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1 **FUEL CHARACTERIZATION AND EFFECTS OF WILDFIRE RECURRENCE ON**
2 **VEGETATION STRUCTURE ON LIMESTONE SOILS IN SOUTHEASTERN**
3 **FRANCE.**

4

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10

11 **Abstract**

12

13 Recurrent fires are more frequent in the Mediterranean basin due to global climate change.
14 The effects of fire recurrence (up to more than three recurrent fires with an interval since the
15 last fire of more or less than fifteen years) on the structure of fuel beds were studied at stand
16 level in southeastern France. Three types of vegetation that are among the most common in
17 the study area (pure pine stands, oak-pine mixed stands and shrublands) were studied to
18 determine the role of fire recurrence on biodiversity. Fuel bed description was carried out on
19 aboveground vegetation at understorey and overstorey levels, and on litter in 39 homogeneous
20 study sites. The structure of the understorey was categorized following a gradient of
21 fragmentation including: (i) isolated shrubs, (ii) vegetation patches made up of a single
22 species and (iii) homogeneous vegetation layers including different species of the same
23 height.

24 The decrease of time interval since the last fire caused an opening of the canopy, except for
25 the lowest vegetation stratum (grasses and low shrubs) that did not vary significantly. There
26 was no significant change in horizontal connectivity between fuel beds (% of layer cover) as a
27 function of the fire regime or the type of vegetation. Conversely, the vertical connectivity (%
28 of tree cover, height of the trees and of the layer) was affected by the fire regime, especially in

29 pure pine stands. Fire regime also influenced the litter layer and litter depth decreased with an
30 increase in the opening of the stand that could be due to fire. These results show that fire risk
31 is greater in the oldest stands (long interval since the last fire).

32

33 *Key words:* wildfire recurrence; fire interval, wildland fuel, vegetation structure; shrubland,
34 *Pinus halepensis*

35

36 **Introduction**

37

38 In recent decades, the number of fires has increased in most regions of the Mediterranean
39 basin (Moreno *et al.*, 1998; JRC, 2006). Humans often play an important role in both temporal
40 and spatial patterns of fire occurrence and over 95 % of current fires in the South of France
41 are ignited by people (Long *et al.*, 2008). The incidence of fire is creating a new ecological
42 situation that may enhance desertification processes (Vallejo, 1997) due to global climate
43 change. As Naveh (1990) pointed out, fire frequency can determine the structure of
44 ecosystems. Going beyond the optimum cycle of disturbances may cause the disruption of a
45 number of basic ecosystem properties such as the pool of soil nutrients. According to Eugenio
46 *et al.* (2006), fire recurrence is defined as the number of fire events occurring at a site during a
47 given period of time. Many studies have only taken into account the effect of the number of
48 fires (Gondelis *et al.*, 2008; Eugenio and Lloret, 2006; Eugenio *et al.*, 2006; Pausas and
49 Lloret, 2007; Kazanis and Arianoutsou, 1996; Clemente *et al.*, 1996). However, the time
50 interval between two successive fires can also have different impacts on the vegetation.
51 Donato *et al.* (2008) showed that much of the native biota was resilient to “extreme” events
52 such as recurrent severe fires. Conversely, short intervals (e.g. less than 4 years in Spanish
53 Catalonia ; Diaz-Delgado *et al.*, 2001) may prevent seed-producing species from replenishing
54 seed banks and resprouters species from replenishing underground reserves (Canadell and
55 Lopez-Soria, 1998; Keeley *et al.*, 1999). High fire recurrence (i.e. short time intervals) may

56 also have deleterious effects on soils causing nutrient deficits that affect plant growth and
57 primary production (Carter and Foster, 2004; Ferran *et al.*, 2005). Fire intensity is also an
58 important parameter to consider because it influences post-fire regeneration in burned areas
59 (Agee, 1998). In spite of enhanced suppression efforts in most Mediterranean countries,
60 mainly using clear-cutting or sometimes prescribed burning, high-intensity large fires are still
61 common (Moreno *et al.*, 1998; Keeley *et al.*, 1999). Prescribed burnings are supposed to
62 decrease the intensity of a subsequent wildfire by disrupting the horizontal and vertical
63 continuity of the fuel complex, but their hazard reduction potential is not easily generalized
64 (Fernandes and Botelho, 2003). Moreover, the effects of fire on vegetation structure and on
65 the resulting changes in the fire regime at large spatial and temporal scales are poorly
66 understood.

