

The use of diachronic spatial approaches and predictive modelling to study the vegetation dynamics of a managed heathland

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Abstract According to the EU Habitats Directive, heathlands are a semi-natural habitat type of community interest. This status aims at conserving these habitats, especially where and when they are threatened by various changes, including natural vegetation succession. We present results of a study of the dynamics of a typical dry heathland plot located in the Fontainebleau massif (France). An exhaustive observation of vegetation changes were made on this area of four hectares between 2000 and 2008, employing a spatial approach. We recorded the expansion of *Molinia caerulea* (L.) Moench at the expense of Ericaceae. The potential future vegetation of the site was modelled using Markov chains coupled to a GIS programme. This model predicted a gradual change in the floristic composition of heathland in favour of *M. caerulea* at the expense of *Calluna vulgaris* (L.) Hull and *Erica tetralix* L., and the expansion of *Pinus sylvestris* L. The study demonstrates how spatial methods can contribute to the design of reliable management methods of habitats such as the heathlands.

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Introduction

In the context of biodiversity loss, some endangered habitats are particularly crucial to preserve for the species they host, or the ecosystem services they provide, including cultural services. The value of heathland has been recognized at the European level, resulting in its insertion in the annex I of the Habitat Directive as a semi-natural habitat type of community interest (Council Directive 92/43/EEC; 21 May 1992). Heathlands are characterised by dwarf shrubs of the botanical family Ericaceae growing on nutrient-poor soils. They are semi-natural formations, shaped and maintained for centuries by humans and their flocks. They exist essentially in the biogeographic zone of the Atlantic of North-Western Europe (Webb 1998) and are disappearing everywhere because of changing agricultural practices and economic priorities. Heathlands are important for several reasons. Although their plant species richness is low, their characteristic and unique plant and animal species make them of high interest to biodiversity conservation efforts. Several species of birds adapted to open habitats use heathland for feeding and breeding purposes (Thompson et al. 1995). Since heather is a food plant for the larvae of a number of leaf beetles and Lepidoptera, several studies have highlighted the importance of this habitat to invertebrate species (Usher 1992; Usher and Thompson 1993). In the UK only 9% of species associated with heathland need heather. However, most require the diversity in structure and species composition found on this habitat (Webb et al. 2010). Finally, heathlands play an important role in apiculture and have a high landscape interest.

The maintenance of heathlands in favourable state of conservation requires permanent management to control two major trends in terms of succession: reforestation by the woody species when the heathland borders a forest, and the invasion by grasses generally linked to nutrient increase from aerial deposition (Miles 1981; Todd et al. 2000). When attempting to thwart the succession to woodland stages one management method often used is regular mechanical treatment, like cutting, and remove the woodland species (Walker et al. 2007). To prevent the invasion by grasses several management methods can be used, usually in combination: controlled burning, mowing, grazing, or the application of herbicides (Webb 1998; Symes and Day 2003) and turf removal or plaggen (Niemeyer et al. 2007).

Our aim in this paper is to quantify the plant community changes and assess the conservation needs of a heathland subjected to natural succession processes and management methods applied for 20 years to control encroachment by woody species.

Our experimental site is situated in the “Man and Biosphere” Reserve of Fontainebleau. This reserve is situated 50 km south of Paris in France in a vast peri-urban forest. At this location, the presence of acid sandy soils and the traditional agro-pastoralism has favoured the establishment of the heathlands for thousands of years. However, its abandonment about 50 years ago caused the progressive disappearance of this high-value habitat. Presently, the heathland covers 1,400 ha, situated within an oak-pine forest.

Additionally, Fontainebleau contains 5% of the total area covered by European dry heathland semi-natural habitat in the French mainland (heathland habitat code 4030, annex I of the Habitats Directive). This reserve also contains 1% of the total area covered by Northern Atlantic wet heaths with *Erica tetralix* L. in the French mainland (code 4010, annex I of the Habitats Directive) (Natura 2000 website). This area is integrated into the Managed Biological Reserves (RBD) (*Réserve Biologique Dirigée*).

The forest services management measures over the last 20 years have been aimed at the preservation of this habitat that is considered to significantly contribute to the high biodiversity of Fontainebleau forest. Since 1990, the National Forests Office (ONF) have attempted to preserve many patches of heathland, by cutting all seedlings and shoots of *Betula pendula* Roth. and seedlings of the conifer *Pinus sylvestris* L. every 2 or 3 years. However, no method is applied at present to prevent the encroachment by grasses.

In this work we studied the dynamics of plant communities using a high-resolution diachronic spatial approach (Glenn-Lewin et al. 1992). We compared vegetation data collected with the same protocol in 2000 and in 2008. The objectives of this study were to (1) identify the processes that could possibly threaten this highly-valued habitat despite the efforts of forestry management, (2) quantify changes in plant communities over an 8-year period, (3) assess these data within the context of future changes. We modelled the predicted changes if the management methods continue to be applied in the same manner as at present. In so doing, we are able to give recommendations for restoration practices.

