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1 **Influence of the spatial variability of soil type and tree colonization on the dynamics of**
2 ***Molinia caerulea* (L.) Moench in managed heathland**

3
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26

27 **Abstract**

28 European heathland communities on acid, nutrient-poor soils have a high ecological value due
29 to their special environmental conditions. Natural succession (tree colonization and the
30 emergence of grasses) poses a threat to this type of habitat and different types of management
31 strategy must be considered if it is to be maintained. A previous study on a dry heathland area
32 located in the Fontainebleau forest (France) showed a gradual shift from a pure ericaceous
33 stand to a mosaic of grasses and *Ericaceae*, despite the application of measures such as
34 removal of woodland species to sustain the habitat. Habitat change was due to local expansion
35 of a grass, *Molinia caerulea* (L.) Moench. The present paper aimed to identify factors
36 responsible for the expansion of *M. caerulea* and the subsequent decrease in ericaceous heath.
37 We focused our study on spatial variability of soil properties (soil horizons, pH, water
38 content) and reforestation (density of birch individuals and proximity to woodland) as a suite
39 of possible factors promoting the expansion of *M. caerulea*. We show that the development of
40 grasses was correlated with thin soil E horizon and spatial distribution of old shoots of
41 birch, *Betula pendula* Roth, which are regularly cut and then resprout. These results suggest
42 that new methods to avoid tree colonization must be introduced if typical heathland is to be
43 maintained.

44 **Keywords:** *Calluna vulgaris*, GIS, soil horizons, soil pH, kriging procedure.

45

46 **1. Introduction**

47 European heathlands are generally restricted to acid, nutrient-poor soils. Tree colonization and
48 the emergence of grasses pose the greatest threats to this habitat. Dwarf shrubs belonging to
49 the Ericaceae are found on oligotrophic soils, where they are better competitors. The dynamics
50 of plant communities are directly associated with the availability of soil mineral resources,
51 which is a structuring factor for vegetation (Miles, 1981). Soil nutrient availability influences
52 the competitive balance and allows grass species to establish on nutrient-rich soils.

53 Heathlands are sub-climax communities (Gimingham, 1972) and, in order to maintain
54 them, management is required to control natural successional processes. Several methods are
55 used in Europe to maintain this habitat in a favourable state for conservation, particularly since
56 ericaceous heathlands have been designated as a natural habitat type of EC community
57 interest in Annex I of the EC Habitats Directive (1992).

58 Ericaceous heathlands have a restricted distribution in the biogeographic zone of Atlantic
59 north-western Europe (Webb, 1998). The presence of acid sandy soils in the Biosphere
60 Reserve of the Fontainebleau forest (Ile-de-France, northern France) (28 000 ha) and the use
61 of traditional agro-pastoral activities have favoured the establishment of heathlands for
62 thousands of years.

63 The abandonment of traditional practices during the second half of the 20th century caused a
64 decrease in heathland, and a concomitant increase in forest vegetation. At present, 1400 ha of
65 heathland remain in fragmented patches embedded in an oak-pine forest that is integrated
66 within a Managed Biological Reserve (RBD). Since heathland contributes significantly to the
67 high level of biodiversity of the massif of Fontainebleau, current management aims to
68 conserve this habitat. In a previous study we conducted an exhaustive observational study of
69 vegetation changes which occurred between 2000 and 2008 on approximately 4 ha of typical
70 heathland, employing a spatial approach (Mobaied et al., 2011). We showed that,

71 despitemanagement measures applied to maintain this typical habitat, there was a gradual
72 change towards a mosaic of grasses and Ericaceae at the expense of pure stands of *Calluna*
73 *vulgaris*(L.) Hull. This vegetation change resulted from the expansion of *Molinia caerulea*
74 (L.).

75 Several studies have shown that increased nutrient availability promotes the establishment of
76 *M. caerulea* (Aerts,1989; Heil and Bruggink, 1987). Increased nutrient availability may be
77 attributed to management methods such as grazing or controlled burning (Grant and Maxwell,
78 1988). In our study site, the only management method used is mechanical treatment. It
79 consists solelyof cutting the trees every two or three years, without any grazing or controlled
80 burning.

81 Increased nutrient availability can also be attributed to atmospheric nitrogen deposition (Aerts
82 and Berendse, 1988; Aerts and Bobbink, 1999; Hogg et al., 1995). Since the Fontainebleau
83 forest is a peri-urban forest, increased atmospheric nitrogen deposition (Ulrich et al., 2007) is
84 almost certainly due to the presence of intensive agricultural land in close proximity and
85 pollution by road traffic. However, the expansion of grasses was spatially limited to a specific
86 area and was not evenly distributed throughout the study site (Mobaied et al., 2011). This
87 suggests the existence of another contributing factor.

88 In the study site, the influence of reforestation on soil fertility and nutrient availability was
89 considered to be particularly favourable to the expansion of *M. caerulea*. Soil acidity and
90 nutrient availability are influenced by dominant plants, especially at early stages of succession
91 (Van Breemen, 1998). Piessens et al. (2006) showthat reforestation can cause an increase in
92 the concentration of nutrients in the soil.

93 This study aimed to identify the relationship between heathland dynamicsand soil spatial
94 variability and, more specifically,to identify the factors potentially responsible for the growth
95 of *M. caerulea* and the subsequent decrease of *C. vulgaris*. These findings, in turn, will

96 contribute to the design of reliable management methods for this area. In order to achieve this
97 aim, we studied the within-heathland spatial variability of reforestation and the thickness of
98 soil horizons and their relationship to grass expansion, by focusing on spatial patterns and
99 associated statistical methods.

100 **2. Materials and methods**

101 **2.1. Study site**

102 The state forest of ‘Les Trois Pignons’ (3,307 ha, 48° 2' N, 2° 3' E) is part of the Fontainebleau
103 forest massif and consists of a mosaic of forest and open habitats, including 83 ha of pure
104 managed heathland, and 540 ha of heathland partly colonized by trees and embedded in a
105 deciduous and conifer forest matrix. The study plot is situated in the Managed Biological
106 Reserve of “La Mare aux Joncs” (Parcel 53). It extends over approximately 4 ha on the edge of
107 a managed heathland (21 ha) and a zone colonized by woodland species. It represents a
108 transition zone between these two vegetation patterns (Fig. 1).

