Journal of Vegetation Science 18: 517-524, 2007

Quantitative prediction of the distribution and abundance of *Vaccinium myrtillus* with climatic and edaphic factors

Coudun, Christophe[1*] & Gégout, Jean-Claude[2,3]

[1]*Centre d'Animation Régional en Matériaux Avancés (CARMA), AREP Center, 1 traverse des Brucs, 06560, Valbonne Sophia Antipolis, France;* [2]*AgroParisTEch, LERFoB, UMR INRA-ENGREF 1092, Ecole Nationale du Génie Rural, des Eaux et des Forêts, 14 Rue Girardet, CS 14216, FR-54042 Nancy Cedex, France;* [3]*E-mail gegout@engref.fr;* [*]*Corresponding author; Tel. +33 (0)4 93001911; E-mail coudun@carma.fr*

Abstract

Question: Can the distribution and abundance of *Vaccinium myrtillus* be reasonably predicted with soil nutritional and climatic factors?

Location: Forests of France.

Methods: We used Braun-Blanquet abundance/dominance information for *Vaccinium myrtillus* on 2905 forest sites extracted from the phyto-ecological database EcoPlant, to characterize the species ecological response to climatic and edaphic factors and to predict its cover/abundance at the national scale. The link between cover/abundance of the species and climatic (65 monthly and annual predictors concerning temperature, precipitation, radiation, potential evapotranspiration, water balance) and edaphic (two predictors: soil pH and C:N ratio) factors was investigated with proportional odds models. We evaluated the quality of our model with 9830 independent relevés extracted from Sophy, a large phytosociological database for France.

Results: In France, *Vaccinium myrtillus* is at the southern limit of its European geographic range and three environmental factors (mean annual temperature, soil pH and C:N ratio) allow prediction of its distribution and abundance in forests with high success rates. The species reveals a preference for colder sites (especially mountains) and nutritionally poor soils (low pH and high C:N ratio). A predictive map of its geographic range reveals that the main potential habitats are mountains and northwestern France. The potential habitats with maximal expected abundance are the Vosges and the Massif central mountains, which are both acidic mountains.

Conclusions: Complete niche models including climate and soil nutritional conditions allow an improvement of the spatial prediction of plant species abundance at a broad scale. The use of soil nutritional variables in distribution models further leads to an improvement in the prediction of plant species habitats within their geographical range.

Keywords: Ecoinformatics; EcoPlant; France; Nitrogen nutrition; Ordinal data; pH; Predictive mapping; Proportional odds model; Species distribution modelling.

Abbreviations: AUC = Area under ROC curve; GLM = Generalized linear model; ROC = Receiver operating characteristic.

Introduction

Plant species distribution models have recently been given much consideration (Guisan et al. 2002, 2006; Lehmann et al. 2002; Scott et al. 2002; Araújo & Guisan 2006; Moisen et al. 2006). Most recent studies focus on the prediction of species presence/absence (e.g. Coudun et al. 2006) and only a few studies have concerned the prediction of species cover/abundance (Guisan & Harrell 2000; Pearce & Ferrier 2001; Guisan 2002; Potts & Elith 2006). Investigating the relationships between species distribution and abundance is, however, important to assess the controls of plant population development (Brown 1984; Brown et al. 1995; Holt et al. 1997; Gaston et al. 2000; Maurer 2002). Knowing the relative abundance of species on a given site is valuable ecological information but it cannot be explored with current geographic range atlases. However, different methods for modelling species distribution and abundance do exist which use other data sources such as plot inventories information (Vincent & Haworth 1983; James & McCulloch 2002; Jones et al. 2002; Potts & Elith 2006).

The current predictive studies of plant species distribution are mostly performed with climatic factors and do not take direct soil nutritional factors into account (*sensu* Austin 1999, 2002). The predictive mapping of *Acer campestre*, a clearly basophilous tree species has, however, been recently investigated (Coudun et al. 2006) with some other studies also including direct nutritional variables (Pinto & Gégout 2005; Seynave et al. 2005), and it illustrates the need to incorporate direct edaphic factors into the models.

Vaccinium myrtillus is one of the most frequent and abundant vascular plant species in northern Europe, being an important species in conifer ecosystems (Ritchie 1956; Flower-Ellis 1971). Many studies have been carried out on this species during the last century, due to the large geographical area occupied by the species, its fruit production and its pharmaceutical properties.

However, its autecology seems poorly known with regard to climatic conditions (see however de Ruffray 1980; Woodward 1986), since most studies have been performed in northern Europe where the species is adapted to most habitats (Ihalainen & Pukkala 2001; Ihalainen et al. 2002, 2003, 2005). France represents the southern limit of its geographic area, and northern France is the southern limit for low altitude areas. Therefore, in the south of France and Europe, the species is only found in mountainous environments. The nutritional requirements of the species have also been identified, especially with regard to nitrogen and mineral nutrition (Mäkipää 1999). *V. myrtillus* is found on acid soils in central and western Europe (Rameau et al. 1989, 1993; Ellenberg et al. 1992). France provides a good study area for assessing the ecological requirements of *V. myrtillus*, with five main mountain areas and many calcareous or acidic soils in the country.

