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**Influence of *Robinia pseudoacacia* L. on plant communities in
Swiss forests**

**Travail de Maîtrise universitaire ès Sciences en comportement, évolution et
conservation**

Master Thesis of Science in Behaviour, Evolution and Conservation

par

Audrey Elsig

Directeur : Dr Pascal, Vittoz

Superviseur (s) : Blaise, Petitpierre

Expert (s) : Anonymous

Department of Ecology and Evolution - DEE UNIL

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1 **Résumé**

2 Dans cette étude nous avons analysé l'influence de l'espèce invasive Robinier faux-acacia
3 (*Robinia pseudoacacia*) sur les communautés végétales de forêts en Suisse romande. Un
4 modèle de distribution de l'espèce en Suisse a été fait pour décrire sa niche écologique. De
5 plus nous avons comparé les sites avec et sans *R. pseudoacacia* du point de vue de leur
6 composition spécifique et de leurs caractéristiques écologiques (l'humus, la richesse en
7 espèces, la canopée, le recouvrement et la fréquence des espèces et certains traits biologiques
8 des espèces). Le modèle de distribution nous a montré que l'aire de répartition de robinier
9 s'étend à l'ensemble du Plateau suisse et aux vallées alpines jusqu'à 1000 m, avec une large
10 amplitude écologique (conditions sèches ou humides). Les résultats montrent que les sites
11 avec *R. pseudoacacia*, comparés aux sites sans, ont un humus montrant une meilleure
12 incorporation de la matière organique, plus de lumière, qu'il y a plus d'espèces nitrophiles et
13 avec un recouvrement de la strate herbacée plus important, en particulier avec le
14 développement des lianes. Compte tenu de sa large amplitude écologique, *R. pseudoacacia*
15 est susceptible d'envahir presque toutes les forêts de basses et moyennes altitudes. Par sa
16 symbiose avec des bactéries fixatrices d'azote, il change la chimie du sol par l'augmentation
17 de l'azote et les conditions du sous-bois par son feuillage clair qui laisse passer plus de
18 lumière. Ceci implique une modification de la flore du sous-bois, en favorisant les espèces
19 nitrophiles et les lianes, qui peuvent mettre en danger les espèces oligotrophes. Il est donc
20 important de ne pas favoriser cette espèce et de lutter dès que possible pour éviter son
21 développement dans les forêts.

22

23

24 **Abstract**

25 In this study we analysed the influence of the invasive species Black Locust (*Robinia*
26 *pseudoacacia*) on forest plant communities in Western Switzerland. A species distribution
27 model in Switzerland was developed to describe its ecological niche. Moreover we compared
28 sites with and without *R. pseudoacacia* to the point of view of their species composition and
29 their ecological characteristics (humus, species richness, canopy, frequency and cover of
30 species, biological traits). The distribution model showed that the potential distribution area of
31 *R. pseudoacacia* extends to the whole Swiss Plateau and alpine valleys up to 1000 m with
32 large ecological amplitude (dry or wet habitats). The results showed that sites with *R.*
33 *pseudoacacia*, compared to sites without, have a humus with a better incorporation of organic
34 matter, more light, more nitrophilous species, and a higher cover of the herb layer,
35 particularly with vines. Considering its large ecological amplitude, *R. pseudoacacia* is
36 susceptible to invade almost all the lowland forests. By its symbiosis with nitrogen-fixing
37 bacteria, it modifies the soil chemistry by increasing nitrogen content, and undergrowth
38 conditions because of its light foliage. This modifies undergrowth plant species composition,
39 with more nitrophilous species and vines, what can potentially endanger oligotrophic species.
40 It is therefore important to not encourage this species and to fight it as soon as possible to
41 prevent its development in the forests.

42

43

44 **Introduction**

45 Invasions of exotic species are among the most significant problems, from a global point of
46 view, in natural ecosystems (Parker et al. 1999). Recent reviews on the homogenization of the
47 world's ecosystems have shown that not only islands and disturbed sites are affected, but
48 mainland areas and little disturbed ecosystems are often invaded and dominated by the same
49 newly established species too (Ehrenfeld & Scott 2001). It is considered that invasive species
50 may be a cause of decline and extinction of native species (Coblentz 1990; Vitousek et
51 al.1997; Zalba et al. 2000). Moreover, major changes often occur when a non-native species
52 acquires a new function in the ecosystem (Vitousek & Walker 1989), which can lead either to
53 loss or alteration of plant communities (Simberloff 1991; Ruesink et al. 1995).

54

55 The nitrogen-fixing ability and the vegetative reproduction of Black locust (*Robinia*
56 *pseudoacacia* L.) are characteristics frequently found in invasive plants (Daehler 1998). This
57 species is considered one of the top 100 of invasive woody species in the world (Cronk and
58 Fuller 1995) and, now, the second most abundant deciduous tree on Earth (Boring & Swank
59 1984). It is native from North America and was introduced in Europe as an ornamental plant,
60 in 1601 by J. Robin in France (Keresztesi 1988). Its very durable wood makes it an important
61 timber producer (Keresztesi 1988), utilized for a diverse range of products including panelling
62 construction boards, firewood, fence posts and livestock forage (Keresztesi1980). Therefore
63 *R. pseudoacacia* is rated as the most important tree species for agro-forestry systems because
64 of its multiple uses. *R. pseudoacacia* is usually planted close to dwellings where previous
65 natural forests had been removed by deforestation (Viorel Blujdea et al. 2011). *R.*
66 *pseudoacacia* is shade intolerant, so it is associated with cleared areas, old pastures, road
67 sides, burned areas, river banks and cities or gardens (Chapman 1935; Ogden 1961; Boring
68 and Swank 1984; Bormann et al. 1993).

