Plant diversity on skid trails in oak high forests: a matter of disturbance, micro-environmental conditions or forest age?

Liping Wei, A. Villemey, F. Hulin, Isabelle Bilger, Yann Dumas, Richard Chevalier, Frédéric Archaux, Frédéric Gosselin

HAL Id: hal-01152839
https://hal.science/hal-01152839

Submitted on 18 May 2015

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5   Liping Wei[a,b,*], Anne Villemey[a], Florian Hulin[a], Isabelle Bilger[a], Dumas Yann[a],

6   Richard Chevalier[a], Frédéric Archaux[a], Frédéric Gosselin[a]

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8   [a]*Irstea, UR EFNO, F-45290 Nogent-sur-Vernisson, France*

9   [b]*Ecole Doctorale SSBCV, Université d'Orléans, 45067 ORLEANS CEDEX 2, France*

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14   *Corresponding author

15   Tel.: +33 23 89 50 96 7; Fax: +33 23 89 50 96 7

16   *E-mail address*: liping.wei228@hotmail.com (L. WEI)

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29   **Abstract**

30   Increasingly mechanized timber harvesting and the repeated use of skid trail

31   networks may affect ground vegetation differently at subsequent stages in the forest

32   rotation. At a fine scale, no studies have yet compared the influence of

33   micro-environmental factors and the effects of skid trail disturbance on ground flora

34   diversity. We investigated understory diversity patterns on skid trails in 30-, 50- and

35   63-year- old oak forests in the northern half of France. Subplots were placed on skid

36   trail center, wheel track, skid trail edge plus an off-trail control. At each subplot, we

37   measured soil moisture, soil compaction (penetration resistance and bulk density) and

38   photosynthetic active radiation and recorded the abundance of all vascular plants. The

39   richness and abundance of ground flora were calculated based on the classification of

40   their life form, seed bank persistence, light preference and moisture requirements. For

41   each ecological group, we found out its best diversity indicator from subplot location,

42   micro-environmental factors (soil moisture and compaction, light) and stand attributes

43   (stand type, basal area), then assessed the magnitude and negligibility of the effect of

44   the best indicator. 1) Higher soil compaction compared to controls was detected on

45   the tracks of skid trails in the 50- and 63-year- old stands. Neither soil moisture nor

46   light varied with subplot location whatever the stand type. 2) The best diversity

47   indicator that showed non-negligible effects included subplot location, and soil

48   moisture or soil compaction. Compared to controls, skid trails in the 50- and

49   63-year-old stands were richer in tree and short-term seed bank species, while skid

50   trails in the 30-year-old plots had no effect on ground flora. The abundance of tree

51   and shade-tolerant species was also higher on skid trails. Soil moisture was positively

52   correlated with the richness of low- and high- humidity species, shade-tolerant species

53   and transient seed bank species as well as with the abundance of short-term seed bank

54   species. Bulk density positively affected heliophilous species richness, while

55   penetration resistance was positively related to shrub abundance. Skid trails and soil

56   compaction in our research area had either no impact or a positive impact on ground

57   flora diversity. Longer-term studies of skid trail effects are needed to validate these

58   main findings.

59

60   Keywords: Ecological group; Soil compaction; Soil moisture; Model comparison;

61   Fine scale; Mechanized harvesting

62   1. Introduction

63

64   Successful forest management requires a thorough understanding of how forest

65   ecosystems respond to disturbances. Disturbances, such as tree harvesting, are a

66   primary factor influencing diversity and floristic composition in the forest (Roberts

67   and Gilliam, 1995 and Berger et al., 2004). During the last several decades, manual

68   felling and logging for forest management have evolved towards mechanized

69   harvesting. Mechanized logging and timber harvesting rely on permanent

70   evenly-distributed skid trail systems (Jarret, 2004), which have the advantage of

71   confining disturbances to relatively smaller areas (Akbarimehr and Jalilvand, 2013)

72   while providing easy access to the forest interior (Avon et al., 2013). The micro-site

73   environment on skid trails is likely to differ from that of the forest interior due to

74   canopy opening, higher soil compaction, soil nutrient loss or increased soil moisture

75   on skid trails compared to undisturbed habitat (Buckley et al., 2003, Zenner and

76   Berger, 2008 and Hattori et al., 2013). These environmental changes might explain the

77   differences in ground flora that is observed between locations on and off skid trails

78   (Swaine and Agyeman, 2008, Wolf, 2008 and Avon et al., 2013). Canopy cover is one

79   of the most important factors that control a site's microclimate (Metzger and Schultz,

80   1984). Opening the canopy along skid trails can influence plant growth and

81   competition patterns, especially between shade-tolerant and -intolerant species (Horn,

82   1971 and Planchais and Sinoquet, 1998). However, light level may not always remain

83   high on skid trails years after logging or cutting operations. The time necessary for

84   canopy closure together with the properties of the residual tree stands (age, height...)

85   can greatly influence light availability on skid trails.

86   Soil compaction, a reduction in the volume of a given mass of soil (Gliński and

87   Lipiec, 1990), is one of the major consequences of mechanized harvesting on skid

88   trails (Ampoorter et al., 2010, Naghdi et al., 2010 and Solgi and Najafi, 2014).

89   Therefore, it is often used as an indicator of forest floor disturbance resulting from

90   machine use on skid trails. Very few studies to date have directly related ground flora

91   to soil compaction measured on skid trails. For instance, Buckley et al. (2003)

92   measured soil compaction in their description of the growth conditions on skid trails,

93   but did not directly link it to ground flora diversity in the statistical analyses. We

94   found only two studies investigating the relationship between soil compaction on skid

95   trails and ground flora, however, their results were not consistent. Roovers et al.

96   (2004) demonstrated that the intensity of soil compaction was highly (negatively)

97   correlated with species cover and composition. On the contrary, Heninger et al. (2002)

98   found that reduced Douglas-fir tree seedling growth on skid trails was unrelated to

99   percentage increases in soil bulk density. Therefore, the role of compaction on skid

100   trails in ground flora diversity needed to be validated.

101   Soil moisture is an important fine-scale factor affecting plants that has been

102   described in many studies (Beckage et al., 2000 and Gray et al., 2012), but those

103   dealing with skid trails did not find consistent results. For example, some studies

104   demonstrated that soil moisture was higher on skid trails due to the removal of the

105   canopy cover which reduced rainfall intercept and increased water intercept in the soil,

106   while others found decreased water holding ability in wheel ruts after the first

107   machine passes (Miller and Sirois, 1986, Buckley, et al., 2003, Ezzati et al., 2012 and

108   Solgi and Najafi, 2014). Since the influence of canopy cover and machine use on soil

109   moisture had not yet been jointly compared, we still need to study the soil moisture

110   level on skid trials and its relation to canopy cover and soil disturbance.

111   Ground flora has the highest species diversity of all forest layers in temperate

112   forests (Thomas et al., 1999). Because the diversity of ground flora is sensitive to a

113   variety of factors such as overstory characteristics (Augusto et al., 2003, Nagaike et

114   al., 2005 and Barbier et al., 2008), soil properties (Brunet et al., 1996), and forest

115   disturbances and management practices (Hammond and Miller, 1998 and Wender et

116   al., 1999), it is an important indicator of forest site quality and of the environmental

117   impact of management (Pregitzer and Barnes, 1982 and Gilliam, 2002). The presence

118   of skid trails, associated with frequent machine entry and accompanying disturbances,

119   favors the introduction of ruderal, non-forest, exotic or heliophilous species (Buckley

120   et al., 2003; Zenner and Berger, 2008; Avon et al., 2013). Identifying species that

121   successfully establish and grow on skid trails, or inversely, that decrease or disappear

122   on skid trails, is an important step for forest managers (Buckley et al, 2003).