67

68 Studies on the impact of fire have been carried out at different levels, for example by
69 Fernandes *et al.* (2008) on the impact of fire severity at tree level. The impact of fire
70 recurrence (especially the number of fires) and of fire severity have frequently been analyzed
71 at stand and landscape level. Variations in fire severity are a potentially important source of
72 diversity that affects vegetation patterns at landscape scale (Christensen, 1993; Chappell and
73 Agee, 1996; Taylor and Skinner, 1998). Variable fire regimes may promote landscape
74 heterogeneity, diversification in vegetation patterns and biotic diversity (Scholes and Walker,
75 1993). Many of the observed patterns in any landscape result from past disturbances and in
76 turn, landscapes patterns can influence the spread of future disturbances (Turner *et al.*, 1989).
77 Probabilistic models have been used to investigate, for example, interactions between
78 landscape patterns and crown fires (Gardner *et al.*, 1987; Turner *et al.*, 1989) revealing the
79 importance of landscape connectivity, and consequently the spatial arrangement of fuels, in
80 controlling disturbance dynamics (Davis and Burrows, 1994; Turner and Romme, 1994).

81

82 In this study, vegetation was analyzed as fuel, with the aim of predicting fire behaviour
83 characteristics (rate of spread, intensity, flame height, etc.), as well as the impact of fire.
84 Wildland fuel is any combustible material available for fire ignition and combustion (Keane *et*
85 *al.*, 2001), mainly live and dead organic matter. Fuels are inherently complex and have many
86 properties that determine fire behaviour, which make them difficult to characterize (Sandberg
87 *et al.*, 2001).

88

89 Pine-dominated ecosystems are one of the main landscape features in the Mediterranean
90 basin, where they account for 25% of forested surface (Barbéro *et al.*, 1998). The most
91 abundant and widespread pine species in the western part of the basin is *Pinus halepensis*,
92 which accounts for 2.5 million ha (Quézel, 2000). This species is known to have expanded
93 during the last century, both due to its widespread use for afforestation and to its ability to
94 invade abandoned fields and pastures (Lepart and Debussche, 1992). In the French
95 Mediterranean Provence, *P. halepensis* forms communities where it coexists with other tree
96 species such as oaks (*Quercus ilex*, *Q. pubescens*, *Q. coccifera*) or *Arbutus unedo*. The forest
97 understorey is dominated by shrubs including *Pistacia lentiscus*, *Phyllirea* sp. pl., *Rhamnus*
98 sp. pl., *Ulex parviflorus*, *Quercus coccifera*, *Rosmarinus officinalis*, *Erica* sp. pl., and *Cistus*
99 sp. Pl.. Such communities have high fuel loads and vertical fuel continuity, and promote high
100 intensity fires that usually kill the entire pine population (Eugenio *et al.*, 2006).

101

102 The aim of this study was to address the effects of fire recurrence at stand level in
103 southeastern France, especially the effect on vegetation structure of the time elapsed since the
104 last fire. A further aim was to determine if these parameters affect forest biodiversity. This
105 study was carried out on limestone soils at the same time as similar studies taking place on
106 acidic soils in Provence, France.

107

108

109 **Methods**

110

111 Study sites

112 In order to prevent variability due to site fertility or physiography, data were collected on sites
113 distributed throughout limestone-derived soils in Provence, southeastern France (Fig. 1) that
114 were selected because of their homogeneity in terms of fertility (medium according to the
115 forest site classification), elevation (less than 300 m), slope (less than 2°) and aspect. A total
116 of 39 study sites were selected using geographical information system (GIS, Esri ArcGis 9.1)
117 by intersecting the following layers: (1) an accurate vegetation map (National Forest
118 Inventory, IFN), (2) fire boundaries for the period 1960¹-2005, and (3) a Digital Elevation
119 Model from the altimetric database provided by IGN (French National Geographical
120 Institute). Within each study site, the vegetation was described in a representative 400 m²
121 georeferenced plot (20 m x 20 m).

122

123 Figure 1

124

125 Vegetation types and fire regimes

126

127 Three representative vegetation types were sampled: pure *Pinus halepensis* stands, mixed
128 pine-oak (pines with *Quercus ilex* and/or *Quercus pubescens*) stands, and shrublands (so-
129 called Garrigue, i.e. evergreen sclerophyllous vegetation type dominated by shrubs). These
130 three types are representative of three sequences of post-fire succession on limestone
131 substrates in Provence and dominate in the study area.

132

133 Sites differed in their fire regime which was defined, first, according to the number of fire
134 events that had occurred during the past 45 years (3 types: no fire, 1 or 2 fires, 3 or more

¹ No spatial records are available on fires occurring before 1960 in the study area.