69

70 By its ability to fix nitrogen, to grow quickly, to reproduce vegetatively and to form dense,
71 monospecific stands, it may supplant native tree species (Mehrhoff et al. 2003) and change
72 plant communities. Many studies have shown the impact of nitrogen fixation on the soil (eg.
73 Stock et al 1995; Von Holle et al. 2006; Yelenik et al. 2004). But, as far as we know, none has
74 investigated the impact it has on the plant community of the forest understorey (shrubs and
75 herbs).

76

77 The aim of this study is to analyse the impact of *R. pseudoacacia* on the community of forests

78 by linking plant inventories in pairs of plots dominated or not by *R. pseudoacacia*.
79 Differences in species composition and differences in species cover between sites were
80 considered. We hypothesize that nitrophilous species are more common and have a higher
81 cover in stands dominated by *R. pseudoacacia*, what could have consequences on distribution
82 of oligotrophic species in forest understorey.

83

84 **Methods**

85 *Species distribution model*

86 To understand the ecological niche of *R. pseudoacacia* (necessary environmental conditions
87 for growth) and to obtain a map of its potential distribution, we did a distribution model with
88 BIOMOD2 (Thuiller et al. 2009) and ArcGIS (ESRI®), according to Guisan & Zimmermann
89 (2000) and Guisan & Thuiller (2005). Data about present occurrences were from
90 www.data.gbif.org, the state of Valais (Département des forêts et du paysage, www.vs.ch),
91 Infoflora (www.infoflora.ch) and from other isolated observations. Twelve environmental
92 variables (WSL: Swiss Federal Institute for Forest, Snow and Landscape Research) were used
93 to generate environmental profiles for our local distribution model and to calculate the
94 importance of the environmental variables in the species distribution model (Fig. 1).

95

96 *Study sites*

97 The study sites areas were located in Western Switzerland (Cantons de Vaud and Valais). The
98 climate of Vaud is humid and temperate. The average rainfall is around 1000 mm per year and
99 mean annual temperature around 9°C in lowland. Valais has a more sub-continental, with
100 lower annual average rainfall, around 600 mm, for similar annual temperatures (Swiss Federal
101 Office of Meteorology and Climatology, www.MeteoSwiss.ch). On the basis of available
102 occurrences and by looking at forests in landscape, we prospected for stands of *R.*
103 *pseudoacacia*. The stands had to meet the following criteria to be retained: presence of *R.*
104 *pseudoacacia* with a minimal cover of 25% in 100 m² of forest, without hedge effect, and an
105 another very close forest of 100 m² without *R. pseudoacacia* but with similar ecological
106 conditions (substrate, slope, aspect). Altogether, we found 27 sites, corresponding to 54 plots:
107 27 with *R. pseudoacacia* and 27 without. 16 sites were in Vaud and 11 sites in Valais. The
108 field observations were carried out between June and August 2013.

109

110 *Field measurements*

111 In plot was defined as a square of 10 x 10 meters. We used a spherical densiometer to
112 measure forest canopy opening from each corner of the square in direction of the centre
113 (Lemmon 1956) and determined the type of humus (Ponge 2011). For that, the thickness of
114 the horizons OL (not or little fragmented litter), OF (mixture of fragmented litter and pellets
115 of organic material), OH (only pellets of organic material) and A (organo-mineral material)
116 were measured if present; the humus was then classified according to the respective
117 importance of the horizons in one of the nine categories: from the very active Mull, with rapid
118 incorporation of organic matter (value 1), to the Mor, with very slow mineralization and
119 absence of incorporation to mineral material (value 9). The topographical values as slope,
120 elevation and aspect were recorded. The point method (Mueller-Dombois and Ellenberg
121 1974) was used to measure the species cover of understorey and low shrubs: The measuring
122 tape was placed every two meters in the square (four lines of 10 m), and species contacts with
123 a 1m-long stick were recorded every 20 centimetres, for a total of 200 points (converted in %
124 cover). Finally, we completed the species list for the whole plot in the three layers (herbs,
125 shrubs and trees) and we estimated visually species cover with a scale in eight classes (Braun-
126 Blanquet 1964; Table 1).

127

128 *Statistical analyses*

129 The estimations of plant cover were converted in numerical values (numerical dominance) for
130 subsequent analyses (Table 1). The following analyses follow suggestions of Borcard et al.
131 (2011). Principal component analysis (PCA) and redundancy analysis (RDA) are linear
132 methods that preserve the Euclidean distance between sites, normally not adapted for analysis
133 with plant species covers. But the Hellinger's transformation of the data was used according to
134 Legendre and Gallagher (2001). A PCA was performed to identify possible shifts between
135 plots of each site: incomplete data set, excluding the tree layer was used to avoid a direct
136 effect of the constant presence of *R. pseudoacacia* in half of the plots. This allowed us to
137 identify the influence of this species on understorey. The plots were distributed in groups by a
138 clustering analysis based on a matrix of similarity.

139

140 The ecological factors collected in the field, canopy (arithmetical means of canopy opening in
141 each corner), slope, aspect and humus type, or from GIS climatic layers (ddeg300, sum of
142 degree day above 3°C) were the explicative variables in the RDA. For this analyse, we kept
143 only the cover herbs species to study the response of the undergrowth to canopy structure and
144 composition. The significance of axes were tested using a permutation test.

145

146 The significance of the global shift between plots of a same pair (with and without *R.*
147 *pseudoacacia*) along the first three axes of PCA was tested by multivariate analysis of
148 variance (MANOVA) by differences of axis scores between plots in sites against the
149 intercept.