123   Furthermore, for those species that are favored by skid trails, it is important to

124   distinguish whether these species are native or non-native species, and whether they

125   are exclusive species. An increase in non-native species may threaten the existence or

126   growth of native species on skid trails, especially when non-native species disperse

127   into the forest interior.

128   The relative importance of different environmental or historical filters (e.g.

129 disturbance) for ground flora diversity may vary with forest stage or stand

130 development (Burton et al., 2011). Stands of different ages and types within a forest

131 frequently experience different management regimes, i.e. they are subjected to

132 varying intensities of machinery use and different distribution patterns of skid trails

133 (Zenner, 2007 and Zenner and Berger, 2008). In addition, more mature forests

134 managed with large machines need wider skid trails for wood extraction, potentially

135 leading to the creation of deeper continuous ruts (Schack-Kirchner et al., 2007 and

136 Picchio, 2012). Furthermore, trees at different ages may intercept different levels of

137 light and water. Some studies have investigated the effect of skid trails on tree

138 regeneration in different forest types (Liechty et al., 2002; Beaudet et al., 2014) but

139 only limited research has compared the plant diversity patterns on skid trails in

140 different forest types. Roovers et al. (2004) examined the effects of trampling on

141 vegetation along skid trails in four vegetation types: two deciduous forest types, one

142 grassland and one heathland, and showed that the increase in floristic dissimilarity

143 from trail to undisturbed vegetation was higher in forests than in the grassland and

144 the heathland, whereas no difference was detected between the two forest types.

145 Fine-scale studies of plant diversity patterns can provide insights into how

146 historical and environmental filters interact across scales to influence vegetation

147 locally (Leibold et al., 2004 and Burton et al., 2011). No previous studies have ever

148 compared the influence of micro-environmental factors with skid trail disturbance to

149 detect their effects on ground flora diversity. In our study, we investigated fine-scale

150 understory diversity patterns in three forest types of varying tree maturity containing

151 skid trail systems. We aimed to find the dominant factors affecting ground flora

152 diversity among subplot location, soil moisture, soil compaction, light, stand type

153 and basal area. We used subplots on and off skid trails to indirectly represent habitat

154 exposed to frequent and infrequent disturbances. In addition, within the skid trails,

155 we used three different locations - the middle of the trail, the wheel track and the

156 trail edge - to represent the within-trail disturbance gradient. Relationships between

157 ecological or functional groupings of plant species and environmental gradients can

158 provide evidence for environmental filtering, particularly when the traits suggest an

159 advantage in the associated environment (McGill et al., 2006 and Burton et al., 2011).

160 The classification of ecological groups was based on the following four species traits

161 (Table 1): life form, seed bank strategy, light and moisture requirements (data

162 sources: Hodgson et al., 1995 and Julve, 2007). Our research questions were as

163   follows: 1) What is the relative importance of subplot location, soil moisture, soil

164   compaction and light on ground flora diversity? 2) Does this importance vary with

165   stand type? 3) Are the dominant factors different among ground flora ecological

166   groups?

167

168   2. Material and methods

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170   *2.1. Study area*

171

172   The Montargis forest (4,090 ha, 48°01' N, 2°48' E, Loiret, northern half of France)

173   is an ancient state forest managed by the French National Forestry Office (ONF)

174   around 110 km south of Paris. Elevation ranges from 95 to 132m a.s.l. Climate is

175   oceanic with a respective mean annual rainfall and temperature of about 647 mm and

176   10.9 C (Chevalier, 2003). Soil conditions are homogeneous, with plateau soils on a

177   chalk substrate. There are small variations in soil texture (sandy to silt-sandy) and

178   stone content (Chevalier, 2003). The dominant tree species are sessile oak (*Quercus*

179   *petraea*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*). The main

180   management goal is to produce quality timber. Therefore, 70% of the area is managed

181   as an oak even-aged high forest, where trees originate from seeds (Helms, 1998).

182   Former standard-with-coppice (SWC) forest management with sessile oak as

183   standards and hornbeam as coppice has been progressively replaced since 1857 by an

184   even-aged high forest system dominated by oak. A high forest rotation is typically

185   180 to 200 years until trees reach 80 cm in diameter (ONF, 1996 and Jarret, 2004).

186   All the even-aged high forest stands have experienced a seed-tree natural

187   regeneration.

188

189   *2.2. Data collection*

190

191   We set up 20 m x 20 m quadrats in 36 even-aged high stands representing three

192   stand types of different average ages (30, 50 and 63 years old - respectively STP30,

193   STP50 and STP63, with 12 quadrats per stand type). The soil profile was tested by

194   one of our authors (Richard Chevalier) in 2000. Site type was controlled to avoid site

195   bias among forest types: variations among the variables related to site type were not

196   significantly strong. We set up a 22-m-radius circular plot around the center of each

197   quadrat and measured the diameter at 1.3 m height ("DBH", in cm) for each tree,

198   following Chevalier (2003). DBH was measured to calculate total tree basal area (all

199   tree species combined, with oak contributing to 82 % of the plot basal area on

200   average). We then selected the skid trail that covered the largest area within the

201   selected quadrat (Fig. 1 (a)). We inventoried vegetation and measured penetration

202   resistance (PR), bulk density (BD) and light on four 0.5 m × 5 m subplots

203   systematically set out in each 20 m × 20 m quadrat (Fig. 1 (a)): (1) on the wheel

204   track of the skid trail (TR); (2) between the two wheel tracks of the skid trail (BE); (3)

205   on the edge of the skid trail (BO); (4) halfway between two skid trails as a control

206   (CO). The four subplots were oriented in the same direction as the skid trail and their

207   centers were aligned orthogonally to the skid trail.

208   Skid trails are created by mowing vegetation during stand regeneration to provide

209   easy access from roads to stand interiors. They are evenly distributed across the stands;

210   this is especially true in lowland managed forests where management is likely to be

211   intense, as is typical in Europe (Avon et al., 2013). The Montargis forest contains two

212   types of parallel skid trails: primary (in STP30) and secondary skid trails (in STP50

213   and STP63). The primary skid trails are spaced 9 m apart and are 1.85 m wide on

214   average (Fig. A1 in Appendix). The primary skid trails are mainly used by small

215   cutting machines entering STP30 to remove shrubs, and wheel ruts are rarely found

216   on most of these trails. The average spacing for secondary skid trails is 22 m. The

217   mean widths of these secondary skid trails are 2.23 m and 2.59 m in STP50 and

218   STP63 respectively (Fig. A1 in Appendix). Wheel rut depths were 5.38 cm and 7.25

219   cm in STP50 and STP63 respectively. The secondary skid trails are mainly used by

220   larger and heavier harvesters and skidders to cut and extract wood from the forest

221   interior. During the maturing process of the stands, two thirds of the primary skid

222   trails will be kept and used as secondary skid trails until the end of the rotation

223   (150-180 years). The remaining primary skid trails are abandoned and gradually

224   become an integral part of the stands.