Materials and methods

The study site

This study focuses on a 4.4 ha heathland stand situated within the state-owned forest called the ‘Trois Pignons’ (3,307 ha) in the west part of Fontainebleau forest (Fig. 1). Heathland covers a total of around 650 ha dispersed across this forest, which is in different reforestation stages. The study stand is included in the Managed Biological Reserves (RBD) of ‘Mares aux Jones’ Parcel (plot) 53 on the edge of the managed heathland and the area colonised by the woodland species. This represents the transition zone between this two vegetation patterns. It is a typical heathland, situated on sandy, acid and poor soil that is essentially sandstone bedrock with sandstone terminals (Roque 2003) resting on stampian

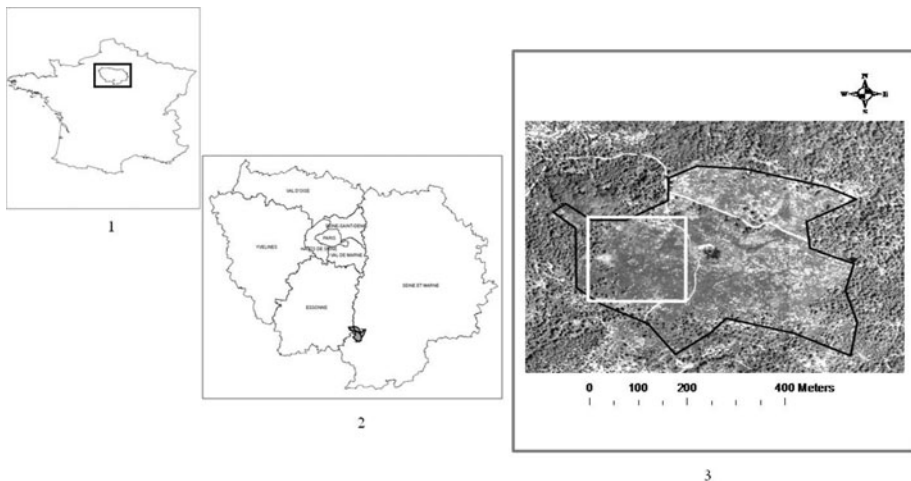


Fig. 1 Location of the study site in: (1) France, (2) Ile de France and the forest of ‘Trois Pignons’ (in gray), (3) The managed heathland 21 ha (black line), the plot study 4.4 ha (white line) in the Mares aux Jones RBD located at coordinates (48°2’N, 2°3’E). France maps vector source: Institut d’Aménagement et d’Urbanisme de la Région d’Ile de-France (IAURIF). Aerial photo source: Institut Géographique National (IGN)

sand (BRGM 1970). The vegetation structure on the site is a mosaic of dry heathland (Habitat 4030 of the annex I of the Habitats Directive) dominated by *Calluna vulgaris* (L.) Hull in different age stages, with patches of *Erica cinerea* L. There are also Northern Atlantic wet heaths with *E. tetralix* (Habitat 4010 of the annex I of the Habitats Directive) and dry open basins with *Campylopus* sp. and lichens. Since 1990, managers have regularly cut the birch and pine shoots and seedlings with the aim of preserving this heathland from reforestation.

Vegetation typology used

We conducted vegetation surveys with the same protocol in 2000 and again in 2008 on the 4.4 ha stand of heathland (include 4.26 ha of vegetation and 0.14 ha of other categories: swamp, path and sandstone). A typology of different vegetation formations was set up, on the basis of floral types, including bryophytes, lichens and vascular plants, using the phytosociological method recommended by Braun-Blanquet (1932) i.e. vegetation type called Mosaic of *C. vulgaris* and *Molinia caerulea* (Cal+M.c) corresponds to the area which *C. vulgaris* cover 25–50% and *M. caerulea* cover 5–25%. Two development phases of *C. vulgaris* were distinguished: (1) open low and discontinuous stands when the heather is dispersed and measured up to 40 cm and, which corresponds to the first phases of the *Calluna* life cycle described by Gimingham (1972): that is the pioneer phase (the colonization of new areas and the regeneration in the area of degeneration of old heather) and the building phase, (2) high and continuous stands when the heather is dense and measured up to 80 cm, and which corresponds to the mature phase in the *Calluna* life cycle. The list of vegetation types is presented in the Table 1.

Table 1 The list of the vegetation typology; the typology was set up, using the phytosociological method recommended by Braun-Blanquet (1932) i.e. vegetation type called (Cal+M.c): mosaic of *C. vulgaris* and *M. caerulea* corresponds to the area which *C. vulgaris* cover 25–50% and *M. caerulea* cover 5–25%

Abbreviation	Elementary vegetation types
Heathland specific species	
Cal.H	High and continuous stands of <i>C. vulgaris</i>
Cal.O	Open low and discontinuous stands of <i>C. vulgaris</i>
Cal+E.c	<i>C. vulgaris</i> and <i>E. cinerea</i>
E.t	<i>E. tetralix</i> pure stands
R.a	Low zone of <i>R. acetosella</i> and <i>Cladonia</i> sp.
Cam+Lich	Dry facies of <i>Campylopus</i> sp. and lichen
M. caerulea communities	
Ca+M.c	Mosaic of <i>C. vulgaris</i> and <i>M. caerulea</i>
E.t+M.c	Mosaic <i>M. caerulea</i> and <i>E. tetralix</i>
WF.M.c	Wet facies of <i>M. caerulea</i>
M.c+J	<i>M. caerulea</i> and <i>Juncus</i> sp.
TP.M.c	Temporary pond of <i>M. caerulea</i> and <i>Sphagnum</i> sp.
Woodlands	
B.p+M.c	<i>B. pendula</i> and <i>M. caerulea</i>
B.p+P.t	High grove of <i>B. pendula</i> and <i>P. tremula</i>
WL.B.p	Woodland of <i>B. pendula</i>
WL.P.s	Woodland of <i>P. sylvestris</i>

Vegetation mapping

The maps of the study zone for 2000 and 2008 were based on the typology of the vegetation. Transects spaced every 10 m were created using compass, topofil, and markers. All vegetation types defined by the typology were mapped (ONF 2000). Subsequently, these data were plotted on grid frameworks with a resolution of 1 m. These data were transferred onto a GIS software programme; in this study we used the software Arc GIS 9.2 (ESRI[®], Ormsby et al. 2004; Environmental Systems Research Institute 2006a, b) to create a map vector file containing polygons, which represent the different vegetation communities. The two maps of the vegetation communities for 2000 and 2008 were then converted into a common raster format (Grid ESRI file), with a resolution of 1 cell = 1 m² (44,000 cells per raster).