150
151 As *R. pseudoacacia* enriches the soil with nitrogen (eg. Stock et al 1995; Von Holle et al.
152 2006; Yelenik et al. 2004), we used the mean ecological indicator values of N (nutrient
153 availability, mainly nitrogen; Landolt et al. 2010) of each relevé (only understorey) to
154 compare the difference in nutrient availability between the relevés with and without *R.*
155 *pseudoacacia*. Their respective cover weighted the importance of the species in the mean. The
156 means of pairs of plots were compared with a paired t-test. We did the same analyses for
157 functional traits as the maximal size (H_{\max} ; according Aeschimann et al. 2004), the specific
158 leaf area (SLA; data from www.leda-traitbase.org, <http://www.try-db.org> and literature),
159 humus type and canopy. The number of understorey species and the total species cover in
160 understorey (measured by the point method) in each site were compared with the same
161 analysis.

162
163 Finally, the frequency (number of occurrences) and the mean cover of each species in the
164 pairs of relevés were calculated. We retained only the species that were present in six or more
165 relevés and which had in at least in one relevé a frequency of three or more.

166

167 **Results**

168 *Potential distribution of R. pseudoacacia*

169 The species distribution model showed that *R. pseudoacacia* has a large ecological amplitude:
170 from plains up to 1000 m, in the Plateau and alpine valleys (annexe 1). The most important
171 variables in the model were annual degree-days (calculated above 3 °C), the minimal
172 temperature and the distance to lake and watercourses (ddeg300, tmin, dist_laceau, Fig. 1).
173 The threshold of degree-days and minimal temperature of suitable area correspond
174 approximately to a mean annual temperature above 5°C.

175

176 *Species composition*

177 The clustering analyse of relevés revealed three distinct groups of plots that approximately
178 correspond to three climatic conditions in three regions: Plateau, Chablais and Valais. The

179 pairs of plots were generally maintained together. For the PCA with tree (Fig. 2a) the first
180 axis explained 8.77% of the total variance in species composition. The second axis explained
181 7.98% of the variance. The plot showed a coherent shift between the plots of a same pair. The
182 shift was highly significant with a MANOVA (p-value < 0.0001). The first axis of the PCA
183 without tree layer explained 9.12% of the total variance and the second axis 7.63% (Fig. 2b).
184 There is less difference between plots but the shift testing was still highly significance (p-
185 value < 0.0001) according to the MANOVA.

186 Redundancy analysis (RDA) underlined the importance of humus (Fig. 3). The RDA was
187 significant according to the permutation test (p-value < 0.001). The projection of ecological
188 variables onto the RDA revealed that the first axis was negatively correlated with degree-day,
189 slope and humus. And the canopy was positively correlated with the second axis. The graph
190 showed a shift between plots with *R. pseudoacacia* and without correlated with the canopy
191 and humus.

192

193 *Species and site characteristics*

194 The differences between the plots with and without *R. pseudoacacia* were significant only for
195 the ecological indicator value for nutrient availability (N, p-value = 0.004), total cover of
196 understorey (p-value = 0.002) and the humus type (p-value < 0.0001) (Table 2). This means
197 that there were more nitrophilous species in the sites with *R. pseudoacacia*, with more active
198 humus on the soil and a higher cover of understorey. For the functional traits (SLA and size),
199 the canopy and the species richness, the difference was not significant (p-value > 0.05) (Table
200 2).

201

202 *Species cover according point method*

203 *Clematis vitalba* was the species with the largest mean difference (diff. cov = 16.85%) of
204 species cover, followed by *Aegopodium podagraria* and *Mercurialis perennis* (Table 3).
205 *Clematis vitalba*, as herb and shrub, *Galium aparine* and *Rubus fruticosus* were noticeable as
206 well for the important difference of presence in plots with and without *R. pseudoacacia*
207 (Table. 3). On the contrary, *Polygonatum multiflorum* and *Fagus sylvatica* had a higher cover
208 in plots without *R. pseudoacacia*, although *P. multiflorum* was more frequent in *R.*
209 *pseudoacacia* stands. We noticed also that the nitrogen indices (N) of species were 4 to 5 for
210 frequent species with *R. pseudoacacia*.

211

212 **Discussion**

213 *Robinia pseudoacacia* grows very quickly, survives to drought and harsh winters. It tolerates
214 infertile and acidic soils (Miller et al 1987). This explains its wide distribution: from the
215 Swiss lowlands up to mountain slopes (~1000 m; www.infoflora.ch). In Switzerland, the
216 model predicts suitable areas mainly on the Plateau and in Alpine valleys up to an elevation
217 corresponding approximately to a mean annual temperature of 5°C. This corresponds to the
218 present distribution of the species in Switzerland, which can be observed from wet forests in
219 lowlands to slopes with southern aspect in the driest region of the country (central Alps in
220 Valais with annual sum of precipitations 570 mm; www.infoflora.ch). The third variable
221 (distance to lake and watercourses; Fig. 1) shows that this species grows better at the edge of
222 lakes and rivers because of the disturbed environment with available space and light. The very
223 high importance of degree-days in models and observations demonstrated that cold is the
224 main constrain to *R. pseudoacacia*, which invades potentially a lot of ecosystems with
225 different climates, environments, soils, etc., as already demonstrated by several studies on
226 invasive species with large ecological amplitude (eg. Fumanal et al. 2008).

227

228 The clustering analysis based on species composition revealed three groups of sites (Fig.1 a
229 and b). The groups corresponded approximately to three climatic conditions, or three
230 geographical regions: The Plateau (annual sum of precipitations ~1000 mm), the Valais
231 (central Alps, <700 mm) and the Chablais (intermediate position and climate). Some plots
232 switched from one group to another according to the presence or absence of *R. pseudoacacia*,
233 but most of the pairs were included in the same group. Hence, species composition of the
234 plots is firstly explained by climatic conditions, and secondly by presence or absence of *R.*
235 *pseudoacacia*.