225   Vegetation in each subplot was sampled once from May to end of July, 2012.

226   Despite the seasonality of our sampling campaign, we were still able to detect vernal

227   species, although probably in reduced abundance. Furthermore, only two vernal

228   species: *Anemone nemorosa* and *Hyacinthoides non-scripta* are present on the mildly

229   acidic soils of the Montargis forest.) Vascular plants below 2 m in height were

230   recorded in each subplot following the Braun-Blanquet abundance-dominance

231   classification with seven coefficients: i, +, 1, 2, 3, 4 and 5 (i, one unique individual,

232   cover < 5 %; +: very few individuals, total cover < 5 %; 1, few to many individuals,

233   total cover < 5 %; 2, many individuals, total cover 5 to 25 %; 3, total cover 25 to 50

234   %; 4, total cover 50 to 75 %; 5, total cover > 75 %). When species abundance was

235   being calculated, the coefficients were transformed into percentage cover classes as

236   follows: i to 0.1 %; + to 0.5 %; 1 to 5 %; 2 to 17.5 %; 3 to 37.5 %; 4 to 62.5 %; 5 to

237   87.5 %.

238   Soil compaction degree was assessed in each subplot from both PR and BD. The

239   measurements were taken at the same time in November, 2012, when soil water

240   content was near field capacity in the Montargis forest; penetrometer readings were

241   thus less likely to be influenced by differences in soil moisture (Miller et al., 2001 and

242   Godefroid and Koedam, 2004a). We took nine PR measurements per subplot. The

243   locations of the PR points were fixed and numbered (1-9) as shown in Fig. 1 (b).

244   Moisture at soil surface was measured simultaneously at the same nine points with a

245   field tetra probe. We recorded PR (MPa) at 1 cm depth intervals while continuously

246   inserting (2 cm/s speed) a penetrologger (Eijkelkamp Agrisearch Equipment, the

247   Netherlands) bipartite probing rod (with a cone-shaped tip of 60 degrees and 1 cm²

248   basal area surface) into the soil until it stopped due to high soil compaction or

249   encountering a root or stone. The maximum measuring depth of a penetrologger is 80

250   cm. In case the probing rod stopped less than 20 cm below ground, we took additional

251   measurements (up to four) in a pre-determined direction and distance (10 cm) from

252   the original point until the probe reached at least 20 cm in depth (Fig. 1 (b)). We also

253   recorded the number of times we renewed the measurement (Nsam). We retained PR

254   values from 0-20 cm in depth since, in previous studies, the strongest soil impact on

255   ground vegetation appeared in this upper layer (Greacen and Sands, 1980 and

256   Ampoorter et al., 2007). Furthermore, this layer is also generally free of the natural

257   compaction that occurs in deeper soil layers (Godefroid and Koedam, 2004a). For the

258   samples that had renewed measurements, we kept the PR and the maximum depth

259   value from renewed measurement only (i.e. the one that had a depth of at least 20 cm).

260   The mean PR of the nine sampling spots at 0-20cm in depth was used as a proxy for

261   soil compaction level for each subplot.

262   We took one bulk density sampling in the center of each subplot (at the same point

263   as PR No.5) at a depth of 10 cm with metallic cylinders 5 cm in diameter and 5cm in

264   height. To calculate BD and water content (Krzic et al., 2003), we weighed the fresh

265 mass of each sample in the lab on the same day the sample was collected. We then

266 dried the sample for 48 hours in an oven (105 °C) and recorded the dry mass.

267 We used four indicators for the degree of soil compaction since we felt that no

268 single one was unambiguously more appropriate than the others: mean PR of the nine

269 sampling spots at 0-20cm in depth, mean number of measurements (Nsam) at each PR

270 point, mean maximum depth of the nine sampling spots (MaxD), and mean BD. Nsam

271 may be a useful predictor of the degree of compaction (the higher the Nsam, the more

272 compacted the soil), although its relevance has not yet been tested. The MaxD

273 decreases with increasing soil compaction and could reflect soil conditions related to

274 plant root penetration. BD is more related to natural soil characteristics such as

275 texture, organic matter content, soil structure (Cassel, 1982) and gravel content

276 (Franzen et al., 1994), while PR mimics a root growing through soil. Relationships

277 between PR and BD are not always consistent and were found to be non-linear in

278 some studies (Smith et al., 1997, Vaz et al., 2001, Whalley et al., 2005 and Ampoorter

279 et al., 2007).

280 We selected 24 of the 36 sampling plots (8 per stand type, randomly distributed

281 throughout the forest) and took light measurements in September, 2013, when the

282 leaves were fully developed. Light transmission at each subplot was measured for 24

283 h with SKP215 (Skye Instruments) sensors in the photosynthetically active radiation

284 spectrum (PAR, 400–700 nm, in $\mu mol.m^{-2}.s^{-1}$) (Balandier et al., 2006). We set one

285 sensor 2 m high above the center of each subplot and placed a control sensor in an

286 open area nearby (hemisphere free of any obstruction) to measure incident radiation.

287 We also placed a sunshine sensor (Delta-T Devices) in the open area to assess

288 diffused radiation and to take into account variations due to weather conditions.

289 Hemispherical photographs were taken to compute the precise time of sunset and

290 sunrise above the tree periphery for each sampling day (Adam et al., 2008). Light

291 transmittance for each subplot was calculated as the ratio between daily mean PAR

292 and daily mean incidence radiation. Light data from sunset to sunrise was omitted.

293 The ratio of diffused to incident radiation was used to correct daily mean PAR data:

294 $PAR_{correct} = PAR \times (1-(diffused\ radiation/incident\ radiation) \times 0.15$. This process

295 enabled us to compare measurements made on different days (i.e. with different sun

296 fluxes) and with different weather conditions (i.e. cloudy or sunny) (Balandier et al.,

297 2006). Finally, relative PAR value (PAR value of each subplot divided by full light

298 PAR) was calculated as a light availability indicator.

299

300   *2.3. Data analysis*

301

302   We modeled the responses of a) species richness − i.e. the number of observed

303   species in the subplot, b) the abundance of ecological groups (Table 1) and c) the

304   abundance of individual common species (defined as those with an occurrence of >

305   25%) to variables that related to subplot location, soil compaction degree, stand

306   attributes, soil moisture and light (Table 2).

307   We applied a total of 27 explanatory models to species richness, abundance of each

308   ecological group (10 groups) (Table 3), and to the abundance of each individual

309   species (15 species). Our first group of ecological models was composed of

310   single-variable models related to subplot location, stand type, basal area, soil

311   compaction degree (PR, MaxD, Nsam, BD) and light (models [2] to [11]). Comparing

312   the single-variable models helped us distinguish the dominant factor on skid trails. To

313   further detect whether ground flora diversity patterns could be better explained by the

314   combined effects of subplot location, soil moisture, soil compaction or light with

315   stand type or basal area, we modeled the interactive effects of subplot location and

316   stand attributes (stand type and basal area) in the second group (models [12] and [13]),

317   as well as the additive effects of soil compaction degree, soil moisture or light and

318   stand type in the third group (models [14] to [20]). The four soil compaction variables

319   (PR, Nsam, MaxD and BD) were included in parallel models from model [14] to [17].

320   The last group of models was composed of quadratic models related to soil

321   compaction degree, soil moisture and light (models [21] to [27]), since in several

322   studies, non-linear relationships between PR and plant species cover were detected

323   (Godefroid and Koedam, 2004a). Only on the 24 plots where light measurements

324   were taken did we compare light models (models [11], [20] and [27]) with the best

325   ones selected from the other 24 models.