109 This area was exploited by man (agriculture, pasture) until the second half of the 20th century,
110 but these practices have since been abandoned. Following this period the heathland was
111 partially colonized by woody species. In 1990, trees were cleared off and management
112 restored the remaining heathland. Since that time, management has consisted of cutting
113 seedlings and shoots of *Betula pendula* Roth and seedlings of *Pinus sylvestris* L. every three or
114 four years.

115 The geological substrate is a flat sandstone table with sandstone terminals (Roque, 2003)
116 resting on Oligocene (Rupelian) sand (BRGM, 1970). The average annual rainfall was 801
117 mm for the period 1999–2008. The vegetation is a mosaic of dry heathland [Habitat 4030, EC
118 Habitats Directive (1992)], dominated by *C. vulgaris* at different growth stages, with patches
119 of *Erica cinerea* L. There are also patches of North Atlantic wet heath with *Erica tetralix* L.

120 [Habitat 4010, EC Habitats Directive (1992)] and dry open basins with mosses(*Campylopus*
121 *sp.*) and lichens.

122 **2.2. Dynamics of the heathland and expansion of *Molinia caerulea***

123 In a related study, all vegetation communities were mapped in 2000 and again in 2008, using
124 transects spaced every 10 m (Mobaied et al., 2011). Vegetation dynamics was mapped
125 between 2000 and 2008 at a resolution of 1 m² per cell. Five types of vegetation communities
126 were distinguished: 1) heathland with specific species (Heath), including *C. vulgaris*,
127 *E. cinerea* and *E. tetralix*; 2) a mosaic of *C. vulgaris* and *M. caerulea* (Cal+M.c); 3) wet facies
128 of *M. caerulea* (WFM.c); 4) deciduous woodland (WLD); and 5) coniferous woodland of *P.*
129 *sylvestris* (WLC). Each cell in this map represented the dynamics that occurred in the plant
130 community in the transition from the initial state in 2000 to the final state in 2008, e.g.:
131 “Heath/Cal+M.c” signifies that heathland with specific species (“Heath”) in 2000 evolved to a
132 mosaic of *C. vulgaris* and *M. caerulea* in 2008 (“Cal+M.c”). When there was no change in the
133 plant community between 2000 and 2008, the vegetation type was noted once (e.g. “Heath”).
134 Results indicated an expansion of *M. caerulea*, in which it replaced *C. vulgaris* (Fig. 2).
135 Within the heathland we distinguished two developmental stages of *C. vulgaris*: 1) open low
136 and discontinuous stands, which correspond to pioneer and building phases of the *Calluna* life
137 cycle as described by Gimingham (1972); and 2) high and continuous stands which correspond
138 to the mature phase of the *Calluna* life cycle. The expansion of *M. caerulea* occurred in open
139 low and discontinuous stands of *C. vulgaris* (CalO). Over eight years, approximately 2000m²
140 of open low and discontinuous stands of *C. vulgaris* turned to a mosaic of *M. caerulea* and *C.*
141 *vulgaris*. Therefore, the dynamics of pioneer and building stages of *C. vulgaris* was examined
142 in greater detail, investigating the spatial and environmental conditions which allowed the
143 colonization of the building phase of *C. vulgaris* by *M. caerulea*.

144 **2.3. Spatial variability of tree colonization**

145 All *B. pendula* shoots present in the site were precisely mapped during fieldwork. Data were
146 integrated into a geographical information system (GIS) as a point-vector map, and
147 subsequently a raster map was generated to represent the density of birch shoots, using the
148 Spatial Analyst module of Arc GIS 9.2 ESRI® software (ESRI, 2006a, b; Ormsby et al.,
149 2004). A given point was identified as a point of high birch density when there were more
150 than six shoots within a circle around it of radius 5 m. Following these rules, we identified
151 areas of high birch density within the site. During fieldwork we also mapped the woodland
152 zone dominated by Scots pine that bordered the study site (Fig. 1) and a polygon-vector map
153 was further generated from these data. Following studies by Piessens et al. (2006), which
154 showed that edge effects were limited in extent to a zone of 8 m into the heathland, we
155 incorporated this edge into reforestation zones.

156 **2.4. Soil survey**

157 Soil profile description, pH and water content measurements were made during a single
158 fieldwork session in 2009.

159 2.4.1. Soil horizons

160 The soil profile was characterized by coring the soil with a cylindrical soil sampler. The soil
161 sampler did not allow exploration of the entire B horizon, due to the presence of a hardpan
162 level below the sandy topsoil. Accordingly, we only considered the topsoil horizons O, A and
163 E in further detail.

164 The description of soil profiles followed Baize and Jabiol (1995) and Jabiol et al. (1995).
165 Measurements of soil horizons were undertaken on 220 points distributed along 22 transects
166 (length of transect 200 m; intervals between transects 10 m; 10 points per transect; intervals
167 between points 20 m). Data were then integrated into GIS in a point-vector map. We
168 distinguished three topsoil horizons that differed in structure, physical composition and

169 organic content: O (organic), A (organo-mineral), and E (mineral, clay-iron eluvial). At the top
170 of the soil profile, the O horizon was composed of litter and accumulated humus that had not
171 been incorporated into the mineral soil. Beneath the organic O horizon, the organo-mineral A
172 horizon was distinguished by its dark colour, due to the presence of organic matter mixed with
173 mineral (sand) products of sandstone weathering. The E horizon was distinguished by its light
174 grey colour, eluviation being the dominant process, which removed clay, iron and strongly
175 humified organic matter.

176 A geostatistical study was conducted in order to obtain a raster map of the thickness of soil
177 horizons based on observation points. To do this, we interpolated values at unobserved points
178 using a kriging procedure. This method allows for the prediction of unknown values from data
179 observed at known locations. Kriging uses variograms to express spatial variation, and
180 minimizes prediction errors by estimating the spatial distribution of predicted values (Isaaks
181 and Srivastava, 1989; Krige, 1951). We used median values of the thickness of the O, A, and
182 E horizons to reclassify each raster into two distributional classes separating the lower half of
183 values (horizon- = from minimum to median value) from the higher half of values (horizon+
184 = from median to maximum value). When a horizon was absent the point was classified in the
185 horizon- class.