236

237 In the PCA analysis, pairs of plots showed coherent and significant shift along the second
238 axis. The differentiation was particularly regularly oriented in the PCA with tree layer (Fig.
239 2a), what is clearly explained by the constant presence of *R. pseudoacacia* in the tree layer of
240 half of the plots. But the preservation of a significant shift in the PCA without tree layer (Fig.
241 2b) is due to differences in the composition of the herb and shrub layers in pairs of plots,
242 although they were systematically set geographically very close to each other and in similar
243 ecological conditions. This shows that the presence of *R. pseudoacacia* clearly influences
244 forest understorey.

245

246 The RDA analysis highlighted the importance of the ecological variables degree-days,
247 canopy, slope and humus to explain species composition in forest undergrowth (Fig. 2). The

248 variable degree-days was the most important, and structured composition according to
249 climatic conditions (corresponding mainly to elevation and geographic region in our study
250 area). But directions of the arrows for canopy and humus were coherent with the general shift
251 observed in pairs of sites with and without *R. pseudoacacia*. Hence, the species shift from
252 absence to presence of *R. pseudoacacia* is related to a decreasing density of canopy, although
253 not significant according to the t-test, and to an improve of humus quality, as low values of
254 humus corresponds to good humus quality (mull) and high values to humus with a bad
255 incorporation of organic matter (mor; Ponge 2011).

256
257 *R. pseudoacacia* is symbiotic with nitrogen-fixing bacteria (Bormann et al. 1993) and we
258 expected that changes would correspond to the presence of more nitrophilous species. This
259 was confirmed by the higher frequency and/or cover of *Galium aparine*, *Aegopodium*
260 *podagraria* and *Rubus fruticosus* (Table 3) under the canopy of *R. pseudoacacia*. The
261 corresponding type of humus in these stands was most frequently mesomull than hemimoder
262 that was most frequently in plots without *R. pseudoacacia*. Humus type, which characterizes
263 the distribution of organic matter in a soil profile (Brêthes et al. 1995), depends on the
264 diversity of animal groups in the soil: the more soil fauna is diversified in forms and sizes, the
265 more plant litter is rapidly incorporated into the soil (Ponge 2000). But the diversity of soil
266 fauna depends firstly on the litter quality (nitrogen content). Therefore, there is a virtuous
267 cycle: *R. pseudoacacia* increases nitrogen content in soil (Bormann et al. 1993), this favours
268 nitrophilous species and increases nitrogen content of the other species, this produces a
269 nitrogen-rich litter, which is better incorporated in soil and delivers quickly nitrogen to the
270 soil (Gobat et al. 2010). The development of this cycle modifies the humus type from
271 hemimoder to mesomull.

272
273 Another species group, which showed a cover increase in *R. pseudoacacia* stands, is vines
274 such as *Clematis vitalba* and *Hedera helix*. This is related to the general increase of
275 understorey cover and shows that the luminosity is higher in sites with *R. pseudoacacia*,
276 although canopy cover was not significantly different as measured with the densiometer. But
277 the thinness of the leaves, clearly leaving more light going through the limb than native
278 species, the low number of branches in the lower canopy and maybe the phenomenon of
279 timidity at the top of this species brings more light to understorey without necessarily having
280 more or larger gaps.

281

282 Luminosity and nitrogen availability may affect SLA of species in understorey, what was only
283 marginally significant in our results (p-value = 0.0851). But the values of SLA were from
284 databases, often measured in unknown situations, and there is a very high intraspecific
285 variability of SLA values in understorey (Reich et al. 1997). SLA differences ought to be
286 evaluated with more relevés and especially with measurements directly on samples from the
287 considered stands.