Data analysis and GIS modelling

The GIS software permits the integration and analysis of complex data to perform a spatial analysis (Aspinall and Pearson 1996; Bridgewater 1993; Pornon 1992; Vietch et al. 1995). This method also permits the predictive simulation of the evolution of the natural system both in space and time (Paegelow and Camacho-Olmedo 2005, 2008). The Geomatics GIS models employ spatial Markov chains and the cellular automata for the simulation of the vegetation dynamics. The Markov chains with memory is used for the temporal aspect (Balzter 2000; Logofet and Lesnaya 2000), and the cellular automata (CA) for the spatial dependence by assigning priority to contiguity (Paegelow et al. 2004). The (CA) are a class of spatially and temporally discrete mathematical systems characterized by local interaction and synchronous dynamical evolution (Von Neumann 1951; Ilachinski 2001).

Many studies have been conducted in an attempt to validate the GIS model (Paegelow et al. 2004) have compared the GIS based model with statistic approaches (nonlinear parametric model and neural networks) their results show a high degree of convergence and a relative similitude of the results obtained by the two statistic approaches compared to the GIS model.

In another study, to validate the methodology, based on available GIS tools Paegelow and Camacho-Olmedo (2005) have used earlier land cover to modeling actual, known land cover, their results give an accurate prediction rate of approximately 75%.

Here we use it to predict the future state of the vegetation communities in the study site through the program module CA-MARKOV of the software IDRISI 32. For this, the two ESRI grids were transferred to the software programme IDRISI.ANDES32 (Clark University, IDRISI Production[®] 1987–2006). The model is probabilistic according to the matrix built for the last 8 years. It uses a 200 × 220 cell grid with square cells each representing 1 m², giving a total grid size of 4.4 ha. The probability estimates are based on the observation of the natural transitions between the communities between these two dates. A transition matrix was built giving the percentage of changes from one stage to the other that occurred between the two dates. The matrix is given in Table 2. To predict the future state of the vegetation communities we used, in 1, 2 and 3 periods of 8 years, with the hypothesis that the management methods are maintained and that all environmental characteristics remain constant. To identify the areas and the nature of the changes, we used the option CROSSTAB “cross tabulation” of the programme IDRISI (Eastman 2006). This software compares the two images, pixel by pixel, and creates a new classified image, where the classes represent the nature of changes. In order to assess the importance of overall change occurred from 2000 to 2008, the CROSSTAB function computes the

Table 2 The transition matrix presents the percentage of changes from one stage to the other between the two dates

Vegetation community	2000															
	Heathland specific species							<i>M. caerulea</i> communities							Woodlands	
	Cal.H (%)	Cal.O (%)	Cal+E.c (%)	E.t (%)	R.a (%)	Cam+Lich (%)	Cal+M.c (%)	E.t+M.c (%)	WF.M.c (%)	M.c+J (%)	TP.M.c (%)	B.p+M.c (%)	B.p+P.t (%)	WL.B.p (%)	WL.P.s (%)	
2008 Heathland specific species																
Cal.H	43	33	-	-	24	-	-	8	-	-	-	-	-	-	-	
Cal.O	48	50	35	5	49	8	-	-	-	-	-	-	-	-	-	
Cal+E.c	4	-	65	-	-	-	-	-	-	-	-	-	-	-	-	
E.t	-	-	-	74	-	-	-	-	-	-	-	-	-	-	-	
R.a	-	-	-	-	18	-	-	-	-	-	-	-	-	-	-	
Cam+Lich	-	-	-	-	-	92	-	-	-	-	-	-	-	-	-	
<i>M. caerulea</i> communities																
Cal+M.c	1	13	-	-	9	-	94	92	-	-	-	-	-	-	-	
E.t+M.c	-	-	-	21	-	-	-	0	-	-	-	-	-	-	-	
WF.M.c	-	-	-	-	-	-	-	-	88	-	-	-	-	-	-	
M.c+J	-	-	-	-	-	-	-	-	-	100	-	-	-	-	-	
TP.M.c	-	-	-	-	-	-	-	-	-	-	100	-	-	-	-	
Woodlands																
B.p+M.c	-	-	-	-	-	-	-	-	-	-	-	100	-	10	-	
B.p+P.t	2.7	-	-	-	-	-	-	-	-	-	-	-	100	-	-	
WL.B.p	-	-	-	-	-	-	-	-	-	-	-	-	-	50	-	
WL.P.s	1.3	3	-	-	-	-	6	-	-	-	-	-	-	-	40	

The bold values represents the no-change diagonal line. (-) = Transition not observed

KAPPA Coefficient of Agreement KIA (Cohen 1960). This statistical measure is a means to test two images, if their differences are due to chance or real disagreement (Monserud and Leemans 1992). The overall Kappa index was carried out using 2000 as the reference map.