326   The variables (Table 2) were included in different generalized linear mixed

327   models (GLMMs) for coefficient estimation and model comparison based on the

328   QAICc (Quasi Akaike Information Criterion corrected for small sample size). Model

329   comparisons based on an information criterion such as AIC make it possible to

330   measure the relative quality of statistical models, and thus to identify the "best" model.

331   They include a trade-off between model goodness of fit and model complexity.

332   QAICc is an extension of the AIC for the analysis of count data with a level of

333 dispersion different from that of the Poisson distribution, and is adapted to limited

334 sample sizes for which the asymptotic results known for AIC do not necessarily apply

335 (Lebreton et al., 1992). This model comparison approach was completed by an

336 analysis of the magnitude of the estimates since model comparison techniques are

337 much more in line with statistical significance than with "biological" significance (e.g.

338 McQuarrie and Tsai, 1999). The lmer function (in the lme4 R package, with the

339 default Laplace approximation to the loglikelihood, Bates and Maechler, 2010) with

340 the Quasi-Poisson "family" was used. The link function was the default (log) for these

341 models. A random "plot" effect was incorporated on the intercept into all the 27

342 models in Table 3. For QAICc, a common dispersion parameter was used for all the

343 27 models being compared for each group, as advocated by Bolker et al. (2009). The

344 common dispersion parameter was taken to be that of the Quasi-Poisson model: PR +

345 STP (where STP is stand type). Analyses based only on statistical significance

346 (*P*-values) are unable to distinguish practically important different situations in trends.

347 This is because, in the usual statistical tests for trends, the failure to reject the null

348 hypothesis of no trend does not prove that the null hypothesis is true, nor does the

349 rejection of the null hypothesis indicate whether or not the trend is ecologically

350 important or non-negligible. The important question is actually whether the true trend

351 is ecologically negligible or not (Dixon and Pechmann, 2005). As did Barbier et al.

352 (2009), we distinguished, for both richness and abundance data, two levels of

353 ecological negligibility in the multiplier of the mean of species richness and

354 abundance – here denoted by β – to a given increase in an ecological variable (see

355 below): a more stringent one (b_1), corresponding to a strict ecological negligibility

356 and a less stringent one (b_2, with ($0 < b_1 < b_2$)). Four different cases occur when

357 describing negligibility effects: (1) negligible weak effects denoted by "0" when the

358 value of the multiplier (β) follows $P(-b_2 < \log(\beta) < b_2) \geq 0.95$, and negligible very

359 weak effects denoted by "00" for the more stringent $P(-b_1 < \log(\beta) < b_1) \geq 0.95$; (2)

360 non-negligible negative and very negative effects: "-" for $P(\log(\beta) < -b_1) \geq 0.95$ and

361 "--" for the stronger $P(\log(\beta) < -b_2) \geq 0.95$; (3) non-negligible positive and very

362 positive effects: "+" for $P(\log(\beta) > b_1) \geq 0.95$ and "++" for the stronger $P(\log(\beta) > b_2)$

363 ≥ 0.95; and (4) negligibility where the estimator cannot be classified   in any of the

364 above categories. In our analysis, we chose $b_1 = 0.1$, $b_2 = 0.2$ for species richness, and

365 $b_1 = 0.25$, $b_2 = 0.5$ for abundance, as in Barbier et al. (2009). In other words, we

366 considered that a change of 10 % in species richness or 25 % in abundance was an

367 ecologically-significant change, while a change of 20 % or 50 % respectively was a

368 strongly significant change (see Table A1 in Appendix). The increases in the

369 continuous ecological variables we considered were of about one standard deviation:

370 0.5 MPa for increment for PR, 1 for Nsam, 10.5 cm for MaxD, 0.25 g.cm^{-3} for BD,

371 6.5 % for moisture, 6 m^3.cm^{-3} for WCS and 5 m^2.ha^{-1} for basal area. For stand type

372 (STP), we calculated the associated multiplicative coefficient by supposing the stand

373 changed from one type to the successive type: STP30 to STP50 stands (STP30to50),

374 and STP50 to STP63 stands (STP50to63). The multiplicative coefficient for subplot

375 location was obtained by calculating the difference between the subplot locations and

376 the control (COtoBE, COtoTR and COtoBO). For quadratic models, we obtained the

377 multiplicative coefficient for the same variation as above but calculated at first,

378 second and third quartile of the explanatory variable. We report the mean value of the

379 multiplier for each variable and its 95% confidence interval.

380   We analyzed the magnitude of the effects of the best models (the lowest QAICc)

381 on the richness and abundance of each ecological group, as well as on the abundance

382 of each species (occurrence > 25%, Table A2). The bootstrap resampling method

383 from the R boot library allowed us to obtain reliable samples of the coefficients in the

384 models, at both the ecological group and species levels, based on 10,000 simulations

385 (Stine, 1990). The bootstrap method resamples the original data with replacement,

386 calculates the index of interest from each bootstrap sample, and estimates the mean,

387 confidence interval and standard error from the replicate bootstrap estimates (Mueller

388 and Altenberg, 1985 and Krebs, 1989).

389   We used generalized linear models (GLMs) with the Gaussian "family" to assess

390 the association between the different soil compaction indicators (PR, Nsam, MaxD

391 and BD) and the variations in soil compaction, soil moisture and light among subplot

392 locations and stand types.

393

394 3. Results

395

396 *3.1 Fine-scale variation of environmental factors*

397

398   PR was significantly greater on wheel tracks (TR) than on controls in STP50 and

399 STP63 and between the two wheel tracks (BE) in STP63 (*P<0.001*) (Fig. 2). Nsam

400 and BD were also significantly higher on TR in STP63. PR, Nsam and BD on the

401 subplot locations BE and TR increased with the increasing age of the stands. No

402 significant variation in MaxD among subplot locations was detected (Fig. 2). BD,

403 Nsam and MaxD were significantly associated to PR (*P<0.001*). Light and soil

404 moisture did not vary among subplot locations whatever the stand type (Fig. 3), but

405 did vary among stand types (*P<0.001*).

406

407 *3.2 Best models*

408

409 The best models fell into two broad categories (Table 3): models related to subplot

410 locations that indirectly represent the disturbance gradient and models related to

411 micro-site factors of soil compaction degree, soil moisture or light.

412 For richness (Table 4), among the 10 ecological groups, two (trees and short-term

413 seed bank species) had best models related to the interactive effects of subplot

414 location and stand type; four groups (herbaceous, shrub, long-term seed-bank and

415 heliophilous species) were best related to soil compaction indices (PR, MaxD or BD),

416 and four groups (transient seed bank, high-humidity, low-humidity and shade-tolerant

417 species) to soil moisture.

418 For abundance data (Table 5), three groups (long-term seed bank, high-humidity,

419 shade-tolerant species) had best models related to subplot location; two groups (tree,

420 heliophilous species) were related to the interaction between subplot location and

421 basal area; three groups (shrub, Low-humidity, transient seed-bank species) were

422 related to PR, and two groups (herbaceous and short-term seed bank species) to soil

423 moisture. Light-only (L) models were preferred to alternative models for heliophilous

424 species richness and long-term seed-bank species abundance (Table 6). The quadratic

425 models combining light and stand type performed the best for herbaceous species

426 richness.