186 By combining the O, A and E horizons, we constructed a map for soil series that grouped all
187 areas with similar soil profiles within our observation limits. Eight soil types were obtained:
188 O-A-E-, O+A-E-, O+A+E-, O-A+E-, O+A-E+, O-A+E+, O-A-E+ and O+A+E+.

189 2.4.2. Soil pH and soil water content

190 Sixty sampling points were selected using a sampling plan that covered the following types of
191 plant cover: 1) heathland specific species (Heath); 2) mosaic of *C. vulgaris* and *M. caerulea*
192 (Cal+M.c); 3) deciduous woodland (WLD); 4) coniferous woodland of *P. sylvestris* (WLC);
193 and 5) mixed woodland (WLM) in the area of overlap between pine and birch. Soil pH and

194 water content measurements were performed according to ISO 10390 and 11465
195 (Anonymous, 1999).

196 **2.5. Data analysis**

197 2.5.1. Vegetation dynamics and soil variability

198 In order to analyse possible correlations between the dynamics of each of the five vegetation
199 communities and the soil spatial variability, we used the cross-tabulation process of the
200 software IDRISI.ANDES32 (Clark University, 1987–2006) to create a contingency table of
201 vegetation dynamics and soil series maps. This contingency table listed the frequency of each
202 possible combination of categories on the two maps (soil types and vegetation dynamics). In
203 other words, it measured the number of pixels of each vegetation dynamics type located in a
204 given type of soil (spatially superimposed). In our raster maps, with pixel size 1 m by 1 m, the
205 spatial contingency table listed areas where vegetation change occurred in relation to soil
206 types. We tested the independence of rows and columns of the contingency table with a Chi-
207 square test to assess whether vegetation dynamics types were dependent on soil type. The
208 contingency table was exported from the GIS software to traditional Excel® software, and a
209 Correspondence Analysis (CA) was then carried out (Benzécri, 1969) using XLSTAT®
210 software (2010) (Addinsoft, 2007).

211 2.5.2. Expansion of *M. caerulea*

212 We compared: (1) spatial patterns of *M. caerulea* expansion versus soil horizons; and (2)
213 spatial patterns of *M. caerulea* expansion versus spatial patterns of tree colonization. For this
214 purpose we used the Map Comparison Kit (MCK) software (Research Institute for
215 Knowledge Systems, 2009; Visser and de Nijs, 2006). Classified maps were compared on a
216 pixel-by-pixel basis. The Kappa statistic (k) of Cohen (1960) provides a statistical measure
217 of the degree of agreement between pixel classifications. Pontius (2000) explains that the
218 Kappa statistic confounds similarity in quantity with similarity of location. He introduces

219 two statistics which allows the separation of similarity of location from similarity of
220 quantity. Two different indices were calculated: the Kappa Location index (Kloc), which
221 depends on the spatial distribution of categories on a map, and the Kappa Histo (quantity)
222 index. For the Kappa statistic (k), Landis and Koch (1977) provide guidelines for
223 interpreting k values as follows: poor ($k < 0$), slight ($0 < k < 0.20$), fair ($0.21 < k < 0.40$),
224 moderate ($0.41 < k < 0.60$), substantial ($0.61 < k < 0.80$) and almost perfect ($0.81 < k <$
225 1.00).

226 2.5.3. Soil pH and soil water content variation

227 To compare soil pH and soil water content values between the different vegetation types we
228 used a one-way analysis of variance (ANOVA) followed by multiple comparisons among
229 means (Tukey HSD) using XLSTAT[®].

230 **3. Results**

231 **3.1. Soil spatial variability**

232 Soil depth varied from 2 cm to 50 cm at the study site. The thickness of the O horizon varied
233 between 2 and 10 cm, with a median of 6 cm. The thickness of the A horizon varied from 1 to
234 18 cm, with a median of 8 cm. The thickness of the E horizon varied from 1 to 20 cm, with a
235 median of 8 cm. By combining the O, A and E horizons, eight soil types were obtained and
236 mapped (Fig. 3).

237 **3.2. Influence of soil spatial variability on vegetation dynamics**

238 Results of the Chi-square test to assess the independence of rows and columns of the
239 contingency table showed that the different types of vegetation dynamics were not
240 independent of soil type ($P < 0.0001$).

241 Vegetation dynamics classes and soil series were projected in the plane formed by the first
242 two factorial axes of CA, which explained 83% of the total variance of the data. The

243 F1–F2biplot suggested a correlation between heathland dynamics and soil types (Fig. 4).
244 WLC, Heath/WLC and WLD/WLC were associated with shallow soil types (O+A-E- and O-
245 A-E-) while WLD and Heath/WLD were associated with deeper soils (O+A+E+ and O+A-
246 E+).
247 The shift from heathland to a mosaic of *C. vulgaris* and *M. caerulea* (Heath/Cal+M.c) was
248 strictly correlated with the soil class O-A+E-. The unchanged heathland (Heath) and the wet
249 facies of *M. caerulea*(WFM.c.) were located near the origin of the factors and were not
250 correlated with any soil types.

251 **3.3. Influence of soil spatial variability on *M. caerulea* dynamics**

252 The expansion of *M. caerulea* occurred on an area of approximately 2000 m² within the
253 former zone of open low and discontinuous stands of *C. vulgaris* (CalOin 2000). The
254 expansion of *M. caerulea* showed a substantial degree of agreement with areas that had a thin
255 O horizon (less than 6 cm, Kloc = 0.619), a moderate degree of agreement with areas that
256 had a thick A horizon (more than 8 cm, Kloc = 0.482) and an almost perfect degree of
257 agreement with areas that had a thin E horizon (less than 8 cm, Kloc = 1) (Fig. 5a, Table 1).

258 **3.4. Influence of the spatial variability of reforestation on the dynamics of *M. caerulea***

259 In the heathland we observed two large areas with a high density of birch shoots. We observed
260 that these birch individuals aggregated together, thus forming an island. Within the previous
261 zone of open low and discontinuous stands of *C. vulgaris* (CalOin 2000) the value of
262 Kloc(0.649) showed a substantial degree of agreement between the area of *M.*
263 *caerulea* expansion and the area of high density of *B. pendula*, while the proximity of
264 woodland dominated by Scots pine did not influence the expansion of *M. caerulea* (Fig.5b,
265 Table 1).