For the treatment of transitions the vegetation communities were grouped into three types: (1) the dynamics of heathland specific species; (2) the expansion of grasses (*M. caerulea* associated community) and finally, (3) the expansion of the woodlands.

Results

Overall vegetation dynamics of the heathland community

Between 2000 and 2008, the vegetation remained stable on 1.9 ha, and changed on 2.36 ha (Fig. 2). The index of agreement from 2000 to 2008 KIA = 0.277 indicating that the agreement between the two maps is poor (Landis and Koch 1977). However the rate of changes was markedly different among vegetation communities, ranging from high stability (80–100%), e.g. the Woodland of *P. sylvestris*, to total disappearance, such as the Mosaic of *M. caerulea* and *E. tetralix* (Table 2, diagonal line). In general there was a loss of the specific heathland community due to an expansion of *M. caerulea* in associated community and an increase of the area invaded by woody species (Table 3).

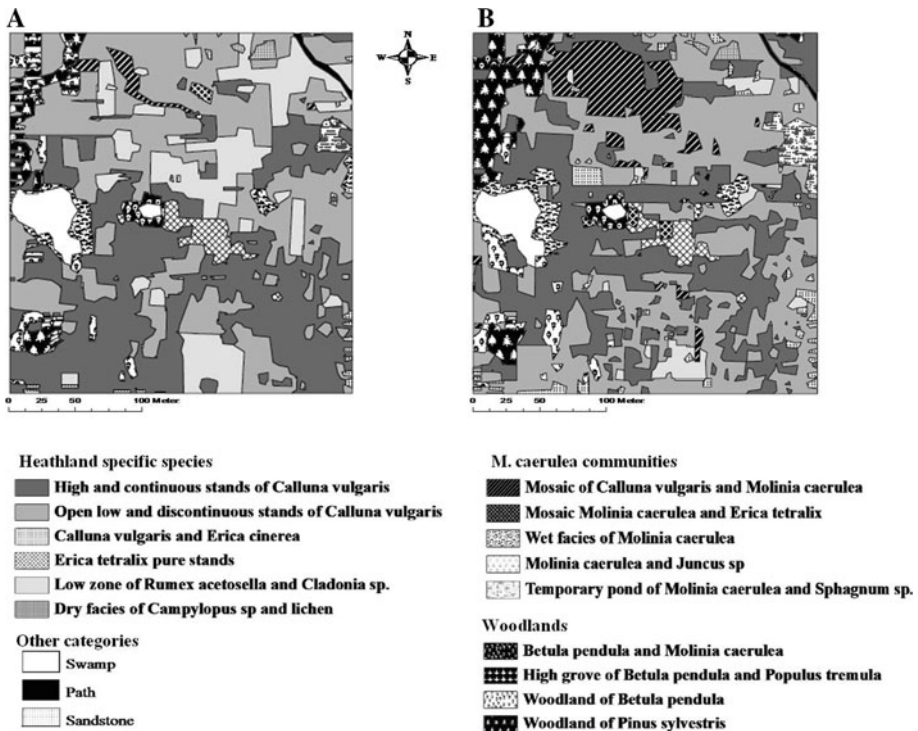


Fig. 2 a Map of plant communities in the study site in 2000. b Map of plant communities in the study site in 2008

Table 3 Change of plant communities between 2000 and 2008

Nom	Vegetation community	Record (m ²) 2000	Record (m ²) 2008	Percentage 2000	Percentage 2008	Percentage of change for the total site area
Heathland specific species						
Cal.H	High and continuous stands of <i>C. vulgaris</i>	38242	33449	89.77	78.52	-11.25
Cal.O	Open low and discontinuous stands of <i>C. vulgaris</i>	14766	13012	34.66	30.54	-4.12
Cal+E.c	<i>C. vulgaris</i> and <i>E. cinerea</i>	16059	17270	37.70	40.54	2.84
E.t	<i>E. tetralix</i> pure stands	252	1093	0.59	2.57	1.97
R.a	Zone of <i>R. acetosella</i> and <i>Cladonia</i> sp.	826	698	1.94	1.64	-0.30
Cam+Lich	Dry facies of <i>Campylopus</i> sp. and lichen	6130	1140	14.39	2.68	-11.71
	<i>M. caerulea</i> communities	209	236	0.49	0.55	0.06
Cal+M.c	Mosaic of <i>C. vulgaris</i> and <i>M. caerulea</i>	1615	5414	3.79	12.71	8.92
E.t+M.c	Mosaic <i>M. caerulea</i> and <i>E. tetralix</i>	456	3305	1.07	7.76	6.69
WF.M.c	Wet facies of <i>M. caerulea</i>	97	207	0.23	0.49	0.26
M.c+J	<i>M. caerulea</i> and <i>Juncus</i> sp.	780	1159	1.83	2.72	0.89
TP.M.c	Temporary pond of <i>M. caerulea</i> and <i>Sphagnum</i> sp.	6	6	0.01	0.01	0.00
	Woodlands	276	737	0.65	1.73	1.08
B.p+M.c	<i>B. pendula</i> and <i>M. caerulea</i>	2743	3737	6.44	8.77	2.33
B.p+P.t	High grove of <i>B. pendula</i> and <i>P. tremula</i>	290	290	0.68	0.68	0.00
WL.B.p	Woodland of <i>B. pendula</i>	13	56	0.03	0.13	0.10
WL.P.s	Woodland of <i>P. sylvestris</i>	1090	1015	2.56	2.38	-0.18
		1350	2376	3.17	5.58	2.41