427

428 *3.3 Magnitude of the effects*

429

430 For richness data, the magnitude and negligibility of the effects estimated from the

431 best models are shown in Tables 4 and 6. Subplot locations of BE and TR had positive

432   effects on tree and short-term seed bank species in STP50, as did the subplots of BE,

433   TR and BO on tree and short-term seed bank species in STP63. Soil moisture showed

434   positive effects on the richness of all the ecological groups with best models related to

435   soil moisture (transient seed bank, low-humidity, high-humidity and shade-tolerant

436   species). For compaction indicators, BD had a positive effect on heliophilous species

437   richness. The effect of MaxD was either weak (long-term seed bank species) or

438   uncertain (shrubs). PR effect was also weak (herbaceous species). The effect of light

439   was either weak (herbaceous species) or uncertain (heliophilous species). The

440   transition of stand type from STP30 to STP50 had a negative effect on shrubs in the

441   additive models of MaxD and STP, while it had a positive effect on herbaceous

442   species richness in the additive models of PR and STP. The transition of stand type

443   from STP50 to STP63 had a positive effect on herbaceous species richness in the

444   quadratic model combining light and stand type.

445   For abundance data (Tables 5 and 6), TR and BE respectively had a positive effect

446   on shade-tolerant and tree species. Soil moisture had a positive effect on short-term

447   seed bank species, whereas its effect on herbaceous species was weak. Similarly, PR

448   had a positive effect on shrubs and a weak effect on transient seed bank species; its

449   effect on low-humidity species was uncertain. The effect of light was weak on

450   long-term seed bank species. The transition of stand type from STP30 to STP50 had a

451   positive effect on herbaceous species and a weak effect on transient seed bank species

452   in the quadratic model combing soil moisture and stand type, while the effect of the

453   transition from stand type STP50 to STP63 on herbaceous transient seed bank species

454   was weak. Basal area had a weak effect on trees and heliophilous species in the

455   models combining subplot and basal area.

456

457   4. Discussion

458

459   *4.1 Best models for ecological groups*

460

461   Disturbance, soil moisture, soil compaction, light, stand type and basal area have

462   been found to be important factors impacting understory diversity (Skov, 1997,

463   Nagaike et al., 2005, Barbier et al., 2008 and Sciama et al., 2009), but few studies

464   have compared the relative importance of these variables to detect which one(s)

465   might be the best indicator(s) under the multiple hypotheses framework (Chamberlin,

466   1965). In our study, we used a model comparison approach to determine the best

467   indicators of ground flora diversity. For the majority of the ecological groups we

468   studied (8 out of 10 groups), the best indicators of species richness were related to

469   micro-environmental factors. Abundance was best indicated by models related to

470   subplot location for half of the groups (5 out of 10) and by micro-environmental

471   factors for the other half (Tables 4 and 5).

472

473   *4.2 Dominant factors affecting ground flora diversity on skid trails*

474

475   In our study, subplot location, soil moisture and soil compaction played

476   non-negligible dominant roles at the fine scale in stands managed with a skid trail

477   system. The dominant effects depended on the ecological group studied and on

478   whether species richness or species abundance was considered. We agree with

479   Brosofske et al. (2001) that disturbance can sometimes override environmental

480   influences. Subplot location, which indirectly represents the disturbance gradient, was

481   the best indicator that showed non-negligible effects on the richness of tree and

482   short-term seed bank species, as well as for the abundance of tree species and

483   shade-tolerant species. However, the effects of subplot location depended on stand

484   types: its positive effects only occurred in the two older stand types. Skid trails in the

485   youngest stands were denser but narrower than in the older stands, and were

486   submitted to fewer and/or less intense disturbances. Indeed, soil compaction values

487   that were significantly higher on skid trails than on the paired forest controls were

488   observed only in the two older stand types (Fig. 2). Furthermore, community stability

489   reflects the ability of resident species to resist change, or, if altered by disturbance,

490   their ability to readjust or recover (Halpern, 1988). Following these criteria, the

491   understory plant community in our research area appears to be resilient to the skid

492   trail system. Skid trails did not appear to negatively impact ground flora diversity. On

493   the contrary, it promoted the diversity of some ecological groups.

494   Soil moisture was the best indicator for the richness of transient seed bank,

495   shade-tolerant, low- and high- humidity species, as well as the abundance of

496   short-term seed bank species. In our study, soil moisture levels varied significantly

497   among stand types, but did not vary along the disturbance gradient in each stand type.

498   Ezzati et al. (2012) obtained a similar finding: there was no moisture difference

499   between skid trail and undisturbed forest 16 to 20 years after skidding operations.

500   According to our results, richness of both low- and high- humidity species was
501   positively affected by soil moisture. As explained by Qian et al. (1997), the trend
502   toward higher diversity in wetter soil conditions generally agrees with findings that
503   diversity peaks at mesic sites (e.g. Burton et al., 1992, Pausas, 1994 and Roberts and
504   Gilliam, 1995).

505   Our study supports the important role of soil compaction only for shrubs
506   abundance (with PR as the best indicator) and heliophilous richness (with BD as the
507   best indicator). Higher soil compaction detected on skid trails does not necessarily
508   mean that it will have significant effects on ground flora. One reason may be that the
509   soil compaction levels in our study were not high enough to affect ground flora. This
510   was supported by Zenner et al. (2007) who found that, though traffic intensity had a
511   negative effect on both aspen density and growth, PR measured from this traffic was
512   not significantly associated with aspen density and growth. Zenner et al. (2007)
513   explained that the PR values after harvest were below the levels that restrict the
514   suckering and growth of aspen. Specific PR values at which root growth is restricted
515   are thought to be between 2,500 and 3,000 kPa for many plant species (Taylor et al.,
516   1966 and Greacen and Sands, 1980). In our study, the critical value of 2,500 kPa was
517   found only on the wheel tracks (TR) in stands aged 50 and 63 years. Heninger et al.
518   (2002) used BD as a soil compaction indicator and found that reductions in tree height
519   were unrelated to percentage increases in soil bulk density in the 0 to 30cm soil
520   horizon. For the four soil compaction indicators we studied (PR, Nsam, MaxD and
521   BD), we found that PR and BD were better soil compaction indicators of floristic
522   biodiversity than Nsam and MaxD. PR and BD were more sensitive than Nsam and
523   MaxD to the variation in degree of soil compaction. In addition, only PR and BD
524   were found to have non-negligible effects on ground flora diversity. Higher soil
525   moisture is usually considered to result in more compacted soils (Williamson and
526   Neilsen, 2000 and McNabb et al., 2001), and vice versa (Greacen and Sands, 1980
527   and Tan et al., 2005). However, in our study, there was no strong relationship between
528   PR and moisture (Pearson's r=0.148, *P*=0.0898). More ecological groups were
529   affected by soil moisture than by soil compaction. Only one study to our knowledge
530   compared the effects of soil moisture and compaction at the stand scale, and found
531   that seedling growth rate in the periods 0–12 and 12–24 months after planting was
532   promoted by higher soil moisture (33%), while PR had no effect (Hattori et al., 2013).
533   Light effect was weak in our study (Table 6). Zenner and Berger (2008) also failed

534 to detect any significant effects of canopy removal intensity on ground flora

535 composition and diversity on plots covered with skid trails. Light did not vary among

536 subplot locations in any stand type in our study. In fact, decades after the creation of

537 skid trails, nearby trees are already tall enough for canopy cover to be fully developed

538 even with disturbance. This was the case even in the youngest stands (30 years on

539 average) we studied because, although the trees were relatively smaller and denser,

540 the skid trails were narrower and the machines used were smaller than in the older

541 stands. Buckley et al. (2003) also found that mean canopy cover was only slightly

542 lower on skid trails than in the forest interior.