266 **3.5. Relationship of soil pH and soil water content with vegetation cover**

267 Recorded pH values varied from 3.3 to 3.8. The lowest pH value was recorded in the
268 coniferous woodland (WLC) rather than in pure stands of *C. vulgaris*. In the heathland the pH
269 value varied from 3.3 to 3.8 and was not significantly different from that in other vegetation
270 types. However, the pH of WLC was significantly lower than for other vegetation types
271 (Fig.6). Within the open zone (Heath and Cal+M.c) soil pH was significantly greater (P
272 <0.05) in high density than in low density birch areas (Fig. 7).

273 The soil water content varied between 15% and 60%, without any significant differences
274 among the five vegetation types (Fig. 8).

275 **4. Discussion**

276 The development phase of *C. vulgaris* was one of the factors suggested to regulate the
277 expansion of *M. caerulea*: in fact only the pioneer and building phases of *C. vulgaris* (CalO)
278 were colonized by this grass. The existence of bare soil in such areas enabled the
279 establishment of *M. caerulea*, contrasting with the mature phase in which high heather covers
280 all the soil.

281 In the study area, two large areas with a high density of birch shoots were observed on
282 different soil types, one within open low and discontinuous stands of *C. vulgaris* (CalO) and
283 the other within high and continuous stands of *C. vulgaris* (CalH). *Betula* spp. can establish in
284 gaps in the centre of mature or degenerate *C. vulgaris* stands (Gong and Gimingham, 1984).

285 This prevents the repetition of the life cycle of heather (Gimingham, 1988), suggesting that
286 after degeneration of heather in CalH areas, cyclical growth processes cannot be restarted and
287 available spaces are instead colonized by other species (Fig. 9).

288 Within open low and discontinuous stands of *C. vulgaris*, colonization by birch exerted
289 significant effects on the expansion of *M. caerulea*. In fact, the area where *M. caerulea*
290 appeared is an area of high density of old birch shoots. In this zone birch, that was cut every

291 four years following prescribed management practices, later resprouted thereby creating a
292 special microhabitat likely to counteract soil acidification (Gardiner, 1968). This influence is
293 well explained by the relationship between the expansion of *M. caerulea* areas and soil types.
294 The transition from heathland to another vegetation type correlated well with soil type; to be
295 more precise, it correlated with the depth of the different topsoil horizons. Scots pine
296 colonization occurred on shallow soils, and this can be attributed to the ability of pines to
297 establish under conditions unfavourable for other tree species (Cañellas et al.,
298 2000; Richardson, 1988). We found deeper and more developed soils in deciduous woodland
299 (groves of *B. pendula* and *Populus tremula* L.). The expansion of *M. caerulea* was correlated
300 with thinner E horizons. Even if there were no significant variation in soil moisture over the
301 study area, it could nevertheless be assumed that drainage was slower on this type of soil,
302 which has a poorly developed layer of sand overlying sandstone, and which may therefore
303 promote the establishment of *M. caerulea*. However, this expansion was not observed in all
304 areas having thin E horizons.

305 Miles (1981) also noted an increase in soil pH in zones having a high density of *B. pendula*.
306 The microhabitat created by birch individuals leads to more 'attractive soils for further species
307 colonization' (Collier and Farrell, 2007), which benefited *M. caerulea* in our study case. Our
308 results agreed well with the podsolization of acidic soils following birch establishment, as
309 demonstrated by Miles (1981). The area affected by *Molinia* development was characterized
310 by thinner E and O horizons and a thicker A horizon, suggesting a faster disappearance of
311 plant debris in the O horizon and the incorporation of organic matter in the A horizon that
312 gradually replaced the E horizon. To confirm this impact, we would need to follow temporal
313 changes in the soil type, which was not possible in the present study (observations of the soil
314 were not performed in 2000). Several studies showed that the conversion of heathland to
315 grassland was primarily caused by a sharp increase in soil nutrient availability (Aerts,

1989; Aerts and Berendse, 1988; Aerts et al., 1990; Heil and Bruggink, 1987). Nitrogen input was identified as the most significant environmental factor for the acceleration of the *Calluna* growth cycle (Lageard et al., 2005), leaving more opportunities for the expansion of *Molinia* in areas where there was a higher nitrogen input. The effects of birch on nutrient availability are mediated by its nutrient-rich broadleaf litter (Sanborn, 2001) and the changes in soil microbial communities, as shown for *Betula pubescens* Ehrh. by Mitchell et al. (2010). Our study showed that heather is preserved in the absence of other invasive species. The successional shift towards grassland was successful only in areas where other factors intervened and potentially led to a change in soil features, e.g. reforestation by birch. This suggests that the method of heathland restoration that was applied for 20 years on the study site (by cutting birch every three or four years) indirectly favoured *M. caerulea*. The proximity to the woodland zone dominated by conifers had no impact on the dynamics of grasses. Reforestation in this area was approximately 11%, a low value that may explain the absence of shadow effect noted at the edge of a coniferous forest by Piessens et al. (2006). In this woody area, *P. sylvestris* expanded to the detriment of *B. pendula* (Mobaied et al., 2011). This suggests that the management procedure applied within the heathland (cutting birch and pine) promoted the expansion of birch by vegetative growth, explaining the clustering of birch individuals, a process which would not be possible if birch had been in competition with pine.

5. Conclusion and implications for practical management

The replacement of ericaceous dwarf shrubs by grasses such as *M. caerulea* is a major threat to heathland conservation. This unwanted trend in plant succession has been noted in most West European heathlands (Berendse, 1990). The conservation of ericaceous heathland habitats greatly depends on the conservation of the soil characteristics necessary for its sustainability. Even in the early successional stages from heathland to woodland, *B. pendula* affected the dynamics of vegetation through its influence on soil, despite the

341 implementation of management strategies to avoid reforestation. The present-day increase in
342 nitrogen deposition rates into terrestrial ecosystems creates an environment in which acid soils
343 become more sensitive. Because of these changes, de-acidification processes become
344 dominant and soils reach a threshold above which the expansion of Poaceae is encouraged, to
345 the detriment of Ericaceae. Management practices which attempt to conserve heathland
346 habitats must become more intensive (Barker et al., 2004) and must take into account the
347 impact of any additional factors on soil acidity and nutrient availability.