288

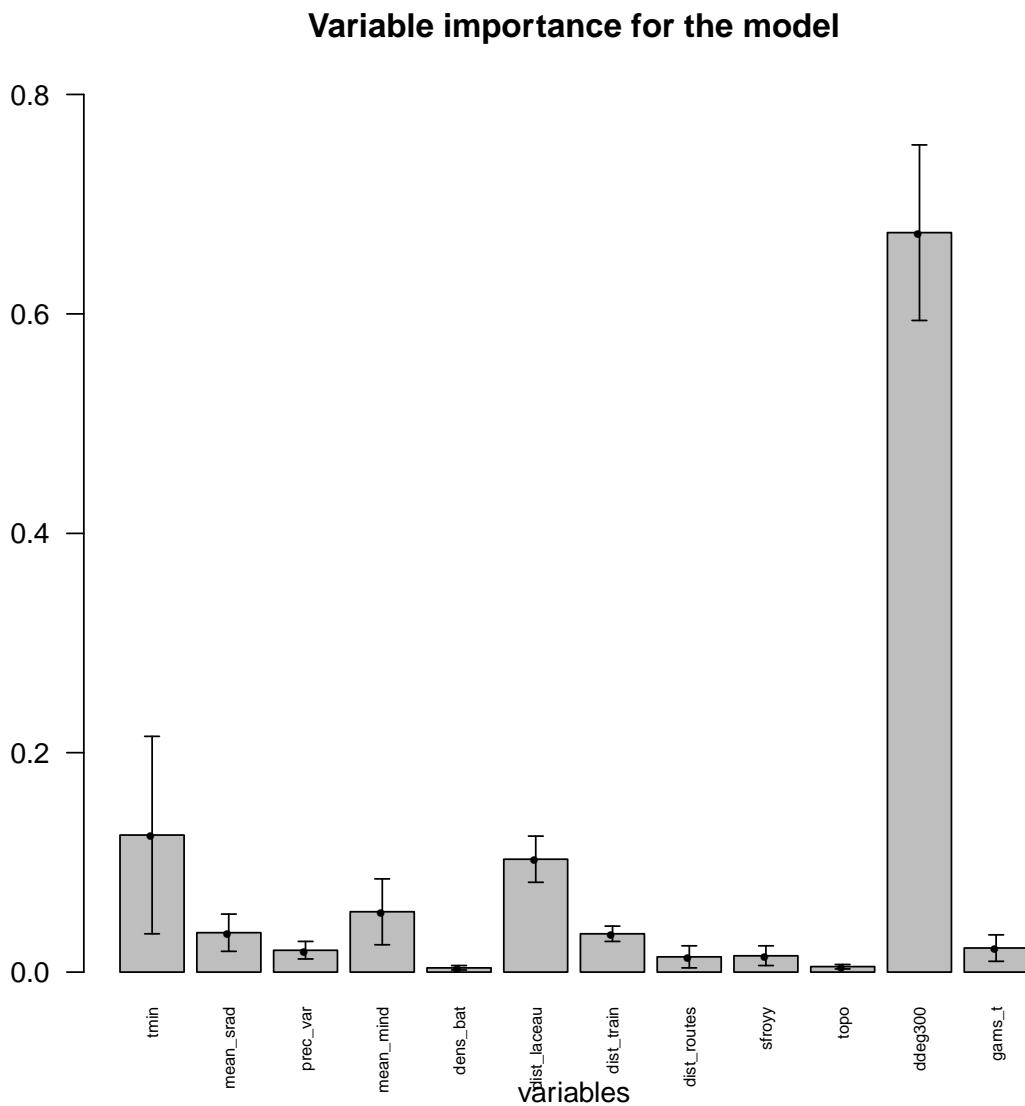
289 The difference of species richness was not significant between the two types of sites, in
290 opposition to stands colonised by another invasive tree, *Prunus serotina*, in Oise region
291 (France; Chabrerie et al. 2007). But, it does not mean that *R. pseudoacacia* does not affect
292 local species richness. As our results showed, species cover increased in *R. pseudoacacia*
293 stands, compared to ecologically similar stands, with a strong development of vines and
294 nitrophilous herbs. It is very likely that these species eliminate by competition some
295 oligotrophic species (Lévêque 2004) as *Polygonatum multiflorum*, which has a higher cover
296 in site without *R. pseudoacacia* (Table 3). As oligotrophic species are globally more often
297 threatened than nitrophilous ones (Moser et al. 2002), the invasion of *R. pseudoacacia* in
298 forests has the potential to increase species rarity of some oligotrophic species, especially
299 combined with general nitrogen deposition by pollution (NABEL 2013), which independently
300 tends to increase proportion of nitrophilous species (Draeger 2011; Kohli 2011). Our results
301 are not able to directly show an impact of *R. pseudoacacia* on rare or threatened species,
302 because the comparison in species cover was limited to frequent species, with presences in at
303 least six plots. Hence, rare species were by definition excluded of the analyses and many
304 more sites, selected around rare species, would be necessary to evaluate more exactly this
305 potential impact. But this would require a huge time investment to find the right sites.

306

307 This study showed that *R. pseudoacacia* settle potentially almost everywhere in lowlands and
308 mountain up to 1000 m, as far as mean annual temperature is above 5°C, with a large
309 ecological amplitude. It means that forests with particular ecological conditions (e.g., wet
310 forests or alluvial forests along river, dry forests on slopes), which often include rare and
311 endangered species, are concerned too. Climate change will very probably extend its
312 available area in the future towards higher elevations (Walkovszky 1998). *R. pseudoacacia*
313 strongly modifies soil chemistry, by increasing nitrogen content, and understorey conditions,
314 because of its light foliage. Therefore, it is able to change the understorey plant composition
315 in climactic forests of Central Europe. Nitrophilous species and vines gradually invade the
316 forest and potentially threaten oligotrophic and short-growing plants. The anthropogenic

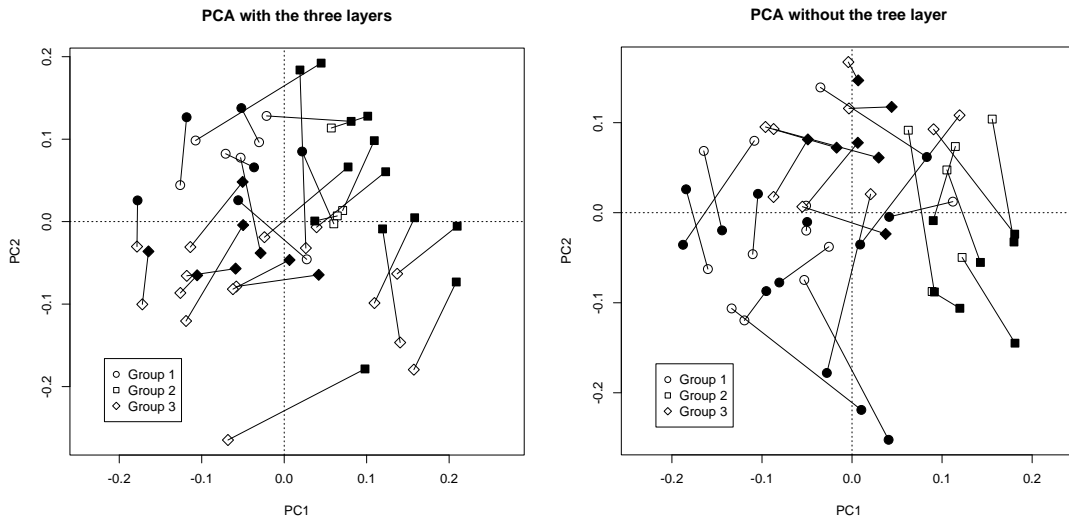
317 disturbances of landscapes facilitate the spread and development of *R. pseudoacacia* (Lee et
 318 al. 2004), and it is still too often favoured or even planted. However, once it has developed
 319 stands in the tree layer, the difficulty to eradicate it was many times demonstrated (e.g.,
 320 Muller 2004), and even colonisation of new areas is difficult to stop. In northern part of
 321 Switzerland, *R. pseudoacacia* is still sparse but it should be monitored more closely in order
 322 to avoid further invasions, any use in forest management has to be banned and efforts have to
 323 be invested to eradicate it, or at least to contain its invasion. Otherwise biodiversity in Central
 324 European forests might dramatically change in the future on large areas.