543

544 *4.3 Responses of ecological groups to their best indicators*

545

546 In our study, the species richness of tree seedlings and saplings was higher on skid

547 trails than in the forest interior (Table 4). The positive role of skid trails on tree

548 recruitment, growth and seedling density has already been repeatedly evidenced in

549 previous studies (Roberts and Harrington, 2008 and Swaine and Agyeman, 2008). A

550 more innovative finding is that the positive influence of skid trails on tree species

551 richness depended on forest type – higher richness on skid trails only occurred in the

552 older stands (50 and 63 year-old) but not in the youngest stands (30 year-old) (Table

553 4). This is because with increasing stand age, the richness of tree seedlings and

554 saplings progressively decreased on controls but did not change on skid trails. For the

555 other two life-form groups (shrubs and herbaceous species), soil compaction has been

556 found to respectively reduce herbaceous cover and increase shrub richness and cover

557 in large plots (60m²) (Zenner and Berger, 2008). Our study also demonstrated a

558 positive effect of soil compaction on shrub abundance at a finer scale. Though the

559 model combining soil compaction and stand type was the best for herbaceous richness,

560 the strongest positive effect was due to the ageing of the stand (from 30 to 50 years),

561 while the effect of soil compaction was weak.

562 Species producing a large number of persistent seeds (alive in seed banks for ≥1

563 year, defined by Thompson and Grime, 1979) seem to be favored by recurring

564 disturbance cycles such as flooding, burning or tree falls; they are awaiting favorable

565 conditions for germination in the soil (van der Valk and Davis, 1978, Thompson and

566 Grime, 1979 and Pugnaire and Lázaro 2000;). As another form of recurring

567 disturbance, man-made skid trails were found to maintain a higher diversity of species

568   with short-term persistent seeds (Avon et al., 2013), which is what we observed in the

569   stands aged 50 and 63 years but not in the younger stands. For transient seed bank

570   species, the dominant factor affecting richness was soil moisture rather than skid trail

571   disturbance.

572   Concerning light-demanding groups, we found a higher abundance of

573   shade-tolerant species on skid trails. Toledo-Aceves et al. (2009) also found that even

574   shade-tolerant species displayed higher densities on skid trails in comparison with

575   closed canopy conditions. Conversely, Avon et al. (2013) found a higher richness of

576   shade-tolerant species in stand interiors and more heliophilous species on skid trails.

577   For heliophilous species richness, BD was a better indicator − associated with a

578   positive non-negligible effect –than light or subplot location. Concerning ecological

579   groups classified by soil moisture, we found that richness for both low- and

580   high-humidity species increased with increasing moisture on skid trails. No previous

581   studies had detected the effects of skid trails on moisture groups.

582

583   *4.4 Conclusion*

584

585   Mechanized harvesting in France is relatively recent and harvesting with heavier

586   machines is likely to occur in the future. Our current study was conducted on plots in

587   relatively young stages in the forestry cycle (30 to 63 years). Investigating skid trail

588   effects in older stands (>63 years) and even younger stands (<30 years) should be

589   considered.

590   Our study compared the effects of skid trail disturbance (represented by subplot

591   location) and micro-environmental factors (light, soil moisture and compaction) on

592   ground flora diversity at a fine scale. The Montargis forest contains two types of

593   parallel skid trails: primary and secondary skid trails. The primary skid trails are

594   mainly used for removing shrubs inside the stand, while the secondary skid trails are

595   mainly for cutting and extracting wood from the forest interior. Not only did we

596   observe that soil compaction was higher on secondary skid trails compared to the

597   forest interior, we also found that compaction on secondary skid trails increased with

598   stand age. The other two environmental factors - light and soil moisture - were not

599   affected by skid trail disturbance. Skid trail disturbance, soil moisture and soil

600   compaction were the best indicators, showing non-negligible effects on ground flora.

601 However, skid trail disturbance only had non-negligible effects in stands with
602 secondary skid trails.

603 Our research was confined to high forest and covered a relatively narrow range of
604 stand ages (30 to 63 years old, i.e. about one sixth of a typical 180-to-200-year
605 rotation). However, we still detected a difference in skid trail effects on plant diversity
606 among stand types. Furthermore, the species groups favored by skid trail conditions
607 were native species (e.g. tree seedlings/saplings, short-term seed bank species) rather
608 than non-native species. This means that skid trails are not systematically a source of
609 exoticspecies. We also checked whether the native species favored by skid trails
610 included competitive species which might potentially limit tree regeneration (Table
611 A2 in Appendix). *Rubus fruticosus* was the only species more abundant on skid trails
612 compared to controls that is known to reduce tree growth (e.g. Schreiner et al, 2000).
613 Even though, in our case, skid trails also favored tree diversity, we cannot reject the
614 hypothesis that skid trails might accelerate the development of *R. fruticosus* at the
615 expense of tree seedlings during the regeneration phase in high forest stands.

616 Unlike coppice-with-standards (CWS) where frequent coppice cuttings conserve
617 the diversity of many functional species groups such as vernal, heliophilous and seed
618 banking species (Ash and Barkham, 1976, Van Calster et al., 2007 and Baeten et al.,
619 2009), the maturing process of high forest stands was found to be accompanied by a
620 generalized decrease in ground flora diversity (Chevalier, 2003); Duguid and Ashton,
621 2013). Yet, according to our results, skid trails could have a positive effect in this
622 respect: while floristic biodiversity did progressively decline within stands, skid trails
623 seemed to allow at least some components of ground flora diversity to maintain a
624 constant level of plant diversity in young to mature high forests. The species favored
625 by skid trails may then be able to recolonize the stand following natural disturbances
626 or cuttings.

627
628 Acknowledgements
629

633

634   References

635

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882

Table 1 Summary of ecological groups

Species trait	Categories	Description
Life form	Tree	
	Shrub	
	Herbaceous	
Seed bank persistence	Transient	1: present during the summer and germinating synchronously in autumn, 2: present during the winter and germinating synchronously in late winter or spring
	Short-term persistence	3 : >5 years but concentrations of seeds in the soil are only high after seeds have just been shed
	Long-term persistence	4: a large bank of long-persistent seeds in the soil throughout the year
Light	Shade-tolerant	Ellenberg L value : 2, 3, 4
	Heliophilous	Ellenberg L value : 5, 6, 7, 8
Soil moisture	Low-moisture	Ellenberg F value : 4
	High-moisture	Ellenberg F value : 5, 6, 7, 8

Data source: Hodgson et al., 1995; Julve, 2007. Ellenberg L value: Ellenberg indicator value of light (Ellenberg et al., 1992); Ellenberg F value: Ellenberg indicator value of soil moisture. The scale value 1 refers to the lowest value of the factor (e.g. very shady for L or very dry for F), and the scale value 9 to the highest value (e.g. full light for L or very wet for F)"

