to green gradient displays the projection of the expected total abundance in

728   amphibians on the whole study area (the greener, the higher expected abundance in

729   amphibians).

730

731   Figure 2: Barplot with standard error of the detection probability P, the naïve site-occupancy

732   estimate Q, the site-occupancy estimate accounting for imperfect detection probability Psi and

733   the probability of non-detection after three visits per site F for the five most common species

734   observed during the survey.

735

736   Table 1: Summary of the environmental variables collected in the study area and related with

737   forest amphibian distribution. Buffer values define the radius of measurement of the variables

738   centred on the ponds. GIS stands for Geographic Information Systems.

739

740   Table 2: Environmental variables content of the 11 different models built for the model

741   selection analysis.

742

743   Table 3: Summary of the GLM analysis investigating relationships between environmental

744   variables and both amphibian species richness and total abundance. Significance codes are

745   defined as usual (0 '***' 0.001 '**' 0.01 '*' 0.05 '•' 0.1 ' ' 1).

746

747   Table 4: Summary from fitting 11 different site-occupancy models to the detection histories

748   data of (A) *Lissotriton helveticus* and (B) *Salamandra salamandra*. ΔAIC for a model is the

749   relative difference between its Akaike information criterion score (AIC) and the AIC score of

750   the most parsimonious model (lowest AIC); w is the AIC model weight; p-value is a measure

751   of model fit resulting from a Pearson chi-square statistic based upon 3000 parametric
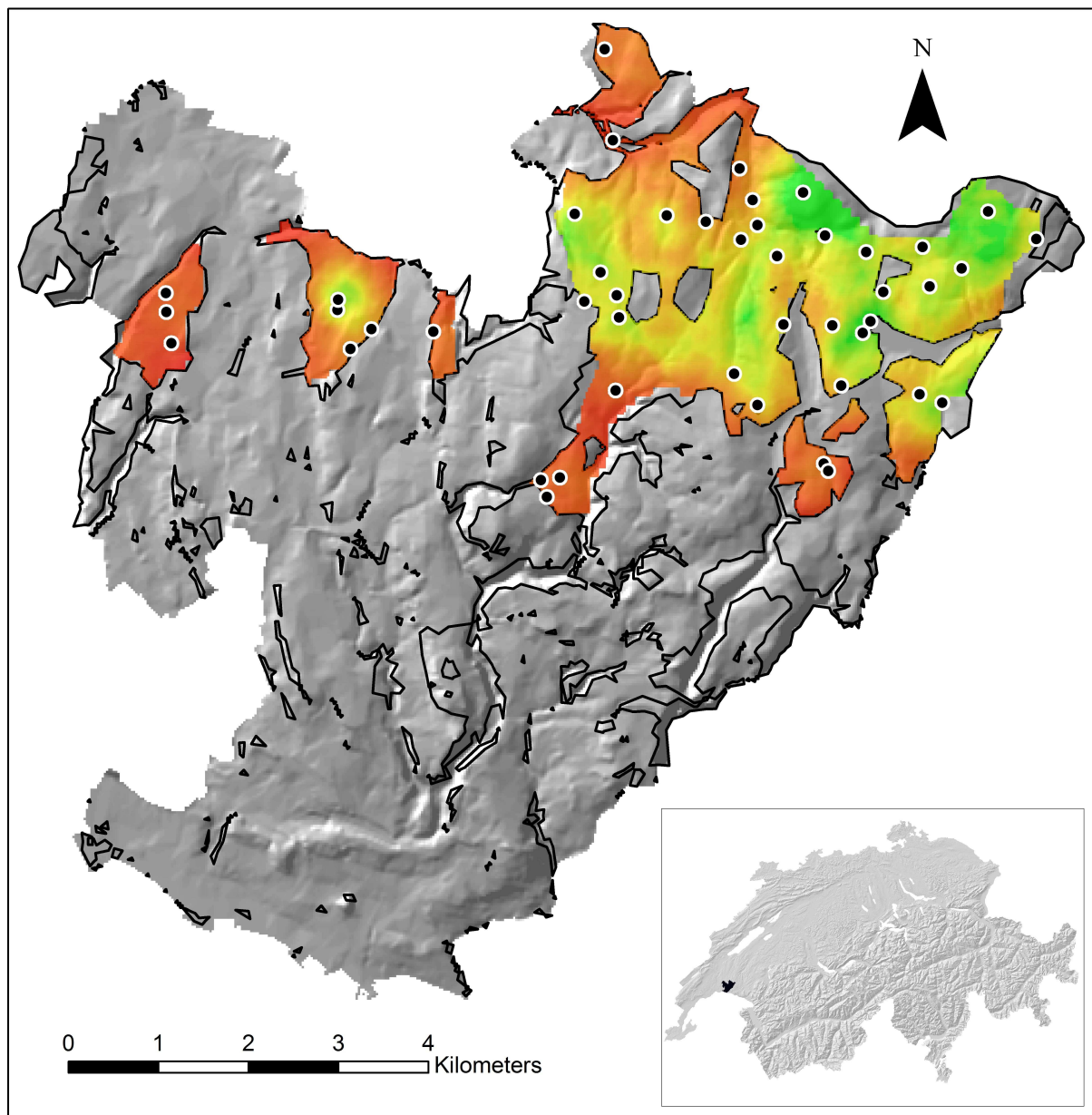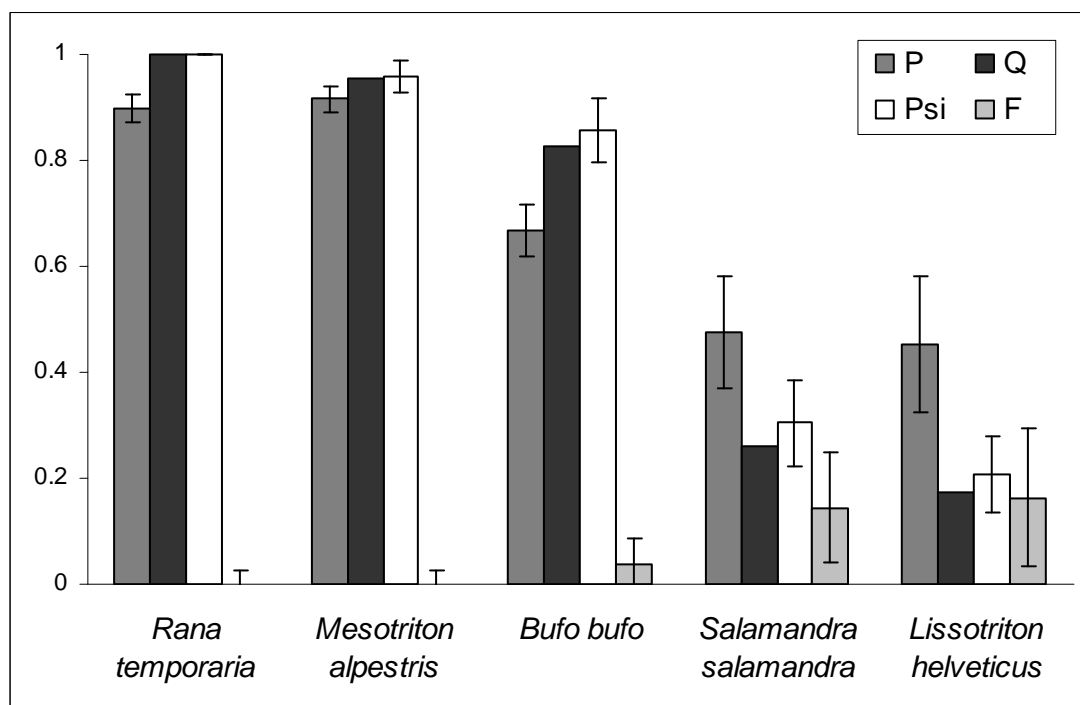
752   bootstraps.

