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

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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 trails 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

169

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 penetrometer (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 penetrometer 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 (N_{sam}). 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 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (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 $\text{PAR}_{\text{correct}} = \text{PAR} \times (1 - (\text{diffused radiation} / \text{incident radiation}) \times 0.15)$. 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 m³.cm⁻³ for WCS and 5 m².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 combining 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 Nielsen, 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

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629

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633

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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)”

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		1.16 [1.03;1.29]								
MaxD + STP	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 m³.cm⁻³ for WCS and 5 m².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		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+PR ² +STP	PR at 1st quartile		1.00 ⁰⁰ [0.92;1.12]
	PR at median		0.91 ⁰⁰ [0.84;0.98]
	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 at 1st quartile		0.94 [0.88;1.00]	
	L at median		0.95 [0.89;1.01]	
L+L ² +STP	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.

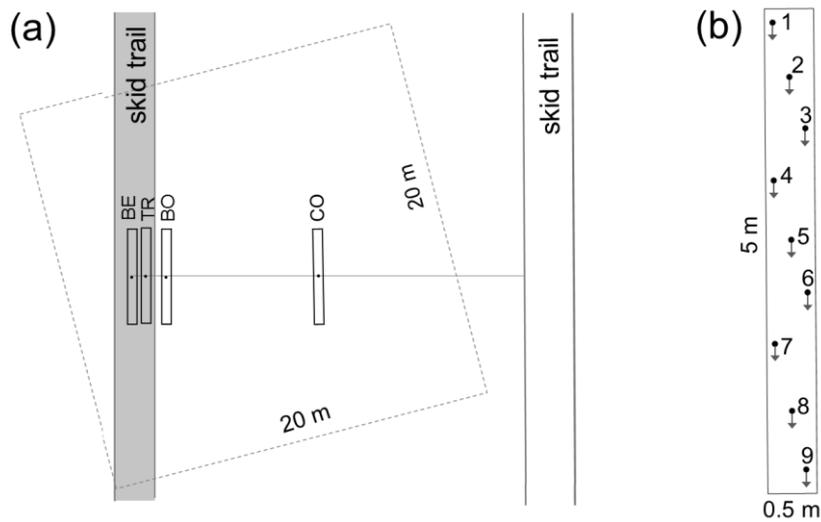


Fig. 1 (a) Subplot location (size: 0.5 m × 5 m) within the 20 m × 20 m quadrats. TR: on the wheel tracks of the skid trail, BE: between the two tracks of the skid trail, BO: on the forest border next to the skid trail, CO: control, undisturbed habitat, halfway between the skid trail and the next parallel 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.