29

Table 2 Ecological variables used in the models

Variable	Description	Mean / SD
Subplot.location	Subplot location: BE: between the two tracks of a skid trail, TR: on the track in a skid trail, BO: on the forest border next to the trail of a skid trail, CO: control, undisturbed habitat, in the forest halfway between two parallel skid trails)	---
STP	Stand type: 3 even-aged high forest stand types with a mean age of 30, 50 and 63 years (STP30, STP50, STP63) (year)	---
G	Basal area at breast height of all the trees in a stand (m^2/ha)	28.21 / 6.41
PR	Mean penetration resistance from 0 to 20 cm in depth (MPa)	1.95/ 0.66
Nsam	Number of PR measurements per subplot (proxy for stone and root density)	1.34/ 0.81
Moisture	Soil moisture (%)	23.58 / 6.47
BD	Bulk density at a depth of between 7.5cm and 12.5cm (g/cm^3)	1.07 / 0.26
WCS	Water content of BD (cm^3/cm^3)	19.58 / 5.95
L	Relative photosynthetic active radiation (PAR) value (%)	1.84/1.91
MaxD	Maximum depth of probe (cm)	47.33 / 10.45

Table 3 Summary of ecological models

Effect	Models
	[1] Null model
Single-variable models	[2-11] Subplot.location, STP, G, PR, MaxD, Nsam, moisture, BD, WCS, L
Interactive models	[12] subplot.location * STP
	[13] subplot.location * G
Additive models	[14] PR + STP
	[15] MaxD + STP
	[16] Nsam + STP
	[17] BD + STP
	[18] Moisture + STP
	[19] WCS + STP
	[20] L + STP
Quadratic models	[21] $PR + PR^2 + STP$
	[22] $MaxD + MaxD^2 + STP$
	[23] $Nsam + Nsam^2 + STP$
	[24] $Moisture + Moisture^2 + STP$
	[25] $BD + BD^2 + STP$
	[26] $WCS + WCS^2 + STP$
	[27] $L + L^2 + STP$

Abbreviations are defined in Table 2.

Table 4 Multiplicative effect of a substantial variation in ecological variables on ecological group richness

Models	RI	Life form			Seed bank			Humidity		Light	
		Tree	Shrub	Herbaceous	Long-term	Short-term	Transient	Low	High	Shade	Heliophilous
Subplot* STP	COtoBO, STP30	0.84 [0.54;1.25]				0.47 [0.16;2.51]					
	COtoTR, STP30	1.13 [0.78;1.59]				1.20 [0.57;2.83]					
	COtoBE, STP30	1.19 [0.81;1.68]				1.24 [0.54;2.48]					
	COtoBO, STP50	1.01 [0.64;1.49]				0.99 [0.29;3.70]					
	COtoTR, STP50	1.49[+] [1.05;2.27]				2.69[++] [1.13;7.95]					
	COtoBE, STP50	1.68[++] [1.20;2.48]				2.52[+] [0.95;7.04]					
	COtoBO, STP63	1.63[++] [1.16;2.52]				3.95[+] [0.86;9.96]					
	COtoTR, STP63	2.39[++] [1.74;3.63]				14.67[++] [4.62;30.34]					
	COtoBE, STP63	2.36[++] [1.77;3.46]				8.91[++] [2.92;19.57]					
MaxD	MaxD				1.06[0] [0.98;1.15]						
MaxD + STP	MaxD		1.16 [1.03;1.29]								
	STP30to50		0.59[--] [0.45;0.76]								
	STP50to63		1.10 [0.86;1.4]								

Moisture	Moisture			1.15[+] [1.09;1.24]	1.51[++] [1.25;1.80]	1.17[+,0] [1.11;1.23]	1.60[++] [1.35;1.78]
	PR	0.96[00] [0.93;1.00]				
PR + STP	STP30to50	1.44[+] [1.16;1.77]				
	STP50to63	1.11[0] [1.01;1.22]				
BD	BD					1.11[+] [1.11;1.27]

Abbreviations are defined in Table 2. Variations were: 0.5 MPa for PR increment , 1 for Nsam, 10.5 cm for MaxD, 0.25 g.cm^{-3} for BD, 6.5 % for moisture, 6 m^3.cm^{-3} for WCS and 5 m^2.ha^{-1} for basal area. For stand type (STP), we calculated the associated multiplicative coefficient by supposing the stand changed from one type to the successive type: STP30 to STP50 stands (STP$_{30to50}$), and STP50 to STP63 stands (STP$_{50to63}$). The multiplicative coefficient for subplot location was obtained by calculating the difference between the subplot locations and the paired control (COtoBE, COtoTR and COtoBO). For quadratic models, we obtained the multiplicative coefficient for the same variation as above but calculated at first, second and third quartiles of the explanatory variable. The multiplicative coefficient for subplot location was obtained by calculating the difference between the subplot locations and the paired control (COtoBE, COtoTR and COtoBO). "0" and "00" indicate that the effect has a *p*-value of at least 0.95 of being negligible at two different levels (see text). "-" and "−" indicate that the effect has a *p*-value of at least 0.95 of being negative and non-negligible at two different levels. "+" and "++" indicate that the effect has a *p*-value of at least 0.95 of being positive and non-negligible at two different levels. Values in brackets are the 95% confidence intervals of the coefficients.

Table 5 Multiplicative effect of a substantial variation in ecological variables on ecological group abundance

Models		Life form			Seed bank			Humidity		Light	
		Tree	Shrub	Herbaceous	Long-term	Short-term	Transient	Low	High	Shade	Heliophilous
Subplot.location	COtoBO				1.16^0 [0.82;1.67]				1.30^0 [1.04;1.62]	1.16 [0.51;2.27]	
	COtoTR				1.28 [0.9;1.77]				1.22^0 [0.96;1.54]	$2.75+$ [1.25;4.6]	
	COtoBE				1.65 [1.16;2.39]				1.51 [1.22;1.86]	2.35 [1.12;3.95]	
Subplot * G	COtoBO	1.34^0 [0.91;1.70]									1.31^0 [0.9;1.7]
	COtoTR	1.63 [1.14;2.02]									1.25^0 [0.84;1.6]
	COtoBE	1.95^+ [1.3;2.4]									1.62 [1.1;2.03]
	G (CO)	0.84^0 [0.60;1.16]									0.83^0 [0.59;1.16]
	G (BO)	1.14^0 [0.89;1.43]									1.15^0 [0.91;1.46]
	G (BE)	1.15^0 [0.95;1.45]									1.15^0 [0.95;1.45]
	G (TR)	1.59^{00} [0.87;1.26]									$1.10^{00,0}$ [0.89;1.33]
PR	PR		$2.20{++}$ [2.15;2.68]					0.72 [0.50;0.95]			
Moisture	Moisture					3.21^+ [1.41;7.16]					
Moisture+Moisture^2+STP	Moisture at 1st quartile			0.93^{00} [0.81; 1.10]							
	Moisture at median			0.86^{00} [0.79;0.96]							

|			
	Moisture at 3rd quartile	0.81^{0} [0.72;0.88]	
	STP30to50	4.35^{++} [2.53;6.25]	
	STP50to63	1.01^{0} [0.81;1.31]	
	PR at 1st quartile		1.00^{00} [0.92;1.12]
	PR at median		0.91^{00} [0.84;0.98]
PR+PR^2+STP	PR at 3rd quartile		0.83^{0} [0.75;0.92]
	STP30to50		0.93^{00} [0.78;1.16]
	STP50to63		1.11^{0} [0.91;1.34]

The legend is the same as for Table 4.