135 fires), and second, according to the time interval since the last fire (3 types: more than 45
136 years with no fire, between 45 and 15 years and 15 years or less) (Table 1). According to
137 Eugenio *et al.* (2006), a period of at least 15 years without a fire appears to be very important
138 for the recovery of *Pinus halepensis* populations. This interval is assumed to be sufficient to
139 favour forest succession towards oak woodlands (Gracia *et al.*, 2002). The fire regime “no fire
140 for 45 years” was used as control.

141

142 Description of vegetation structure

143

144 Study plots were marked with differential GPS sub-metre post-processed positioning using
145 EGNOS (Gauthier *et al.*, 2003). Fuel structural elements were referenced according to the
146 geographical coordinates of the plot using decameters. The aboveground vegetation and litter
147 of each plot were described:

148 - Aboveground vegetation

149 Aboveground vegetation strata were assumed to be composed of live fuel. The stand
150 description took three structural elements into account: (i) isolated trees or shrubs, (ii)
151 vegetation patches made up of a single species and (iii) continuous fuel beds in the
152 understorey vegetation, including different species of the same height, defined as a
153 “vegetation layer” Therefore, the variation of structures was also assumed to be part of
154 landscape diversity.

155 The following parameters were recorded for each type of vegetation structure:

- 156 (i) Isolated shrubs and trees: height (m) of the first live branch and trunk
157 circumference (m) at 1.30 m height giving the diameter at breast height (dbh) only
158 for the trees, crown diameter measured on both North-South and East-West axes
159 (m), total height (m) of the plant and its species,
- 160 (ii) Vegetation patches: patch diameter measured on both North-South and East-West
161 axes (m), mean patch height (m) and its species,

162 (iii) Vegetation layers: the vegetation was sampled along parallel transects laid out
163 every three metres, perpendicularly to the side of the plot, within the continuous
164 fuel bed. Every three metres along each transect, the main species, its height (m)
165 and its percentage cover per 1 m² were recorded.

166 Isolated shrubs, patches and layers generally composed the understorey in the forest. The tree
167 density (number of trees per hectare) and the volume of tree crowns (m³·ha⁻¹), the percentage
168 cover of the different heights of the vegetation strata (0-1 m, 1-3 m, 3-6 m, 6-10 m, >10 m),
169 the percentage cover and mean height (m) of each structural element (tree, shrub, patch and
170 layer) were also calculated.

171

172 Litter

173 Litter is the ground fuel layer made up of dead vegetation which is more or less decomposed
174 (leaves, needles, twigs, etc.). All measurements were made in April-July, just after the peak of
175 leaf/needle fall and before their decomposition, which occurs in autumn-winter in the study
176 area. Litter depth (cm) and percentage cover were recorded in 1 m² quadrats, placed
177 systematically every two metres (Fig. 2). The average of the values gave the mean depth and
178 mean cover for each plot.

179

180 Figure 2

181

182 Statistical analyses

183 The effects of both factors “type of vegetation” and “fire regimes” on the fuel structure
184 variables were analyzed using one-way analysis of variance (one-way ANOVA). In addition
185 to tests of overall significance with ANOVA, the LSD test was used to test significant
186 differences between vegetation types or fire regimes. The α level for all tests was 0.05. In all
187 cases, when the distribution of data did not follow the expected parametric pattern and when
188 the log- or square root-transformations were not efficient, a non-parametric Kruskal-Wallis

189 test was used instead of a parametric ANOVA. Then, for each type of vegetation, different
190 fire regimes were compared with respect to the cover of vegetation strata and of the fuel
191 structural elements, using a non-parametric Kruskal-Wallis test because of the small number
192 of data in each sample analyzed. The relationship between litter variables was analyzed using
193 regression and the Pearson correlation coefficient. A significant relationship between the
194 variables was assumed when the probability was less than 0.05 (Statgraphics Centurion XV).

195

196

197 **Results**

198

199 - Aboveground vegetation

200 The following vegetation structure parameters differed significantly according to the types of
201 vegetation (Tab. 2 and 4):

202 (i) Height of shrubs, vegetation patches and layer. The lowest values were
203 recorded in shrublands and the highest in pine-oak mixed stands. Tree height
204 did not vary significantly between the different stands.

205 (ii) Cover of vegetation strata, except for the 1-3 m stratum which did not vary
206 from one type to another. The cover of the lowest stratum (0-1m) increased
207 with a decrease in the canopy cover, unlike the cover of the highest strata
208 which displayed the reverse trend.

209 (iii) Cover of trees, shrubs and vegetation patches which decreased more in more
210 open environments, i.e. in shrublands. The cover of the vegetation layer did not
211 vary from one ecosystem to another.

212 (iv) Tree density and volume of tree crowns per hectare. The highest values were
213 obtained in *Pinus halepensis* stands.