The dynamics of heathland specific species

Within the area that is consistently heathland since 2000, changes were nevertheless observed. A large part of the zone of *Rumex acetosella* and *Cladonia* sp. became stands of *C. vulgaris* (Table 2). The open low and discontinuous stands of *C. vulgaris* mapped in 2000 remained stable on 50% of their area (8,500 m²) and progressed to maturity phase on 33% (5,280 m²) i.e. became high and continuous stands of *C. vulgaris* (Table 2). The surface occupied by the high and continuous stands of *C. vulgaris* in 2000 was stable over 43% (6,400 m²) in the mature phase, while 48% (7,000 m²) changed into the degeneration phase i.e. the branches withered and collapsed which led to opening tufts of *C. vulgaris* (Gimingham 1972). Subsequently, they reverted back to open stands of *C. vulgaris* (see the life cycle Fig. 6). Mixed *C. vulgaris* and *E. cinerea* community occupied around 250 m² in 2000. It quadrupled its surface in 2008. This expansion occurred in high and continuous stands of *C. vulgaris*. Globally there was a loss of 11.25% of the specific heathland (Table 3).

The expansion of *Molinia caerulea* formation

The expansion of *M. caerulea* has been more important within the patches of open and discontinuous stands of *C. vulgaris* than in the mature ones. Approximately 2,000 m² (13%) of this stand was transformed into a mosaic of *C. vulgaris* and *M. caerulea* (Table 2). The second formation colonised by *M. caerulea* was the zone of *R. acetosella* and *Cladonia* sp. with about 9% of its area. This expansion was less important (1%) in the zones of high and continuous stands of *C. vulgaris*. The zone of pure stand of *E. tetralix* was colonised on 21% of its area by *M. caerulea*. We also observed that *E. tetralix* had disappeared from a mixed patch of *E. tetralix* and *M. caerulea* (90 m²). Globally there was an expansion of 9% of the *M. caerulea* in associated community (Table 3).

The expansion of woodland

The afforestation in the heathland is due principally to two main species: *B. pendula* and *P. sylvestris*. Between 2000 and 2008 we observed the expansion of the *P. sylvestris* wooded heathland on 1,000 m² on the perimeter of the old wooded zone. This *P. sylvestris* wooded heathland replaced on 400 m² (40%) the *B. pendula* wooded heathland mapped in 2000 where *P. sylvestris* existed in shrub layer. Since then, it has developed and in 2008, this species forms the tree layer of this area. *P. sylvestris* had also colonised 480 m² (3%) in the open and discontinuous stands of *C. vulgaris* and 200 m² (1.3%) in the zones of high and continuous stands of *C. vulgaris* (Table 2). We observed an expansion of the zone of high grove of *B. pendula* and *Populus tremula*. Additionally, we observed that the expansion of the wooded zones has been spatially limited to the perimeter of the old wooded zones of the two formations. More generally there was an increase of 2.3% of the woodland vegetation type (Table 3; Fig. 3).

Predictive simulations

According to our simulations, the future changes concerning the heathland relate to: (1) the decrease in the surface area occupied by *C. vulgaris*; (2) the continuing decline of the area occupied by the pure stands of *E. tetralix*, which is replaced by a mosaic of *E. tetralix* and *M. caerulea*, (3) the stability of the area occupied by *E. cinerea*, (4) the continued expansion of the wooded area by *P. sylvestris* (Fig. 4). The model also predicts a large

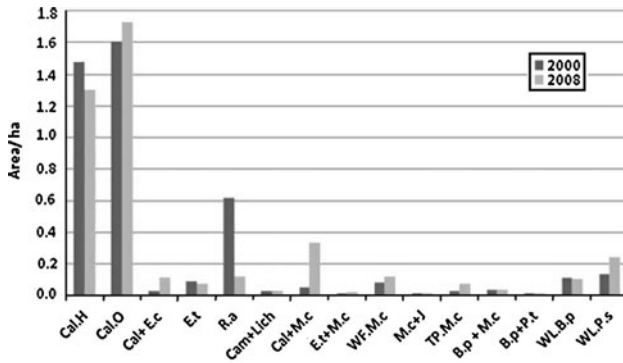


Fig. 3 The area of each type of vegetation community in 2000 and 2008

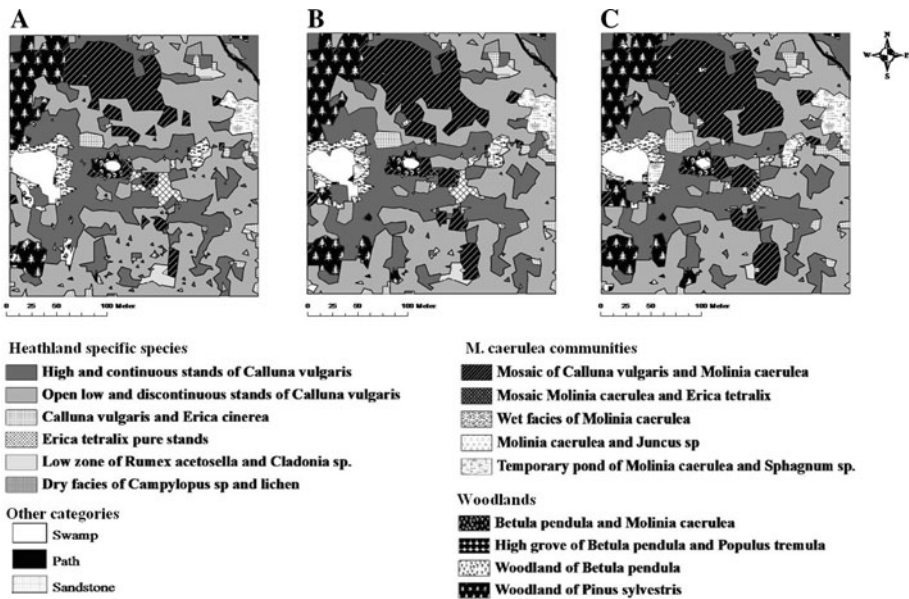


Fig. 4 Simulation map of plant communities in the study site in 2016 (a), in 2024 (b) and in 2032 (c)