325 **Figures**



326
 327 Figure 1: Environmental variable importance in the species distribution model of *R.*
 328 *pseudoacacia*. The 12 environmental variables are: tmin: Minimal annual temperature; mean
 329 srada: Annual mean of daily average of potential short wave radiation; prec. var.: Variance of
 330 precipitations; mean mind: Mean of monthly moisture index; dens. bat.: Density of building;

331 dist. laceau: Distance to lake and watercourse; dist. train: Distance to railway; dist. routes:
 332 Distance to routes; sfroyy: Average number of frost days during the growing season (core
 333 90% of the vegetation period, the days with a mean daily temperature above 3°C); topo:
 334 Topographic position (concave to convex); ddeg300: Annual degree-day; gams t:
 335 Continentality index of Gams (general seasonality of climate derived from annual
 336 precipitation and mean annual temperature).

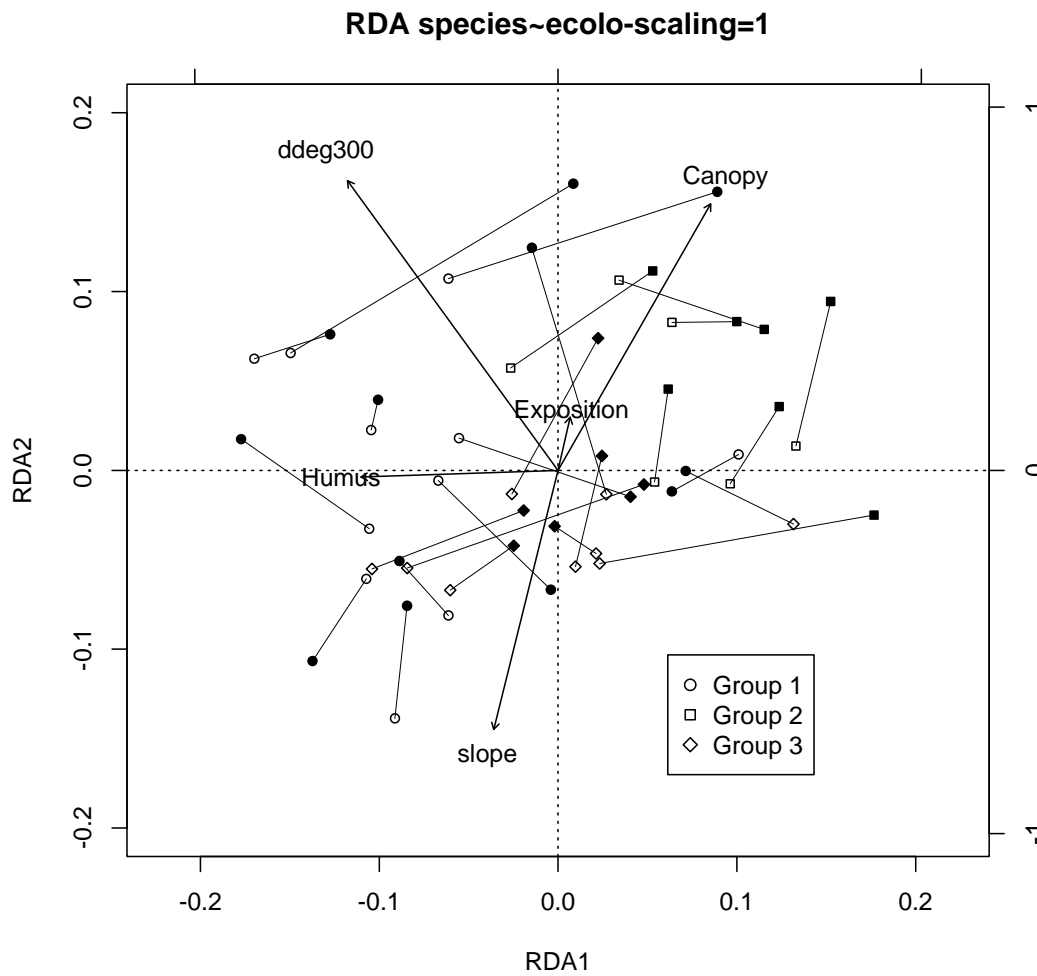


337

338 a

b

339 Figure 2: PCA of plots based on species (a) with tree and (b) without tree layer. The pairs of
 340 plots are joined. The black symbols represent the plots with *R. pseudoacacia* and the white
 341 without *R. pseudoacacia*. Group: groups of plots according to a hierarchical clustering.



343

344 Figure 3: RDA of plots, considering only undergrowth (herb and shrub layers) with the
 345 ecological variables ddeg300 (degree day), canopy, humus type, slope and exposition. The
 346 pairs of plots are joined. The black symbols represent the plots with *R. pseudoacacia* and the
 347 white without *R. pseudoacacia*. Groups: groups of sites according a hierarchical clustering.

348

349 **Tables**

350 Table 1: Scale used for plant cover estimates in the field, with corresponding cover (Braun-
 351 Blanquet 1964) and the transformations used in the analyses.