214

215 The fire regimes entailed the following significant changes in vegetation structure (Tables 3
216 and 4):

217 (i) A decrease in the height of the trees and of the vegetation layer with fire. Patch
218 height remained constant regardless of the fire regime. Shrub height only
219 varied significantly with the number of fires.

220 (ii) A decrease in strata cover, especially in the case of recent fires (in the 3-6 m
221 and 6-10 m strata), except in the lowest stratum (0-1 m) in which the cover
222 remained constant regardless of the fire regime.

223 (iii) A decrease in tree cover with fire, while the other types of vegetation remained
224 constant.

225 (iv) A decrease in tree density and in the volume of tree crowns with fire.

226

227 Effect of fire regime on vegetation structure within each vegetation type

228 The previous results, especially those concerning the impact of vegetation types and fire
229 regimes on the cover of vegetation strata and of fuel structural elements were refined by
230 comparing each fire regime within each vegetation type. These two variables were considered
231 to be the most significant in describing the forest diversity at landscape level.

232 Thus, in shrublands, there was no variation in the stratum cover according to the fire regime
233 except in the 1-3 m stratum in which the cover was significantly higher ($KW=9.48$, $p=0.023$)
234 in unburned stands or in stands that burned a long time ago (1-2 fires > 15 years ago) than in
235 stands that burned recently after a short interval (1-2 fires ≤ 15 years ago and ≥ 3 fires < 15 years
236 ago).

237 The same trend was found in mixed stands in the upper strata, 3-6 m and 6-10 m ($KW=8.06$,
238 $p=0.018$ and $KW=5.6$, $p=0.05$). The cover of the highest stratum (>10 m) was significantly
239 higher in unburned stands (40%) than in burned stands (0%) regardless of the number of fires
240 and the interval since the last fire ($KW=10.5$, $p=0.005$). There was no variation in the cover of
241 the lower strata (0-1 m and 1-3 m) as a function of the fire regime.

242 In *Pinus halepensis* stands, the impact of the fire regime on the cover of strata was significant
243 only in the highest stratum (>10m), and there was a marked decrease in cover from unburned
244 stands to burned stands (KW=6.32, p=0.042) (Table 5; Fig. 3).

245 Concerning the fuel structural elements cover, our results showed that, in shrublands, the
246 impact of the fire regime was not significant regardless of the structural element concerned
247 (isolated trees or shrubs, patches, layers). In mixed and pure pine stands, the impact of the fire
248 regime was significant only for tree cover (KW=10.35, p=0.006 for mixed stands and
249 KW=8.44, p=0.014 for pine stands) with a decrease in tree cover from unburned or previously
250 burned stands (> 15 years) to recently burned stands (\leq 15years) (Table 5; Fig.4).

251

252 These results showed that, in shrublands, the fire regime did not lead to a variety of vegetation
253 patterns. In both pure pine and mixed stands, the variation in vegetation structure due to fire
254 could involve a variation of landscapes only at tree level. As the sampling was only carried
255 out on 39 study sites, all of which were representative of limestone Provence, this could
256 explain the lack of variation in our results.

257

258 Figures 3 and 4

259

260 Figure 5 shows the cover of the main species recorded on the study sites according to
261 vegetation types and fire regime. The minimum number of main species was observed in pure
262 pine stands that had never burned (2 species) and in shrublands that had burned repeatedly.
263 The maximum (4 or 5 species) was observed in the three types that had burned once or twice
264 with a long interval since the last fire (>15 years) and in mixed stands that had burned once or
265 twice with a short interval (\leq 15 years) since the last fire.

266

267 Figure 5

268

269

270 - Litter

271 Results showed that both fire the regime and the vegetation type had a significant influence on
272 litter depth (ANOVA, $F=6.17$, $p=0.002$; $F=8.17$, $p=0.0013$) whereas only the fire regime had
273 a significant influence on the cover of litter (ANOVA, $F=5.08$, $p=0.0053$). The lowest values
274 of these variables were linked to the highest number of fires and to open land (shrublands).
275 An LSD test showed that differences were significant only between shrublands and mixed
276 stands, and between shrublands and *Pinus* stands for vegetation types. Concerning the fire
277 regime, differences were significant between the oldest fires (0 fire since 1960 and 1 or 2 fires
278 > 15 years) and recent fires (<15 years regardless of the number of fires). There was a
279 significant decrease in litter depth and cover with an increase in the number of fires and with a
280 decrease in the interval since the last fire, especially for shrublands (Fig. 6).