decrease in the area occupied by *B. pendula*. In general, we observe a shift in the balance of species along a trajectory from a *Calluna*-dominated to a *Calluna–Molinia* mosaic. According to our model, by 2032 the site will possess only 63% heathland, while the *M. caerulea* communities will cover 25% and woodlands 12% of the total site area (Fig. 5).

Discussion

Changes of species composition in open areas

Individuals of *C. vulgaris* pass through four distinct phases during their life history: pioneer, building, mature and degenerate phase followed by the death of the plants

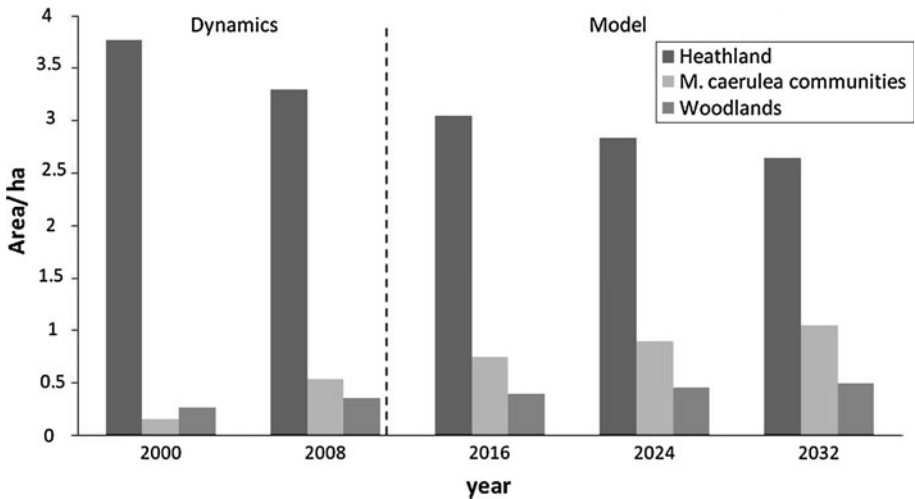


Fig. 5 The area of heathland, *M. caerulea* communities and woodlands in 2000, 2008, 2016, 2024 and 2032

(Gimingham 1972). The changes of *Calluna* formations (high and continuous stands of *C. vulgaris* and open low and discontinuous stands of *C. vulgaris*, during the period of 8 years can be largely attributed to the life cycle of this species. The decrease in the continuous and high formations of *C. vulgaris* corresponds to the transition from the mature phase to the degenerate phase. In open areas the pioneer and building phase establishes after the phase of degeneration.

This succession was nevertheless disrupted by the invasion by *M. caerulea*. We observed that this grass settled during the pioneer phase and/or the building phase of the life cycle of *C. vulgaris* (Fig. 6). This process occurred on an area of 3,000 m² that shifted the heathland from the *C. vulgaris* in pure stands to a mosaic of *C. vulgaris* and *M. caerulea*, thereby threatening the maintaining of a favorable conservation status of the habitat European dry heathland (code 4030, annex I of the Habitats Directive). Finally we detected the colonisation of 700 m² of European dry heathland by *P. sylvestris*.

The reduction of the zone occupied by the Northern Atlantic wet heaths with *Erica tetralix*. (code 4010, annex I of the Habitats Directive) was due to its invasion by *M. caerulea*. Of the two zones where *E. tetralix* was found in 2000, the first disappeared (loss of 90 m²), and in the second zone, 700 m² remained in pure stand of *E. tetralix* while 128 m² changed to a mosaic of *M. caerulea* and *E. tetralix*. The increase of the *E. cinerea* surface between 2000 and 2008 was due to the appearance of this species in an area where it was absent and where it replaced stands of high *Calluna* individuals and *R. acetosella*.

Several studies on the transition of heathland communities to stands dominated by grasses showed that increased nutrient availability promotes the establishment of *M. caerulea* (Aerts 1989; Heil and Bruggink 1987). This increased availability of nutrients has been attributed to several factors (Lagan 1999): (1) an increased atmospheric nitrogen deposition due to factors such as intensive agriculture in the neighborhood or by pollution by road traffic (Aerts and Berendse 1988; Aerts and Bobbink 1999; Hogg et al. 1995); (2) management trials, by grazing or controlled burning (Grant and Maxwell 1988) and (3) the lowering water tables, which leads to increased rates of mineralisation (Berendse et al. 1994; Aerts and Ludwig 1997), and finally (4) an increase of the concentration of nutrients in the soil due to reforestation (Piessens et al. 2006).