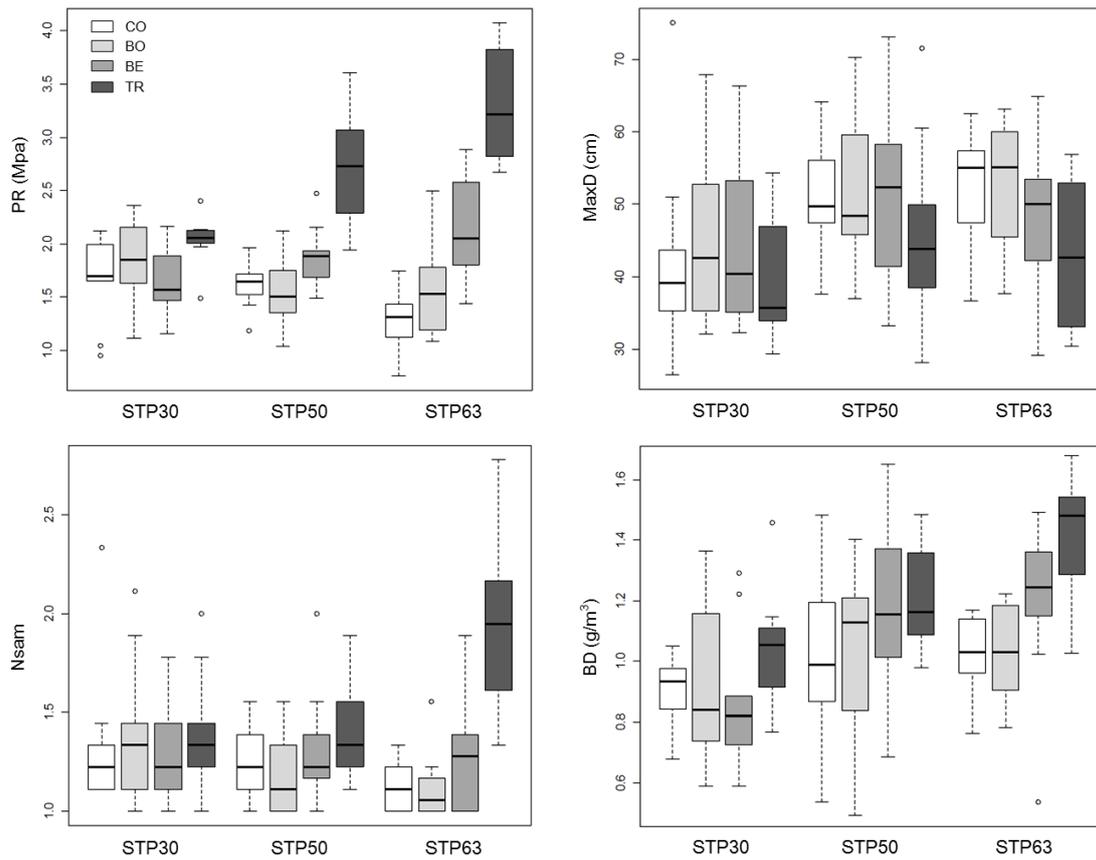


Fig. 2 Distribution of (PR), MaxD, Nsam and BD depending on subplot location (CO, BO, TR and BE) and stand type (STP30, STP50 and STP63). PR, MaxD, Nsam and BD, TR, BE, BO and CO are defined in Table 2.

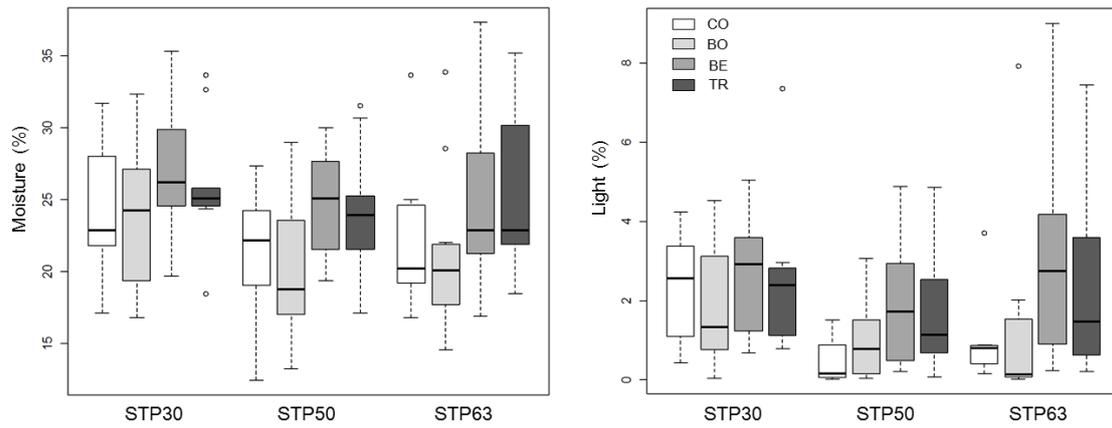


Fig. 3 The distribution of moisture and light in each subplot location (CO, BO, TR and BE) in the three stand types (STP30, STP50 and STP63). PR, MaxD, Nsam and BD, TR, BE, BO and CO are defined in Table 2. OK