281

282 There was a moderate positive correlation between litter depth and the cover of the 1-3 m
283 stratum (correlation coefficient=0.53, $p=0.02$), and the cover of the 6-10 m stratum
284 (correlation coefficient=0.52, $p=0.02$). The correlation was the same between the cover of the
285 litter and the cover of the 1-3 m stratum (correlation coefficient=0.55, $p=0.014$). There was no
286 correlation between litter parameters and tree basal area or between litter parameters and tree
287 cover.

288

289 Figure 6

290

291

292 **Discussion**

293

294 Change in vegetation structure

295

296 The results of our study showed that the minimum cover of trees, shrubs and patches was
297 observed in shrublands, early stages in the post-fire succession (Quézel, 1998), and that
298 coverage increased with stand aging. In the both types of forest, tree cover decreased with a
299 decrease in the time since the last fire (i.e. short time interval since the last fire), as no trees or
300 a few trees were recorded in the case of a recent fire (≥ 3 fires or 1-2 recent fires and ≤ 15
301 years). This was especially true in the case of the cover of the highest stratum (>10 m) in *P.*
302 *halepensis* stands, which were the most mature encountered in the study area. Indeed, several
303 studies have shown that tree cover was the most relevant variable to explain differences in the
304 characteristics of Mediterranean plant communities (Gondelis *et al.*, 2008; Eugenio and
305 Lloret, 2006; Eugenio *et al.*, 2006; Pausas and Lloret, 2007; Kazanis and Arianoutsou, 1996;
306 Clemente *et al.*, 1996). In these studies, fire intervals ranging from 2 to 10 years negatively
307 affected most ecosystem attributes such as soil organic matter, and led to structural
308 simplification of the vegetation. For example, in *Pinus halepensis* populations, the percentage
309 of pines decreased while that of shrubs increased. In our study sites, the cover of understorey
310 (shrubs, patches and layers) did not vary significantly between burned and unburned sites
311 regardless of the type of vegetation (Table 5). Nevertheless, the layer was the main structural
312 element (always more than 40% cover) allowing high horizontal connectivity between fuel
313 beds, regardless of the vegetation type or the fire regime.

314

315 Tree cover, tree density and volume were the highest in pure pine stands in which *Pinus*
316 *halepensis* had the largest crowns and dbh, but these values decreased with the recurrence of
317 fires. This revealed a loss of resilience of the *P. halepensis* population with an increase in the
318 number of fires and/or a decrease in the time interval since the last fire (Eugenio *et al.*, 2006).
319 In recently burned sites, *P. halepensis* was dominant only in pure pine stands, but not in
320 mixed stands. Several authors (Bradstock *et al.*, 1997; Pausas, 1999) showed that recurrent
321 fires favoured seeders only if the fire interval enabled plant maturation and production of
322 seeds.

323

324 Generally, the cover of every stratum except the lowest (0-1 m) decreased with a decrease in
325 the canopy cover. Their values were the lowest in shrublands and in the case of recent fires
326 (short time interval since the last fire) and the highest in pine stands for the highest stratum
327 (>10 m). The cover of the lowest vegetation stratum (0-1 m), made up of grasses and low
328 shrubs, remained constant regardless of the fire regime and was highest in shrublands.

329

330 Some *Pinus* trees were present above the shrublands in one plot and in mixed stands. These
331 trees were as high as those in pure pine stands, explaining why tree height did not vary
332 according to the type of vegetation in the study site. Only tree height and layer height
333 decreased in recent fires leading to a decrease in vertical connectivity. This decrease in tree
334 growth also reflected loss of resilience as reported by Eugenio *et al* (2006). The height of
335 understorey was lowest in shrublands and highest in mixed stands, which were more open
336 than mature *Pinus halepensis* stands where the soil is too acidic to allow development of an
337 important understorey (Barbier *et al.*, 2008). Vertical connectivity was higher in mixed stands
338 than in pure pine stands.

339

340 In the study sites, shrublands were mainly composed of *Quercus coccifera* as was the
341 understorey of *P. halepensis* stands (Figure 5) regardless of the fire regime. Indeed, this
342 species regenerates after fire by resprouting (Deletti *et al.*, 2005) and has been shown to be
343 very resilient to wildfire (Trabaud, 1990; Canellas and San Miguel, 1991; Papio, 1994)
344 because of its extensive root system (Papatheodorou *et al.*, 1998; Canellas and San Miguel,
345 2000). Several authors showed that, after a period of a few years, plant species composition
346 becomes similar to prefire composition, the most efficient being the resprouters, especially in
347 shrublands (Vallejo *et al.*, 1998; Nunez and Raffaele, 2007; Delitti *et al.*, 2005). Our results
348 also showed that *Quercus ilex*, another resprouting species, was the main understorey species
349 in both unburned and recently burned plots in mixed stands (up to 73%) while *Ulex*