348 Several recommendations can be drawn from our study: (1) cutting of tree individuals would
349 be more effective in summer after extraction of soil nutrients by tree canopies and before
350 recycling of nutrients to the soil through annual litterfall; (2) *Betula* shoots should be
351 extracted when they are at a high density; (3) a specific management should be implemented
352 for grasses; and (4) heathland areas should be selected that will be easier to conserve and/or to
353 restore, by surveying the soil and then focusing on areas where spatial conditions prevent
354 grass expansion and reforestation, and hence which favour the long-term stability of
355 heathland. According to our results, management priority should be given to those heathland
356 areas that are located on shallow soils where the thickness of the A horizon is less than 8 cm.
357 This study provides several threshold values which are of practical value for heathland
358 conservation in similar regions. Specifically, we provide indications of the soil condition, with
359 respect to the factors that influence the expansion of grasses to the detriment of Ericaceae, e.g.
360 more than six *Betula* shoots in a circle of 5 m radius, pH values higher than 3.5, and thickness
361 of the E horizon lower than 8 cm. These values can be measured easily in the field and could
362 possibly prevent the colonization of the area by grasses, and in so doing would avoid the need
363 for more drastic interventions once grasses are established.

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Table 1: Kappa indices (k , k_{Loc} and k_{histo}) to measure of the degree of agreement between *Molinia caerulea* expansion and soil horizons or spatial patterns of birch colonization.

	<i>Kappa</i>	<i>Kappa Location</i>	<i>Kappa Histogram</i>
Comparisons between <i>Molinia caerulea</i> expansion and soil horizons.			
Thick O horizon (O+)	-0.078	-2.613	0.030
Thin O horizon (O-)	0.262	0.619	0.424
Thick A horizon (A+)	0,474	0.482	0.982
Thin A horizon (A-)	-0.097	-2.376	0.041
Thick E horizon (E+)	-0.124	-2.170	0.057
Thin E horizon (E-)	0.243	1	0.243
Comparisons between <i>Molinia caerulea</i> expansion and spatial patterns of tree colonization.			
Areas of high density of <i>Betula pendula</i>	0.431	0.649	0.665
Areas without <i>Betula pendula</i> shoots	-0.082	-5.071	0.016
Areas in proximity of woodland zone dominated by coniferous trees	0.077	0.097	0.795

469
 470

471 **Figure captions**

472 **Figure 1.** Location of the study site in: (1) France, (2) Ile-de-France and the state forest of
473 TroisPignons (in gray), (3) the 21 ha of managed heathland (black line), the study plot 4.4 ha
474 (white line) in the Mare-aux-JoncsManaged Biological Reserve located at coordinates 48 ° 2
475 'N, 2 ° 3'E.

476 France mapsvector source: Institut d'Aménagement et d'Urbanisme de la Région d'Ile-de-
477 France (IAURIF). Aerial photographic source: InstitutGéographique National (IGN)

478

479 **Figure 2.**Map of the dynamics of vegetation between 2000 and 2008

480 Heath = heathland unchanged; Heath/WLC = change from heathland to *Pinus sylvestris*
481 woodland; Heath/WLD = change from heathland to deciduous woodland;Heath/Cal+M.c =
482 change from heathland to mosaic of *Calluna vulgaris* and *Molinia caerulea*; Cal+M.c =
483 unchanged mosaic of *Calluna vulgaris* and *Molinia caerulea*; WFM.c = wet facies of
484 unchanged *Molinia caerulea*; WLC = unchanged *Pinus sylvestris* woodland; WLD/WLC =
485 change from deciduous woodland to *Pinus sylvestris* woodland; WLC =unchanged deciduous
486 woodland; P= pathway; S=swamp area.

487

488 **Figure 3.** Map of soil series; O- = thin or no O horizon; O+ = thick O horizon; A- = thin or no
489 A horizon; A+ = thick A horizon; E- = thin or no E horizon; E+ = thick E horizon.

490

491 **Figure 4.** Correspondence analysis (CA)biplot: projection of classes of vegetation dynamics
492 and soil series in the plane of axes 1–2.

493

494 **Figure 5.** (a) Maps of the zone of expansion of *Molinia caerulea* versus soil horizon
495 thickness.

496 (b) Maps of the zone of expansion of *Molinia caerulea* versus spatial patterns of tree
497 colonization.

498

499 **Figure 6.** Comparison of soil pH values among ground cover plant categories: a same italic
500 letter indicates non-significant differences (HSD procedure, $P < 0.05$).

501

502 **Figure 7.** Comparison of soil pH values amongst spatial patterns of *Betula*: a same italic letter
503 indicates non-significant differences (HSD procedure, $P < 0.05$).

504

505 **Figure 8.** Comparison of soil water content values among ground cover plant categories: a
506 same italic letter indicates non-significant differences (HSD procedure, $P < 0.05$).

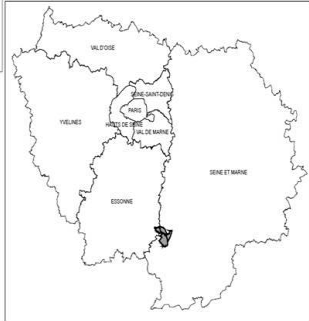
507

508 **Figure 9.** The influence of spatial variability of soil and tree colonization on restart of cyclical
509 growth of *Calluna* and on expansion of *Molinia caerulea* following heather degeneration.