352

Cover classes	% Plant coverage	Values used in the analyses
r	One individual	1
+	<1%	2
1	1-4%	3
2a	5-14%	4
2b	15-24%	5
3	25-49%	6
4	50-75%	7
5	>75%	8

353

354

355 Table 2: Standardized mean differences of variables for the two types of plots [95%Wald CI]
 356 and p-values of the paired t-test. Canopy is the measured proportion of gaps in the tree layer.
 357 H_{max} is the maximum size of the understorey plants. Species richness is the number of
 358 different species in plots. SLA is the specific leaf area [mm^2/mg]. Total cover is the total
 359 species cover of undergrowth. N is an index (1-5) of nutrient availability (mainly nitrogen;
 360 Landolt et al. 2010).

Variables	Standardized mean difference [95%Wald CI]	P-value (paired t-test)
Canopy	0.218 [-0.315; 0.751]	0.2379
Humus	-2.901 [-3.503; -2.436]	< 0.0001
Total cover	0.724 [0.191; 1.257]	0.0025
Species richness	0.387 [-0.145; 0.921]	0.1454
H_{max}	0.372 [-0.160; 0.906]	0.1486
SLA	0.353 [-0.179; 0.887]	0.0851
N	0.157 [0.054; 0.261]	0.0043

361

362

363 Table 3: Difference of species frequency (nb of occurrences in the plots; Freq.) and mean
 364 species cover (measured by point method, in %; Cov_mean) in the plots with (a) and without
 365 *R. pseudoacacia* (b). Species are sorted according to the difference of mean cover (diff.
 366 mean). N is the ecological indicator value (1-5) for nutrient availability (mainly nitrogen;
 367 Landolt et al. 2010). B after species is the shrub and H the understorey layers. We retained
 368 only the species that were present in six or more relevés and who had in at least one plot a
 369 cover of three or more.

Species	Freq_a	Freq_b	Mean Cov. A %	Mean Cov. B %	Diff. Cov. %	N
<i>Clematis.vitalba</i> .H	10	4	19.60	2.75	16.85	3
<i>Aegopodium.podagraria</i> .H	3	5	24.33	12.70	11.63	4
<i>Mercurialis.perennis</i> .H	3	3	15.67	5.33	10.33	3
<i>Galium.aparine</i> .H	6	0	5.75	0.00	5.75	5
<i>Rubus.fructicosus</i> .H	16	10	10.53	4.90	5.63	4
<i>Clematis.vitalba</i> .B	13	4	6.81	1.50	5.31	3
<i>Corylus.avellana</i> .B	15	16	9.73	5.22	4.51	3
<i>Robinia.pseudoacacia</i> .B	12	0	4.29	0.00	4.29	4
<i>Rubus.fructicosus</i> .B	16	11	13.94	10.55	3.39	4
<i>Hedera.helix</i> .H	18	21	29.31	26.71	2.59	3
<i>Brachypodium.sylvaticum</i> .H	8	4	9.19	7.63	1.56	3
<i>Prunus.avium</i> .B	8	7	4.31	2.86	1.46	3
<i>Lamium.galeobdolon</i> .H	10	7	6.00	4.64	1.36	3
<i>Hedera.helix</i> .B	3	4	1.67	0.63	1.04	3
<i>Abies.alba</i> .B	4	3	2.00	1.00	1.00	3
<i>Crataegus.monogyna</i> .B	9	9	2.00	1.06	0.94	3
<i>Ligustrum.vulgare</i> .H	7	8	2.86	2.00	0.86	3
<i>Juglans.regia</i> .B	3	4	1.83	1.00	0.83	4
<i>Stachys.sylvatica</i> .H	7	6	8.57	7.83	0.74	4
<i>Acer.platanoides</i> .B	3	3	1.00	0.67	0.33	3
<i>Allium.ursinum</i> .H	4	3	1.13	0.83	0.29	3
<i>Alliaria.petiolata</i> .H	4	2	1.75	1.50	0.25	5
<i>Juglans.regia</i> .H	4	5	0.88	0.80	0.08	4
<i>Cornus.sanguinea</i> .H	9	9	1.72	1.67	0.06	3
<i>Lonicera.xylosteum</i> .H	2	4	1.00	1.00	0.00	3
<i>Carpinus.betulus</i> .B	4	3	1.88	2.00	-0.13	3
<i>Acer.platanoides</i> .H	3	4	1.67	1.88	-0.21	3
<i>Picea.abies</i> .B	2	4	1.00	1.25	-0.25	3
<i>Viburnum.opulus</i> .B	4	4	2.13	2.38	-0.25	3
<i>Acer.pseudoplatanus</i> .H	8	8	1.44	1.75	-0.31	3
<i>Fraxinus.excelsior</i> .B	15	13	2.07	2.38	-0.32	3
<i>Acer.campestre</i> .H	2	4	0.50	0.88	-0.38	3
<i>Corylus.avellana</i> .H	6	4	1.75	2.13	-0.38	3
<i>Lonicera.xylosteum</i> .B	12	11	3.42	3.91	-0.49	3
<i>Prunus.avium</i> .H	5	4	0.80	1.38	-0.58	3
<i>Fraxinus.excelsior</i> .H	15	14	3.87	4.46	-0.60	3
<i>Acer.campestre</i> .B	4	5	1.63	2.80	-1.18	3
<i>Ligustrum.vulgare</i> .B	6	8	5.08	6.56	-1.48	3
<i>Cornus.sanguinea</i> .B	12	10	6.08	7.80	-1.72	3
<i>Acer.pseudoplatanus</i> .B	10	8	2.80	4.63	-1.83	3
<i>Fagus.sylvatica</i> .B	9	9	3.28	7.50	-4.22	3
<i>Fagus.sylvatica</i> .H	4	6	1.63	7.42	-5.79	3
<i>Polygonatum.multiflorum</i> .H	5	2	1.70	8.00	-6.30	3