350 *parviflorus*, an obligate seeder, was one of the dominant understorey species in recently
351 burned plots (up to 44%). This result differs from that of Delitti *et al.* (2005) who found that,
352 on the most frequently burned sites, the cover of herbaceous and sub-shrub species showed a
353 tendency to increase while that of the obligate seeding shrubs (*U. parviflorus*) decreased with
354 both the frequency of fires and a decrease in the interval since the last fire. According to
355 Clemente *et al.* (1996), obligate seeders have different patterns of recovery, some species
356 being more abundant just after a fire (*Cistus monspelliensis*, *Cistus albidus* in the recent fires
357 regimes), while others display delayed yet continuous recruitment during post-fire succession
358 (*Rosmarinus officinalis* after old fires and the control). In the present study, for both fire
359 regimes (old or recent fires), *Pinus halepensis* remained the main species in pure pine stands.
360 *P. halepensis* is a seeder and a serotinous species that forms a canopy seed bank (Goubitz *et*
361 *al.*, 2003; Daskalakou and Thanos, 1996;). Post-fire regeneration of the species relies
362 exclusively on the canopy seed bank, due both to the transient nature of the soil seed bank and
363 to the destruction by fire of all seeds on or near the soil surface (Habrouk *et al.*, 1999; Izhaki
364 *et al.*, 2000; Núñez and Calvo, 2000).

365

366 Relationships between fuel accumulation and wildfire activity have been reported in Europe
367 by Rego (1991). The management of the wildfire risk involves the control of the understorey
368 growth, generally by clear-cutting or prescribed burning. The latter is generally used at wide
369 scale even if the fuel accumulation rate frequently limits prescribed burning effectiveness to a
370 short post-treatment period according to Fernandes and Botelho (2003).

371

372 Impact of fire recurrence on litter

373 Litter depth decreased in the case of recent fires as a function of the decrease in tree cover and
374 height. Litter depth values were lowest in shrublands where species did not produce a large
375 amount of litter whereas understorey productivity was the highest in open stands (Wimberly
376 and Kennedy, 2008). The litter was thicker under the oldest stands (>15 years) than under

377 recently burned stands which had a greater tree cover. According to Cseresnyes *et al.* (2006),
378 needlefall increased with stand age and Williams and Wardle (2007) showed that mean annual
379 pine needlefall was 2.5 times greater in unburned areas than in burned areas. Indeed, they
380 found a significant reduction in leaf shed in both species and a significant reduction in
381 litterfall for up to four years following the fire.

382 Litter cover also decreased in the case of recent fires regardless of the type of vegetation.
383 Williams and Wardle (2007) showed that the majority of pine litter (70%) fell directly below
384 the pine canopy, whereas the proportion decreased in mixed stands.

385 The correlations between litter parameters and vegetation strata (1-3 m and 6-10 m) cover
386 were intermediate. The 1-3 m stratum was one of the two strata with the highest cover
387 especially in mixed stands (>55%). This stratum was essentially made up of tall shrubs with a
388 cover of more than 30% regardless of the type of vegetation and the fire regime (except when
389 the frequency of fires was too high: ≥ 3 fires) and played an important role in litter production.

390 Litter cover remained homogeneous in the plot regardless of the tree cover and no correlation
391 was found between litter cover and the cover of the other strata. In mixed stands, litter
392 comprised a mix of *Q. pubescens* leaves and *Pinus halepensis* needles. The oak leaves formed
393 thick well-ventilated litter in contrast to pure needle litter which was much more compacted
394 and decomposes more slowly than sclerophyllous leaf litter (Madeira and Ribeiro, 1995; Paul
395 and Polglase, 2004) due to a high initial lignin/nitrogen ratio (Madeira and Ribeiro, 1995).

396

397

398 **Conclusion**

399

400 The fire regime, which is partly induced by human activities in limestone Provence, clearly
401 influenced the structure of the stands. As diverse fire regimes within ecological limits are
402 essential for maintaining biodiversity, the variation in vegetation structure may play a role in
403 diversity at local and landscape scales (De Grandpré *et al.*, 2000; Burrow, 2008). In our study,

404 the decrease in the interval since the last fire led to the opening of the canopy similar to a
405 level of an early successional stage. Only the cover of the lowest stratum (0-1 m),
406 corresponding to grasses and low shrubs, did not vary as a function of the fire regime and its
407 values were higher in shrublands whereas the cover of the other strata decreased with a
408 decrease in the canopy cover. The horizontal connectivity between fuel beds did not change as
409 a function of vegetation type or fire regime because of the resilience of the resprouters *Q. ilex*
410 and *Q. coccifera* in the understorey. In this case, the risk of surface fire remains high
411 especially when the weather conditions are severe. In contrast, the vertical connectivity
412 decreased with fire recurrence especially in *Pinus halepensis* stands which become less
413 resilient (Eugenio *et al.* 2006), thus decreasing the risk of crown fire. However, there was a
414 high risk of fire in mixed stands in which no fire had occurred because of higher vertical
415 connectivity and higher fuel amount.