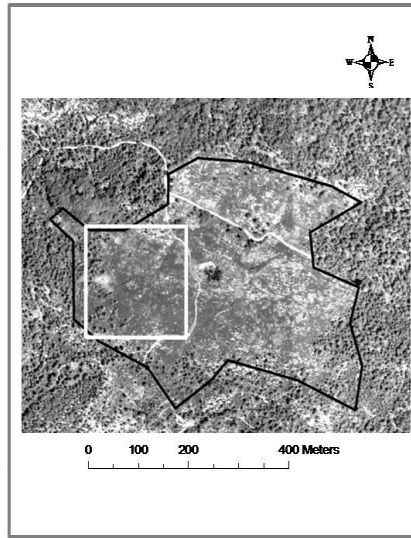
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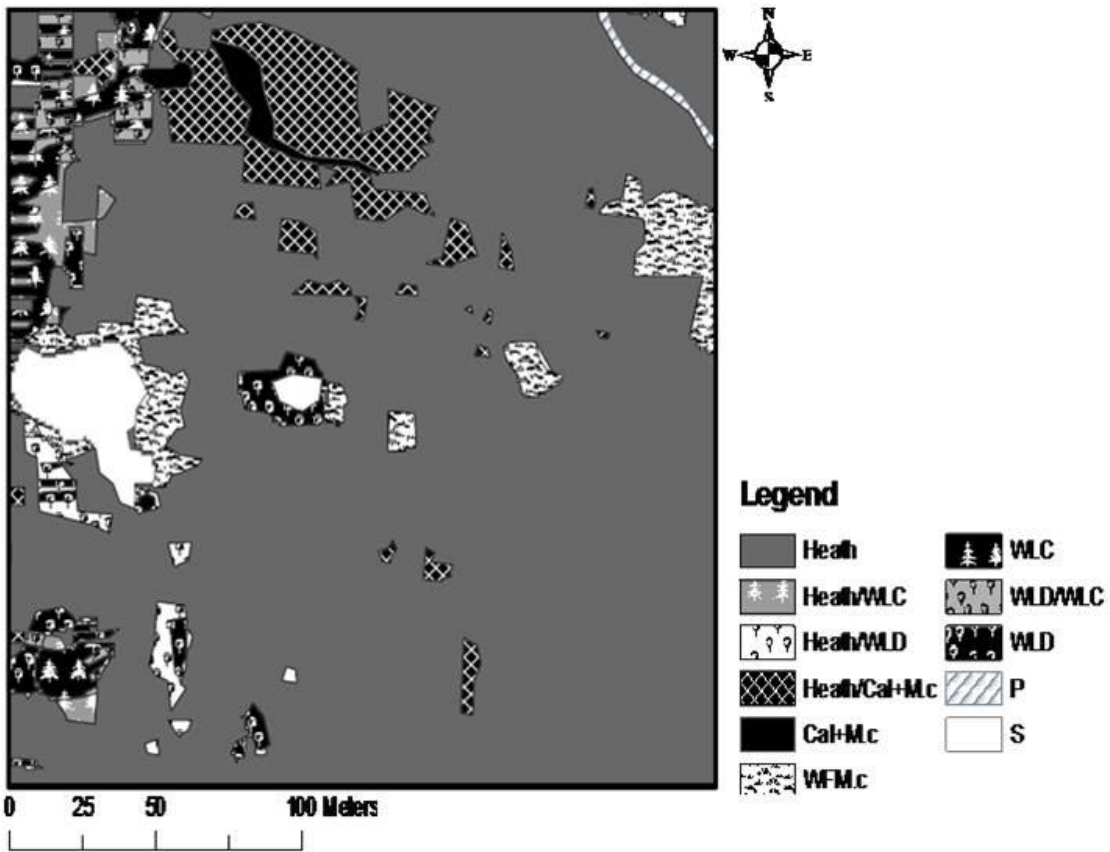


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512 Fig. 1

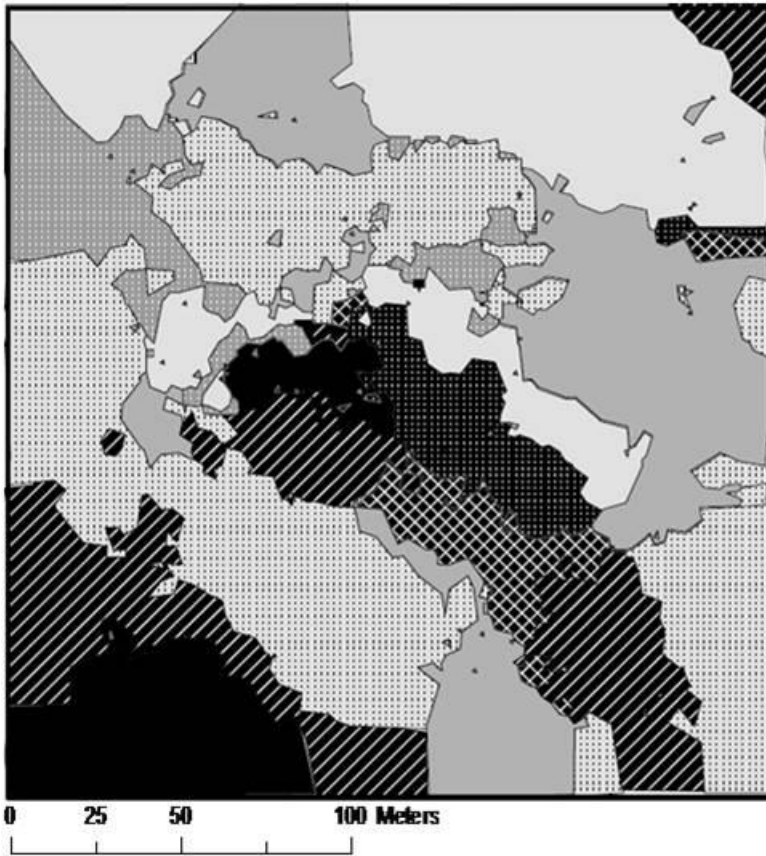
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515 Fig. 2