370

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377

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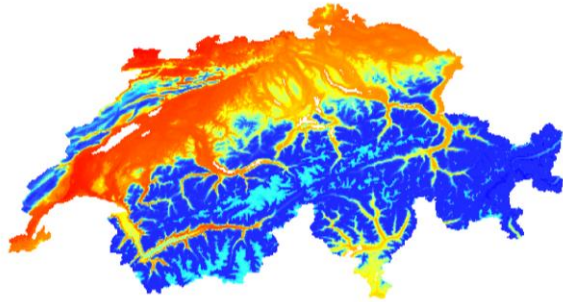
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525

526 **Annexes**

527



528

529 Annexe1: Map of model projection of *Robinia pseudoacacia* in Switzerland. Red: more
530 probable presence, to blue: less probable presence.

531

532 Annexe 2: Table of species cover (with visual estimation) of the 54 plots. Each plot code
533 contains the indication of presence (a) or absence (b) of *Robinia pseudoacacia* and the region
534 in which the stand is located (vd, Vaud, up to east extremity of Lake of Geneva; ch, Chablais,
535 Rhone valley in upland of Lake of Geneva, up to Martigny; vs, Central Valais, with low
536 annual precipitations). NO-ISFS is the official code of the species in Switzerland
537 (www.infoflora.ch). Tree (A), shrub (B) and herb (H) layers are indicated after species name
538 for trees and shrubs species.

Annexe 3 Environmental factors measured in the stands.

	Site	Region	Robinia	Elevation [m]	Slope [°]	Exposition [°]	Canopy	Humus
1a_vd	1	vd	Yes	405	0	0	8	hemimoder
1b_vd	1	vd	No	405	0	0	7.75	hemimoder
2a_vd	2	vd	Yes	393	0	0	17.75	mesomull
2b_vd	2	vd	No	393	0	0	11	hemimoder
3a_vd	3	vd	Yes	395	0	0	9.25	mesomull
3b_vd	3	vd	No	395	0	0	10.25	hemimoder
4a_vd	4	vd	Yes	389	0	0	6.25	hemimoder
4b_vd	4	vd	No	397	0	0	8.25	oligomull
5a_vd	5	vd	Yes	456	0	0	11.25	mesomull
5b_vd	5	vd	No	440	0	0	10.25	mesomull
6a_vd	6	vd	Yes	443	0	0	9.25	mesomull
6b_vd	6	vd	No	425	0	0	5.75	hemimoder
7a_vd	7	vd	Yes	439	0	0	6.75	mesomull
7b_vd	7	vd	No	446	0	0	7.75	hemimoder
8a_vd	8	vd	Yes	448	0	0	9	mesomull
8b_vd	8	vd	No	445	0	0	5.25	hemimoder
9a_vd	9	vd	Yes	461	45	44	4	mesomull
9b_vd	9	vd	No	474	45	43	4.75	hemimoder
10a_vd	10	vd	Yes	497	0	0	5.75	mesomull
10b_vd	10	vd	No	495	0	0	5.5	hemimoder
11a_vd	11	vd	Yes	560	45	62	3	mesomull
11b_vd	11	vd	No	551	10	66	3.5	hemimoder
12a_vd	12	vd	Yes	585	41	37	6	mesomull
12b_vd	12	vd	No	567	12	34	7.75	hemimoder
13a_ch	13	ch	Yes	438	0	0	8.5	mesomull
13b_ch	13	ch	No	426	0	0	4.25	hemimoder
14a_ch	14	ch	Yes	427	23	312	9.25	mesomull
14b_ch	14	ch	No	437	0	0	4.5	hemimoder
15a_ch	15	ch	Yes	474	15	322	4	mesomull
15b_ch	15	ch	No	473	11	329	5.5	hemimoder
16a_ch	16	ch	Yes	484	10	217	5.75	mesomull
16b_ch	16	ch	No	469	12	223	5.25	hemimoder
1a_vs	1	vs	Yes	485	0	0	12	mesomull
1b_vs	1	vs	No	485	0	0	7	hemimoder
2a_ch	2	ch	Yes	461	45	138	4.25	mesomull
2b_ch	2	ch	No	534	32	122	4.25	mesomull
3a_ch	3	ch	Yes	464	0	0	5.5	mesomull
3b_ch	3	ch	No	451	0	0	7	hemimoder
4a_vs	4	vs	Yes	472	0	0	6.25	mesomull
4b_vs	4	vs	No	478	0	0	5.75	hemimoder
5a_vs	5	vs	Yes	769	0	0	6.5	mesomull
5b_vs	5	vs	No	754	0	0	7.25	hemimoder
6a_vs	6	vs	Yes	959	64	198	4.25	mesomull
6b_vs	6	vs	No	975	39	195	4.25	hemimoder
7a_vs	7	vs	Yes	620	0	0	10	mesomull
7b_vs	7	vs	No	613	0	0	10.75	hemimoder
8a_vs	8	vs	Yes	587	0	0	7.25	mesomull
8b_vs	8	vs	No	577	0	0	10.5	hemimoder
9a_vs	9	vs	Yes	496	0	0	4.5	mesomull
9b_vs	9	vs	No	515	0	0	7.25	hemimoder
10a_vs	10	vs	Yes	907	36	290	6.5	mesomull
10b_vs	10	vs	No	934	61	325	4.25	hemimoder
11a_vs	11	vs	Yes	651	0	0	7	mesomull
11b_vs	11	vs	No	652	0	0	6.25	hemimoder