416

417 The litter parameters were also affected by the recurrence of fires and by a decrease in the
418 interval since the last fire. The increase in litter depth with stand closure increased the risk of
419 fire. The positive correlation between litter parameters and tree cover was mainly due to the
420 oak stratum (6-10 m) in mixed stands as oak leaves were less compacted than litter that
421 contained only pine needles.

422

423 It will be interesting to compare these results to those obtained in acidic soils of Provence and
424 determine whether the effects of fire recurrence on vegetation structure are the same, since the
425 site fertility and the species composition of the fuel complex are different.

426

427 These results underline the need to control the growth of understorey vegetation to reduce the
428 risk of fire. Prescribed burning may be an efficient technique for this purpose, but is not often
429 applied in the French Mediterranean region.

430

431

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433

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438

439

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599

TABLES

600

601 Table 1: Number of study sites sampled in each vegetation type as a function of the fire
602 regime (number of fires/interval since the last fire).

603

Fire regime	Types of Vegetation			Total
	Shrublands	Mixed stands	Pure pine stands	
No fire/>45 years	3	4	4	11
1-2 fires/>15 years	4	4	4	12
1-2 fires/<15 years	4	4	4	12
≥ 3 fires/<15 years	4	0	0	4
Total	15	12	12	39

604

605 Table 2: Mean (standard deviation) values of the different vegetation structures as a function
 606 of the fire regime.

607

Vegetation structures / Fire regimes		No fire	1-2 old fires	1-2 recent fires	>=3 fires
Percentage cover of stratum	Stratum >10 m	39.7 (37.9)	7.1 (12.3)	5.0 (8.7)	0.0
	Stratum 6-10 m	11.9 (17.9)	16.2 (14.4)	0.2 (0.2)	0.0
	Stratum 3-6 m	17.0 (12.9)	17.2 (18.3)	3.7 (5.6)	0.0
	Stratum 1-3 m	53.6 (15.1)	58.3 (4.7)	45.6 (30.0)	1.7 (2.4)
	Stratum 0-1 m	70.3 (6.8)	62.5 (19.4)	58.7 (16.3)	73.7 (12.5)
Percentage cover of structural elements	Trees	69.7 (44.6)	33.8 (31.7)	10.1 (17.5)	0.0
	Shrubs	7.0 (4.4)	10.7 (7.5)	17.4 (15.5)	1.4 (1.7)
	Patches	5.4 (6.6)	16.0 (17.7)	19.4 (12.4)	0.4 (0.7)
	Layers	52.0 (16.9)	64.8 (6.0)	46.8 (4.7)	66.6 (12.5)
Height (m) of structural elements	Trees	11.9 (3.8)	8.9 (1.2)	6.2 (1.2)	-
	Shrubs	2.2 (0.8)	2.2 (0.6)	1.9 (0.4)	0.6 (0.1)
	Patches	1.5 (1.1)	2.1 (0.5)	1.4 (0.4)	0.5 (0.1)
	Layers	1.2 (0.5)	0.9 (0.4)	0.8 (0.4)	0.3 (0.1)
Tree density (nb ha ⁻¹)		394 (153)	204 (92)	117 (87)	0
Crown volume (m ³ ha ⁻¹)		87121 (37934)	24218 (20683)	25874 (18046)	0.00

608

609

610 Table 3: Mean (standard deviation) values of the different vegetation structures as a function
 611 of vegetation types

Vegetation structures / Vegetation types		Shrublands	Mixed stands	<i>P.halepensis</i> stands
Percentage cover of stratum	Stratum >10 m	0.6 (0.8)	13.3 (23.1)	37.9 (34.4)
	Stratum 6-10 m	0.6 (0.8)	20.1 (17.4)	7.7 (11.7)
	Stratum 3-6 m	1.0 (1.2)	21.6 (18.7)	15.6 (6.3)
	Stratum 1-3 m	32.3 (30.3)	60.0 (18.0)	53.3 (13.7)
	Stratum 0-1 m	77.6 (5.9)	58.7 (6.5)	56.7 (15.9)
Percentage cover of structural elements	Trees	4.6 (9.2)	43.0 (45.5)	64.4 (34.9)
	Shrubs	4.3 (2.0)	14.1 (4.5)	15.9 (16.7)
	Patches	3.5 (4.1)	22.6 (17.1)	13.5 (10.7)
	Layers	62.8 (9.3)	55.5 (13.7)	46.6 (11.1)
Height (m) of structural elements	Trees	9.9 (3.4)	8.1 (2.0)	10.5 (2.2)
	Shrubs	1.6 (0.4)	2.5 (0.8)	1.8 (0.5)
	Patches	0.7 (0.2)	2.5 (0.9)	1.5 (0.7)
	Layers	0.7 (0.23)	1.1 (0.5)	1.1 (0.5)
Tree density (nb ha ⁻¹)		15 (25)	248 (122)	448 (178)
Crown volume (m ³ .ha ⁻¹)		3284 (5688)	58333 (20839)	74502 (48240)