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754 \Figures

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756 Figure 1

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759   Figure 2

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762

763   Table 1

764

Variable	Abbreviation	Description	Mean (range)	Buffer	Data source
Pond scale variables					
Pond size (ln)	Size	Natural logarithm of the pond surface area [m^2]	4.86 (1.1 - 8.48)	Pond	Field
Aquatic vegetation	Aqua-Veg	Percentage of the pond covered in emergent aquatic vegetation	34.48 (0 - 97.5)	Pond	Field
Water supply	Water	Presence/absence of a running water supply	0.3 (0=absence - 1=presence)	Pond	Field
Canopy closure	Canopy	Canopy density above the pond expressed as a percentage	54.78 (7.44 - 91.68)	Pond	Field
Forest management scale variables					
Coarse woody debris (ln)	CWD	Natural logarithm of the amount of dead wood at ground level [m^3]	2.44 (1.49 - 4.02)	100 m	Field
Understory vegetation	Veg	Percentage of the herbaceous vegetation cover	76.24 (30 - 98)	100 m	Field
Stand age	Age	Presence/absence of recent (20th century) forest stand close to the pond	0.28 (0=absence - 1=presence)	100 m	GIS
Tree diameter	Diam	Mean diameter at breast height of the forest stand [cm]	36.4 (29.83 - 46.25)	500 m	GIS
SD tree diameter	Sd-Diam	Standard deviation of the mean diameter at breast height [cm]	10.76 (5.28 - 13.83)	500 m	GIS
Coniferous rate A	Conifer-A	Percentage of coniferous stems close to the pond	41.9 (0 - 88.18)	100 m	GIS
Coniferous rate B	Conifer-B	Percentage of coniferous stems around the pond	48.93 (2.76 - 75.76)	500 m	GIS
Forest exploitation	Exploit	Proportion of forested landscape without logging during the last decade	0.03 (0 - 0.13)	500 m	GIS
Landscape scale variables					
Elevation	Elev	Elevation of the pond [m.a.s.l.]	798 (582 - 910)	Pond	GIS
Connectivity	Connect	Distance-weighted connectivity index	5.63 (1.93 - 8.64)	Pond	GIS
Forest cover	Forest	Proportion of landscape covered by forest	0.75 (0.4 - 1)	500 m	GIS
Hydrology	Hydro	Proportion of streams density	0.07 (0 - 0.15)	500 m	GIS