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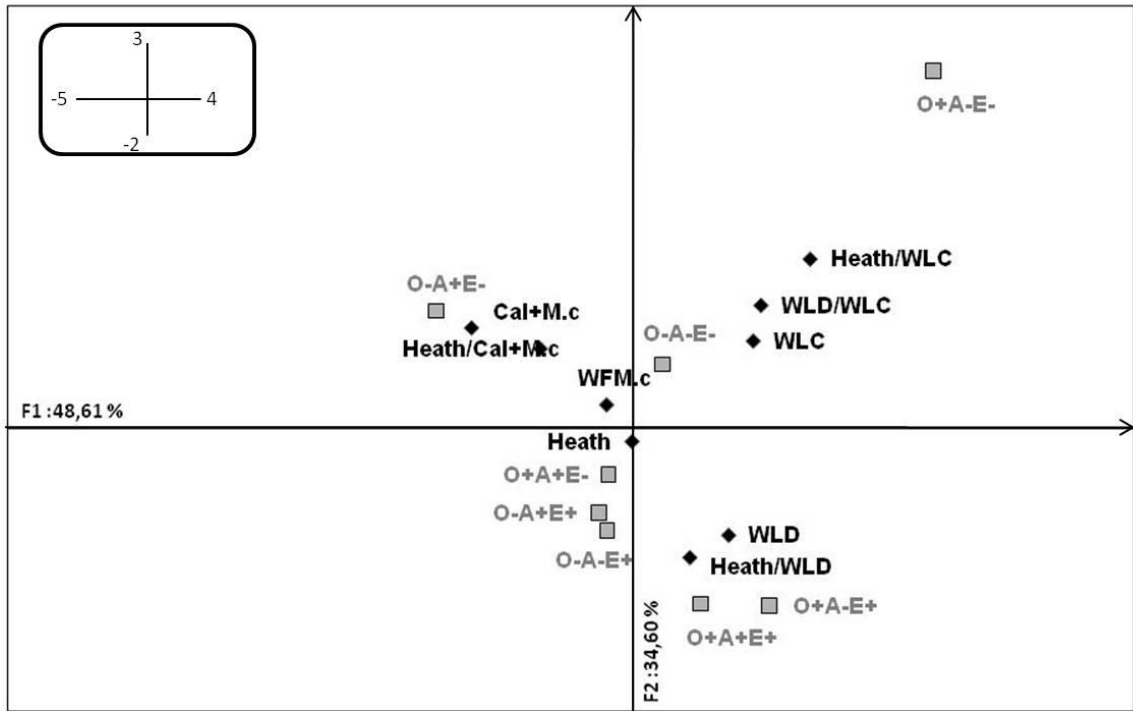
Legend

	0-A-E-		0-A+E+
	0+A+E-		0+A+E+
	0-A+E-		0-A-E+
	0+A-E-		0+A-E+

517

518 Fig. 3

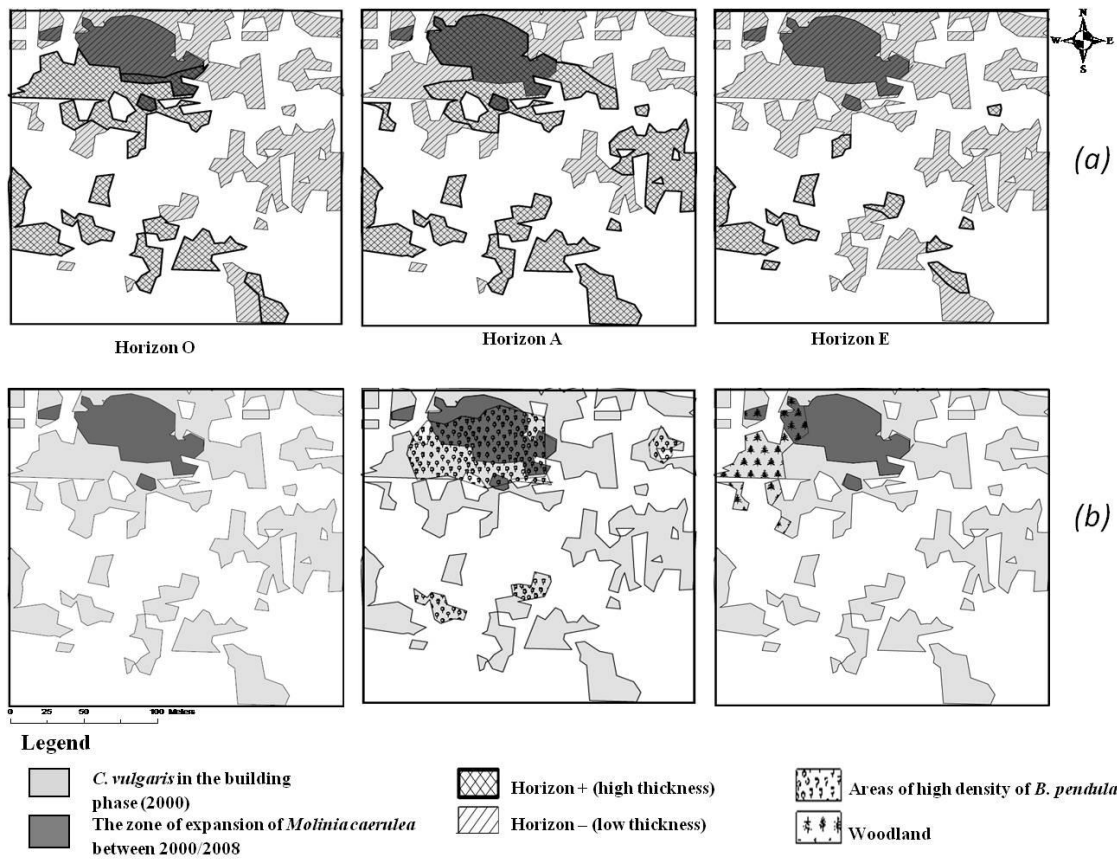
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521 Fig. 4

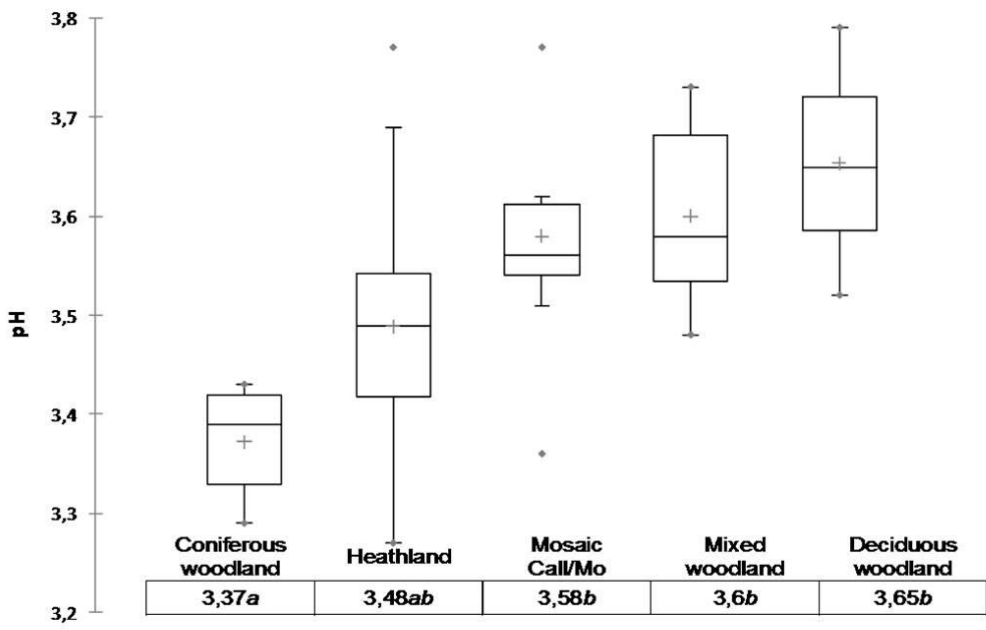
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524 Fig. 5