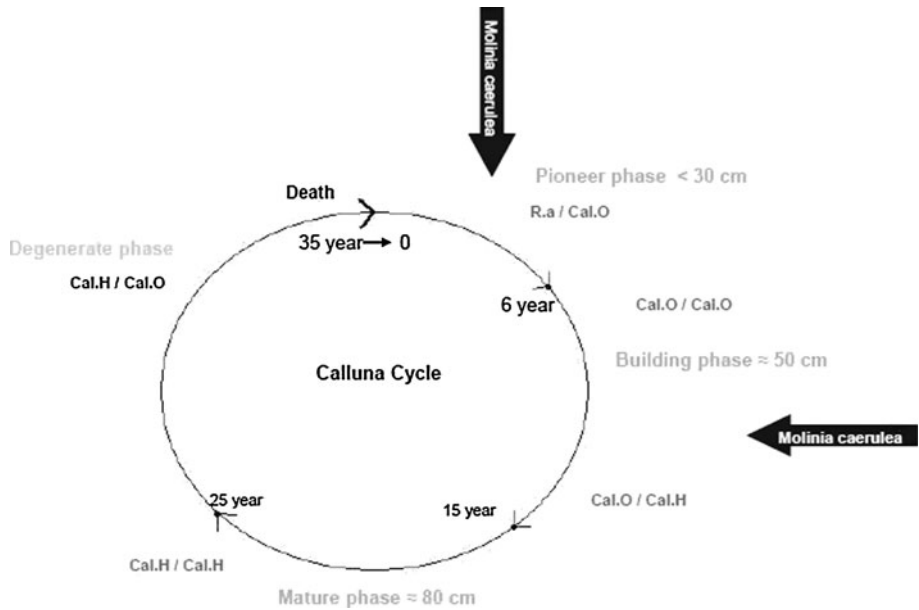


Fig. 6 The positioning of transition classes and the appearance of *M. caerulea* relative to the phases of *C. vulgaris* cycle described by Gimingham (1972)

In the case of our site, several reasons for the observed pattern can be proposed. Firstly, the site experienced a drought period from 2003, which was characterised by lower rainfall levels and higher summer temperatures. The drought could have caused the lowering of groundwater thus induced the increased mineralisation levels. These circumstances would favour *M. caerulea* especially in the zone of wet heaths with *E. tetralix*. This drought may have also accelerated the drying of the high and continuous stands of *C. vulgaris*. The opening of this formation led to the establishment of open low and discontinuous stands of *C. vulgaris*. It created a new space that could have been colonised by *C. vulgaris* and *M. caerulea* forming a mosaic of *C. vulgaris* and *M. caerulea* or by *C. vulgaris* and *E. cinerea* on other areas. Secondly, the increase atmospheric nitrogen deposition in this zone is undeniable (Ulrich et al. 2007). Of particular relevance is that Fontainebleau forest that is crossed by an important highway (A6) and is also located in a region of intensive agriculture, which adds to the levels of nitrogen. In the stand, the changes we observed were concentrated in a specific area and not scattered throughout the site. This observation could suggest a local increased of the concentration of nutrients in soil. To confirm this hypothesis, a more detailed study has been launched on the influence of spatial variability of soil and spatial distribution of individuals of woody species in the heathland and their role in increase of soil nutrients.

The modelling analysis (Fig. 7) predicted that the dynamics of the *C. vulgaris* zones are not stable and will probably continue to decrease in the future. Two succession trajectories can lead to new pure stands of *C. vulgaris*: first, the establishment of a pioneer and building phase after the degeneration of the old stands of *C. vulgaris*. During this process, the invasion by *M. caerulea* is frequent, and results in the disappearance of pure stands of *C. vulgaris* in favour of mosaic areas of *C. vulgaris* and *M. caerulea*. Secondly, *C. vulgaris* could invade the *R. acetosella* zone, however this zone was so reduced between 2000 and 2008 that *C. vulgaris*

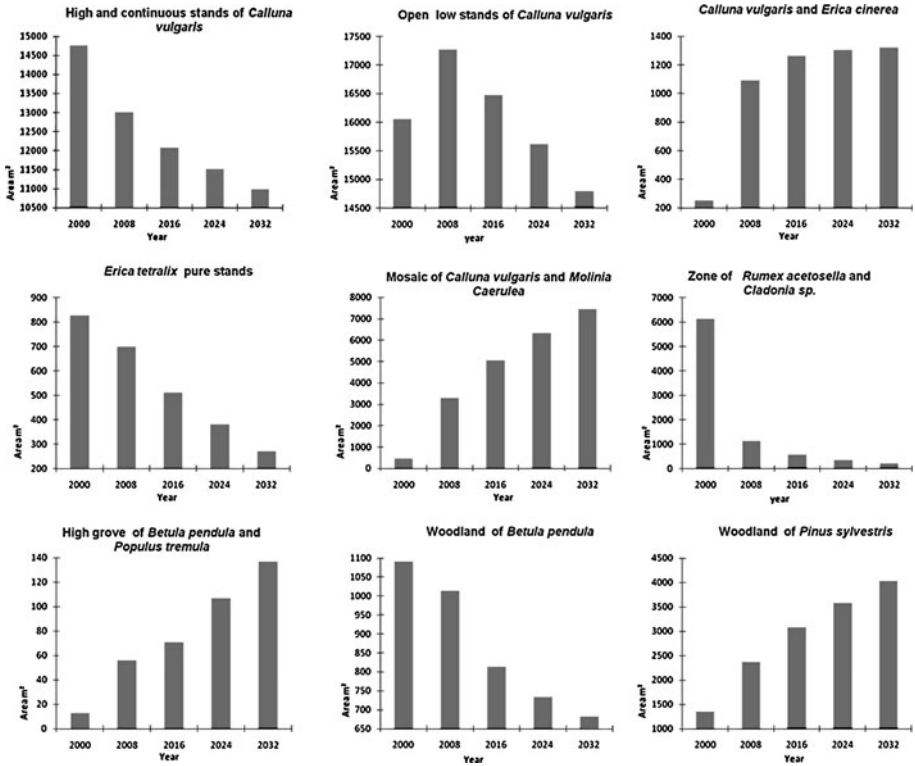


Fig. 7 The area of each type of vegetation community in 2000, 2008, 2016, 2024 and 2032