612

613

614 Table 4: Results of the one-way ANOVA showing the effects of vegetation types and fire

615 regimes on vegetation parameters (F: Fisher test ; KW: Kruskal-Wallis test ; p: probability ; NS: non

616 significant; degree of freedom=1 in all the tests)

617

Vegetation parameters	Vegetation types	Interval since last fire	Number of fires
Tree height	NS	KW=8.51; p=0.014	KW=8.08 ; p=0.004
Shrub height	F=4.20; p=0.025	NS	KW=6.41; p=0.040
Patch height	F=8.90; p=0.003	NS	NS
Layer height	KW=7.48; p=0.024	KW=13.45; p=0.004	KW=12.96. p=0.001
Tree cover	F=19.93; p=0.000	KW=16.41; p=0.000	KW=13.32; p=0.001
Shrub cover	KW=9.33; p=0.009	NS	NS
Patch cover	KW=7.32; p=0.026	NS	NS
Layer cover	NS	NS	NS
Tree density	KW=21.13; 0.000	KW=13.28; p=0.001	KW=11.58; p=0.003
Tree volume	KW=18.89; p=0.000	KW=15.27; p=0.000	KW=13.72; p=0.001
0-1 m stratum cover	F=3.40; p=0.045	NS	NS
1-3 m stratum cover	NS	NS	KW=9.12; p=0.010
3-6 m stratum cover	KW=15.30; 0.000	KW=15.23; p=0.000	KW=9.51; p=0.008
6-10 m stratum cover	KW=11.63; p=0.003	KW=9.19; p=0.010	NS
>10 m stratum cover	KW=10.08; p=0.006	KW=18.12; p=0.000	KW=18.05; p=0.000

618

619

620 Table 5: Comparison between the effects of the different fire regimes on strata cover and on
 621 the cover of structural elements in shrublands, mixed stands and pure pine stands (NS: non
 622 significant variation, *: significant variation, unburned: no fire, previously burned: 1-2 fires >15years ago,
 623 recently burned : 1-2 fires ≤15years ago or ≥3 fires <15years ago in shrublands).

624

	Shrublands		Mixed stands	Pure pine stands
Strata cover	0-1 m	NS	NS	NS
	1-3 m	* Unburned or previously burned vs recently burned	NS	NS
	3-6 m	NS	* Unburned or previously burned vs recently burned	NS
	6-10 m	NS	* Unburned or previously burned vs recently burned	NS
	>10 m	NS	* Unburned/Burned	* Unburned vs Burned
Cover of structural elements	Trees	NS	* Unburned or previously burned vs recently burned	* Unburned or previously burned vs recently burned
	Shrubs	NS	NS	NS
	Patches	NS	NS	NS
	Layers	NS	NS	NS

625

626

FIGURE CAPTIONS

627

628 Figure 1: Study sites and sampling in limestone-derived soils in Provence, France. Inner lines
629 indicate municipalities (BD Carto ® IGN 2003).

630

631 Figure 2: Description of the litter in a 20m x 20m plot

632

633 Figure 3: Variation in the cover of the vegetation strata as a function of the fire regime of each
634 vegetation type.

635

636 Figure 4: Variation in the cover of structural elements as a function of the fire regime of each
637 vegetation type.

638

639 Figure 5: Percentage cover of the main species recorded on the study sites as a function of
640 vegetation type and fire regime (P.h: *Pinus halepensis*, Q.c: *Quercus coccifera*, Q.i: *Q. ilex*, Q.p: *Q.*
641 *pubescens*, R.o: *Rosmarinus officinalis*, J.o: *Juniperus oxycedrus*, C.m: *Cistus monspelliensis*, C.a: *C. albidus*,
642 P.a: *Phillyrea angustifolia*, P.l: *P. latifolia*, U.p: *Ulex parviflorus*)

643

644 Figure 6: Variation in litter depth (cm) and in percentage cover as a function of vegetation
645 type and fire regime.

646