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

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Abstract

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

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

1. Introduction

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

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

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

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

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

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

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

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

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

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

2. Materials and methods

2.1. Study site

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

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

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

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

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

In a related study, all vegetation communities were mapped in 2000 and again in 2008, using transects spaced every 10 m (Mobaied et al., 2011). Vegetation dynamics was mapped between 2000 and 2008 at a resolution of 1 m² per cell. Five types of vegetation communities were distinguished: 1) heathland with specific species (Heath), including *C. vulgaris*, *E. cinerea* and *E. tetralix*; 2) a mosaic of *C. vulgaris* and *M. caerulea* (Cal+M.c); 3) wet facies of *M. caerulea* (WFM.c); 4) deciduous woodland (WLD); and 5) coniferous woodland of *P. sylvestris* (WLC). Each cell in this map represented the dynamics that occurred in the plant community in the transition from the initial state in 2000 to the final state in 2008, e.g.: “Heath/Cal+M.c” signifies that heathland with specific species (“Heath”) in 2000 evolved to a mosaic of *C. vulgaris* and *M. caerulea* in 2008 (“Cal+M.c”). When there was no change in the plant community between 2000 and 2008, the vegetation type was noted once (e.g. “Heath”). Results indicated an expansion of *M. caerulea*, in which it replaced *C. vulgaris* (Fig. 2).

Within the heathland we distinguished two developmental stages of *C. vulgaris*: 1) open low and discontinuous stands, which correspond to pioneer and building phases of the *Calluna* life cycle as described by Gimingham (1972); and 2) high and continuous stands which correspond to the mature phase of the *Calluna* life cycle. The expansion of *M. caerulea* occurred in open low and discontinuous stands of *C. vulgaris* (CalO). Over eight years, approximately 2000 m² of open low and discontinuous stands of *C. vulgaris* turned to a mosaic of *M. caerulea* and *C. vulgaris*. Therefore, the dynamics of pioneer and building stages of *C. vulgaris* was examined in greater detail, investigating the spatial and environmental conditions which allowed the colonization of the building phase of *C. vulgaris* by *M. caerulea*.

2.3. Spatial variability of tree colonization

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

2.4. Soil survey

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

2.4.1. Soil horizons

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

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

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

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

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

2.4.2. Soil pH and soil water content

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

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

2.5. Data analysis

2.5.1. Vegetation dynamics and soil variability

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

2.5.2. Expansion of *M. caerulea*

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

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

2.5.3. Soil pH and soil water content variation

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

3. Results

3.1. Soil spatial variability

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

3.2. Influence of soil spatial variability on vegetation dynamics

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

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

F1–F2biplot suggested a correlation between heathland dynamics and soil types (Fig. 4). WLC, Heath/WLC and WLD/WLC were associated with shallow soil types (O+A-E- and O-A-E-) while WLD and Heath/WLD were associated with deeper soils (O+A+E+ and O+A-E+).

The shift from heathland to a mosaic of *C. vulgaris* and *M. caerulea* (Heath/Cal+M.c) was strictly correlated with the soil class O-A+E-. The unchanged heathland (Heath) and the wet facies of *M. caerulea*(WFM.c.) were located near the origin of the factors and were not correlated with any soil types.

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

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

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

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

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

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

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

4. Discussion

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

In the study area, two large areas with a high density of birch shoots were observed on different soil types, one within open low and discontinuous stands of *C. vulgaris* (CalO) and the other within high and continuous stands of *C. vulgaris* (CalH). *Betula* spp. can establish in gaps in the centre of mature or degenerate *C. vulgaris* stands (Gong and Gimingham, 1984). This prevents the repetition of the life cycle of heather (Gimingham, 1988), suggesting that after degeneration of heather in CalH areas, cyclical growth processes cannot be restarted and available spaces are instead colonized by other species (Fig. 9).

Within open low and discontinuous stands of *C. vulgaris*, colonization by birch exerted significant effects on the expansion of *M. caerulea*. In fact, the area where *M. caerulea* 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

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

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

Figure captions

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

France maps vector source: Institut d'Aménagement et d'Urbanisme de la Région d'Ile-de-France (IAURIF). Aerial photographic source: Institut Géographique National (IGN)

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

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

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

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

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

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

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

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

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

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

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Fig. 2

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