765   Table 2

766

Model name	Site covariables implemented	Number of site covariables implemented
Null model		
psi(.) p(.)	-	0
Full model		
psi(full) p(.)	Size, Aqua-Veg, Water, Canopy, Elev, Connect, CWD, Veg, Age, Diam, Sd-Diam, Conifer-A,Conifer-B, Exploit, Forest, Hydro	16
Pond scale models		
psi(larvae survival) p(.)	Size, Aqua-Veg, Water, Canopy, Conifer-A	5
psi(pond management) p(.)	Size, Aqua-Veg, Water, Connect, Hydro	5
Forest management scale models		
psi(adult survivial) p(.)	Conifer-B, Exploit, CWD, Veg, Age, Diam, Sd-Diam, Forest, Elev	9
psi(forest management) p(.)	Canopy, Conifer-A, Conifer-B, Exploit, CWD, Veg, Diam, Sd-Diam	8
Landscape scale models		
psi(metapopulation survival) p(.)	Connect, Hydro	2
psi(landscape) p(.)	Forest, Elev, Age	3
Hybrid models		
psi(larvae survival & pond management) p(.)	Size, Aqua-Veg, Water	3
psi(larvae survival & forest management) p(.)	Canopy, Conifer-A	2
psi(adult survival & forest management) p(.)	Conifer-B, Exploit, CWD, Veg, Diam, Sd-Diam	6

767

768

769   Table 3

770

Variable	Estimate ± Standard error	
	Total abundance in amphibians ($R^2 = 0.73$)	Amphibian species richness ($R^2 = 0.49$)
Pond surface area (Size)	0.338 ± 0.071 ***	0.193 ± 0.070 **
Emergent aquatic vegetation cover (Aqua-Veg)	-0.005 ± 0.003 •	-0.005 ± 0.004
Presence of a running water supply (Water)	-	0.688 ± 0.218 **
Canopy closure above the pond (Canopy)	-	-0.009 ± 0.006
Pond elevation (Elev)	0.005 ± 0.003	-0.003 ± 0.001 *
Pond connectivity (Connect)	0.181 ± 0.055 **	-
Volume of large dead wood at ground level (CWD)	0.182 ± 0.165	-
Presence of recent forest stand close to the pond (Age)	-	0.606 ± 0.223 **
Heterogeneity of forest stand (SD-Diam)	0.166 ± 0.057 **	0.102 ± 0.059 •
Coniferous rate around the pond (Conifer-B)	-0.021 ± 0.011 •	-
Forest exploitation intensity (Exploit)	-6.796 ± 4.738	-
Forest cover (Cover)	2.146 ± 0.688 **	-
Streams density (Hydro)	-5.041 ± 2.986	-

771

772 Table 4

773

774 A

Model	ΔAIC	w	p-value
psi(pond management) p(.)	0	0.42	0.48
psi(metapopulation survival) p(.)	0.85	0.28	0.50
psi(full) p(.)	1.88	0.17	0.14
psi(forest management) p(.)	2.43	0.13	0.07
psi(adult survival & forest management) p(.)	9.39	0.00	0.00
psi(juvenile survival & forest management) p(.)	11.26	0.00	0.01
psi(.) p(.)	12.29	0.00	0.01
psi(adult survival) p(.)	15.34	0.00	0.00
psi(juvile survival) p(.)	15.37	0.00	0.00
psi(juvenile survival & pond management) p(.)	16.2	0.00	0.01
psi(landscape) p(.)	16.29	0.00	0.01

775

776 B

Model	ΔAIC	w	p-value
psi(juvenile survival) p(.)	0	0.41	0.69
psi(pond management) p(.)	0.15	0.38	0.59
psi(full) p(.)	1.28	0.21	0.21
psi(juvenile survival & pond management) p(.)	10.86	0.00	0.01
psi(metapopulation survival) p(.)	20.23	0.00	0.00
psi(.) p(.)	21.27	0.00	0.01
psi(landscape) p(.)	21.39	0.00	0.00
psi(adult survival & forest management) p(.)	22.44	0.00	0.01
psi(juvenile survival & forest management) p(.)	22.97	0.00	0.00
psi(adult survival) p(.)	24.91	0.00	0.00
psi(forest management) p(.)	25.23	0.00	0.01

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