Table 6 Multiplicative effect of a substantial variation in ecological variables (in the models related to light) on ecological group richness and abundance

| Models	Variables	Richness		Abundance
		Heliophilous	Herbaceous	Long-term seed bank
L	L	1.15 [1.01;1.26]		1.18^{0} [1.05;1.34]
L+L^2+STP	L at 1st quartile		0.94 [0.88;1.00]	
	L at median		0.95 [0.89;1.01]	
	L at 3rd quartile		0.96^{0} [0.90;1.01]	
	STP30-50		1.50 [1.17;1.97]	
	STP50-63		1.14^{+} [1.00;1.29]	

The legend is the same as for Table 4.
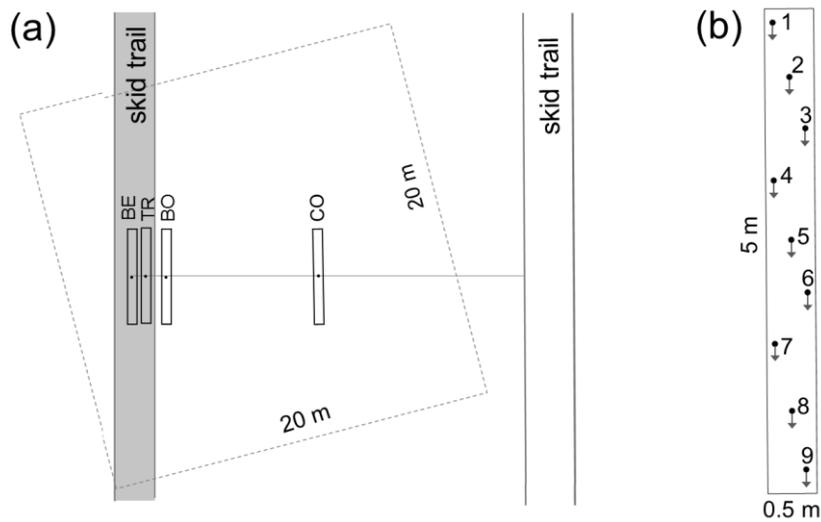
Fig. 1 (a) Subplot location (size: 0.5 m × 5 m) within the 20 m × 20 m quadrats. TR: on the wheel tracks of the skid trail, BE: between the two tracks of the skid trail, BO: on the forest border next to the skid trail, CO: control, undisturbed habitat, halfway between the skid trail and the next parallel skid trail). Numbers 1-9 represent the 9 penetration resistance (PR) measurement points; arrows represent the direction of a renewed measurement when the probing rod encountered a stone or root above 20 cm in depth. The bulk density sample was taken at point No. 5.
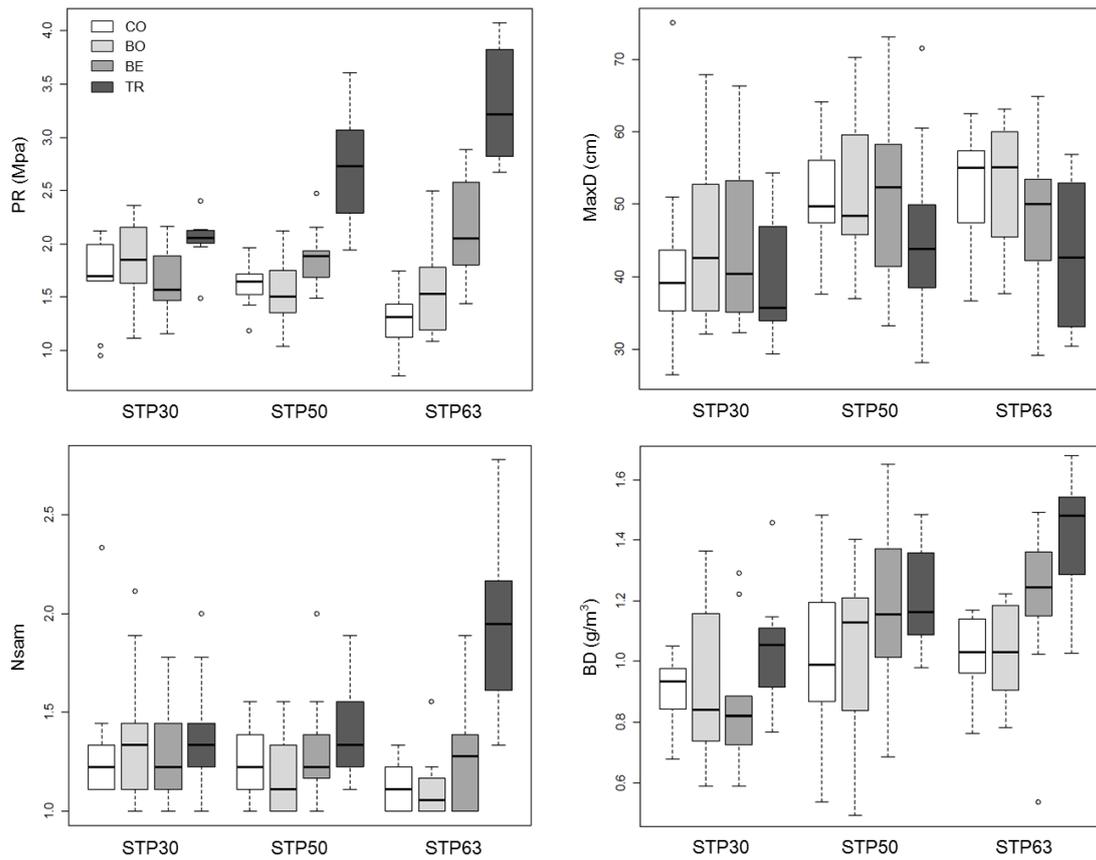
Fig. 2 Distribution of (PR), MaxD, Nsam and BD depending on subplot location (CO, BO, TR and BE) and stand type (STP30, STP50 and STP63). PR, MaxD, Nsam and BD, TR, BE, BO and CO are defined in Table 2.
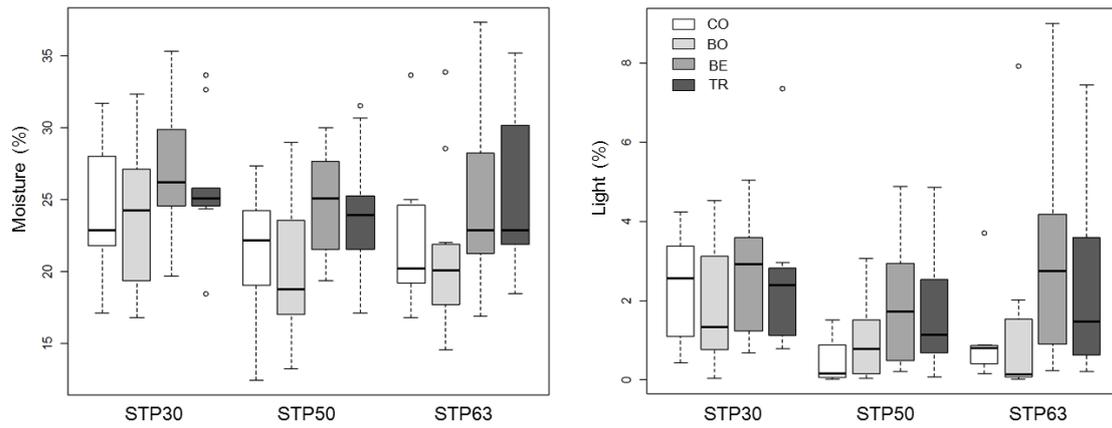
Fig. 3 The distribution of moisture and light in each subplot location (CO, BO, TR and BE) in the three stand types (STP30, STP50 and STP63). PR, MaxD, Nsam and BD, TR, BE, BO and CO are defined in Table 2. OK

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