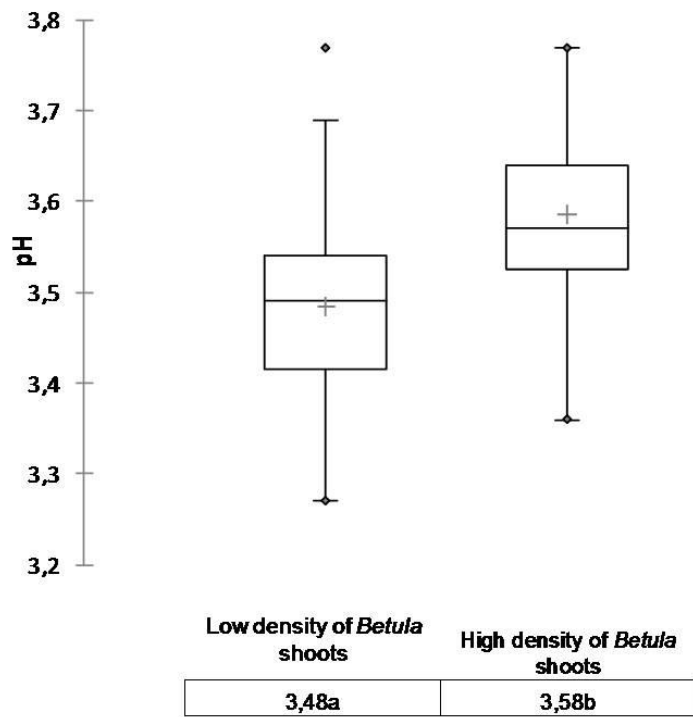
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527 Fig. 6

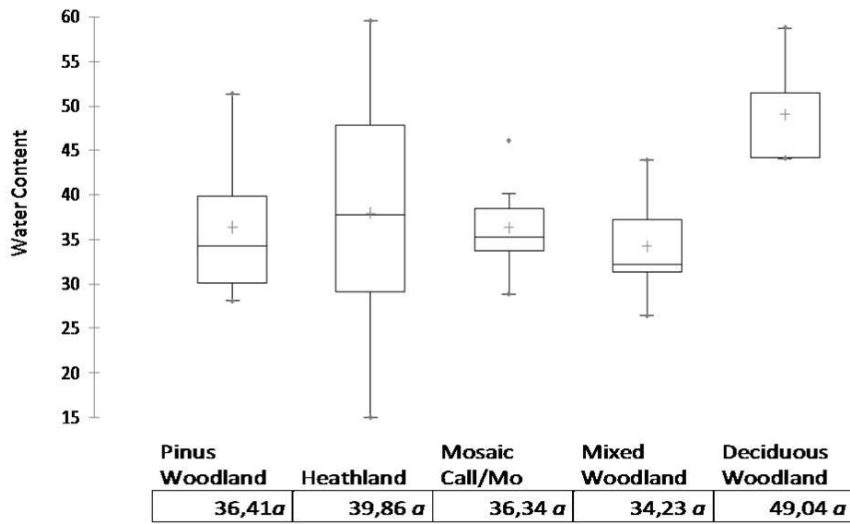
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530 Fig. 7

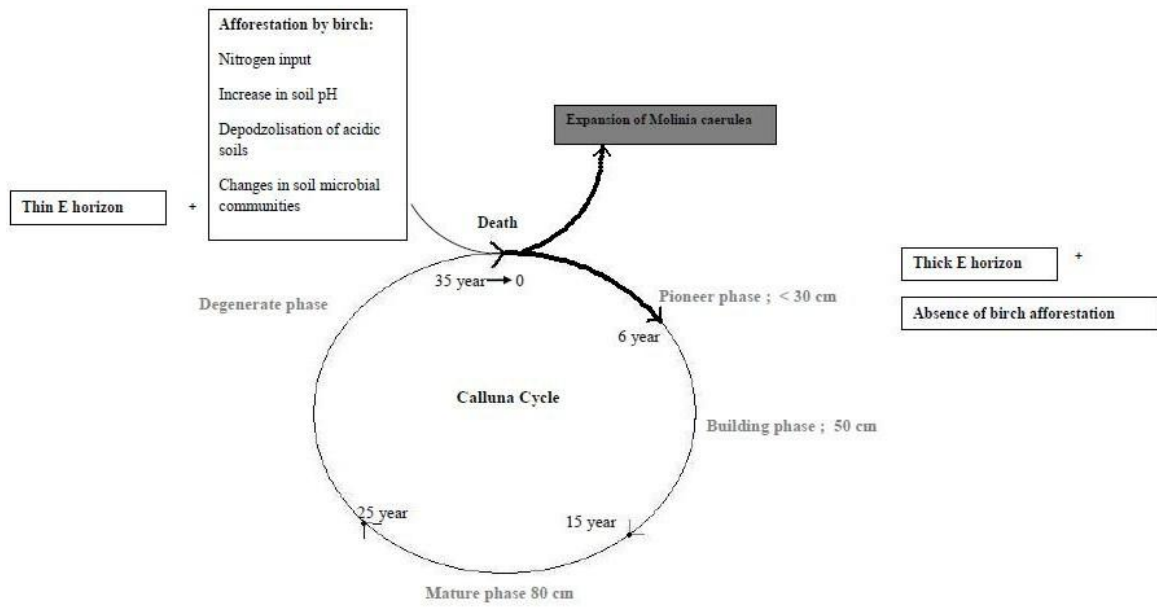
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533 Fig. 8

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535

536 Fig. 9