will probably not be able to expand in the future. On the contrary, processes that replace pure stands of *C. vulgaris* by other communities will continue to occur.

The model also predicts that the areas occupied by *E. cinerea* will remain stable in the south of the site. The colonisation of a zone by *E. cinerea* in the centre of the site did not have a pronounced effect on the dynamics of this community. The probability of a replication of this event, based on the percentage of changes between 2000 and 2008 is small compared to other types of changes experienced by cells that have the same starting position.

The modelling of the dynamic of *E. tetralix* predicts a decrease of the area occupied by this species resulting from two processes: the invasion by *M. caerulea* in the pure stands of *E. tetralix*, and the disappearing of *E. tetralix* where it co-occurred with *M. caerulea* in 2000. The model predicts the recurrence of this scenario in the future.

Afforestation

The expansion of woodlands dominated by *P. sylvestris* has two causes: (1) progression of this conifer species in the heathland areas, and (2) colonisation of wooded areas previously dominated by *B. pendula*. The species is characterised by an invasive ability and tolerance of dry conditions, which mean that *P. sylvestris* is constantly colonising new areas. With regards to *B. pendula*, between 2000 and 2008, it occupied roughly the same area but our model predicts a decline due to its replacement by *P. sylvestris*. Two reasons explained the

non-appearance of new areas of woodland dominated by *B. pendula* in the predictive model: (1) According to the model, the probability of a pixel of woodland of *B. pendula* to evolve towards woodland of *P. sylvestris* is higher than the probability of creating a new pixel of *B. pendula* woodland from other formations (Table 2), and (2) areas of woodland of *B. pendula* are fragmented patches. Apart from this, the model also emphasises the concept of contiguity by applying the principle of ‘cellular automata’, so it reduces the probability that a pixel of woodland *B. pendula* surrounded by a large number of other types of formations, remains stable or colonises neighbouring pixels.

The expansion of *P. sylvestris* woodland is currently spatially restricted due to the strict management efforts applied to the open areas of the heathland. Conversely, in the margin of the “heathland-forest” that is not so rigorously managed, new individuals of woody species have established in the perimeter of an ancient woodland in the west of the site.

Conclusion

The Markov chain models are employed by ecologists for study the vegetation dynamics and the succession process (Leps 1988). Other authors have criticised Markov chain models for not taking the spatial effects on the dynamics of vegetation into account (e.g. Usher 1981; Lippe et al. 1985). Other studies have used models based only in a cell-based spatial simulation (Britton et al. 2001). The Geomatics GIS model employed in this study assembles Markov chains with memory for the temporal aspect, and the cellular automata for the spatial dependence. This diachronic spatial approach yields a very high degree of precision (data on vegetation were collected on 1 m² grids) that allows us to assess the changes of our study site between 2000 and 2008 by means of transition matrix. This tool enabled us to understand and quantify the processes that threaten the heathlands in detail.

However, the use of the predictive model meant that several assumptions had to be made, and that certain types of data were omitted. In particular, we did not integrate spatial and temporal heterogeneity of the environmental characteristics e.g. soil properties or climate that could have affected the transition rates. At the scale of this study, only the transition probabilities and the spatial distribution of communities affect the projected vegetation dynamics. The effects of other restricted factors such soil properties and hydrology have not been observed. These factors could be integrated in the predictive model as multi criteria to assist spatial implementation of predicted time transitions by suitability maps.

The general trend of predicted changes to the studied heathland is primarily the increase of the areas occupied by the mosaic of *M. caerulea* and the *Ericaceae* at the expense of *Ericaceae* species in pure stands. The present competitive ability of *M. caerulea* could have been reinforced by the current drought experienced in our study site, but also by the soil nutrient enrichment. The increased atmospheric nitrogen deposition has probably also influenced the afforestation in the heathland. The current management methods i.e. the cut of all the small pines and birches, limit the afforestation of the site. However, we noticed an increasing area covered by the wooded heathland and a shift in the species composition, with *P. sylvestris* replacing *B. pendula*. This pattern could also have been accelerated by the drought experienced in this region. Even if the future speed of colonisation cannot be directly deduced from that observed during the previous 8 years, we assume that the trends predicted will certainly occur if the management methods continue to be applied as they are.

We conclude that, the conservation of heathland specific species in relatively small patch in the middle of a forest matrix will require very strong efforts, since the region is

facing major and unavoidable environmental changes (climate and nitrogen deposition). This is particularly important at the interface with woodlands, where the cut of seedlings and shoots of *B. pendula* and seedlings of the conifer *P. sylvestris* will have to be undertaken more regularly and systematically without delay to export the plant residues to avoid enrichment of the soil. The operations should also integrate the management of the grasses e.g. by grazing that will inevitably replace the *Ericaceae* if we let them.

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