The first objective of this study is to investigate nutritional and climatic requirements of *V. myrtillus* simultaneously in order to confirm the need of edaphic variables in predictive distribution models. The second objective is to investigate whether those variables are also useful to predict the spatial patterns of abundance of plant species.

Material and Methods

Calibration data set: EcoPlant

We used 2905 relevés extracted from EcoPlant, a phyto-ecological database for French forests that was developed to store complete floristic relevés with associated climate and precise soil information (Gégout 2001; Gégout et al. 2005). Floristic information was available through Braun-Blanquet (1932) cover/abundance scores on 400-m^2 sites, consistent with current phytosociological practice (Mueller-Dombois & Ellenberg 1974). In order to get a better distribution of cover/abundance scores (van der Maarel 1979; Noest et al. 1989), we recoded the original Braun-Blanquet scores into three classes: Class 1 was when the species was present and its cover was < 5% of the relevé (corresponding to Braun-Blanquet values + and 1), class 2 was cover between 5% and 50% (corresponding to Braun-Blanquet values 2 and 3) and class 3 for cover > 50% (corresponding to Braun-Blanquet values 4 and 5). Among the 2905 relevés, *V. myrtillus* was found in 377 relevés (Fig. 1), with 178 relevés in class 1, 156 in class 2 and 43 in class 3.

For each relevé, we had access to 65 climatic variables from the geographical information system AURELHY (Benichou & Le Breton 1987), among which were one annual and 12 monthly values for mean

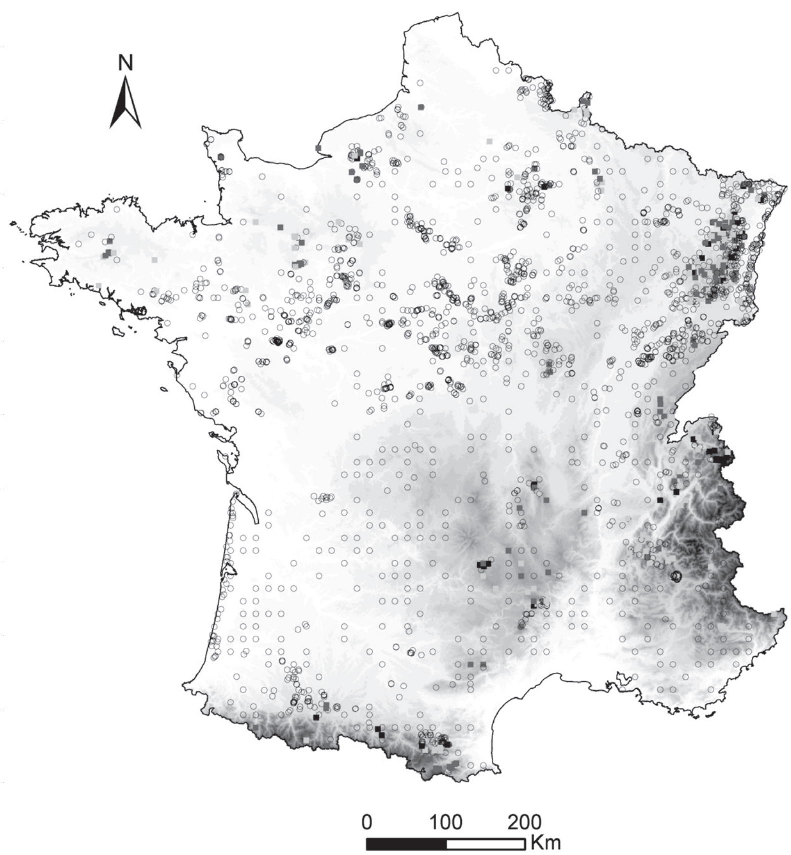

Fig. 1. Geographic location of the 2905 forest relevés, indicating absence (empty circles) and abundance (presence with cover < 5% = light grey squares, cover between 5% and 50% = dark grey squares, cover > 50% = black squares) of *Vaccinium myrtillus* in the calibration data set extracted from EcoPlant.

Table 1. List of available climatic and edaphic variables to model the distribution and abundance of *Vaccinium myrtillus* in French forests, with minimum, mean and maximum values. 2905 relevés were available.

Code	Variable	Unit	Minimum	Mean	Maximum
T	Annual temperature [1]	°C	4.0	9.8	15.5
R	Annual radiation [1]	$kJ.cm^{-2}$	265	429	646
P	Annual rainfall [1]	mm	385	950	2390
PET	Potential evapotranspiration [1, 2]	mm	335	676	1005
WB	Water balance (yearly sum of monthly P-PET) [1, 2]	mm	–479	270	1887
PH	$pH(H_20)$ of the first mineral soil horizon	-	3.0	5.2	8.5
C:N	C:N ratio of the first mineral soil horizon	-	10	17	35

[1] Monthly values were also available, and were tested in the models. [2] The method used to compute potential evapotranspiration was based on Turc (1961).

temperature, precipitation, radiation, evapotranspiration and water balance. (Table 1). We also had access to two measured soil variables: soil pH and C:N ratio of the first organo-mineral horizon A. The selected calibration points are all separated from each other and from the validation points by at least 500 m in order to avoid spatial autocorrelation in the models (Coudun 2005; Coudun et al. 2006).

Evaluation data set: Sophy

We had access to 9830 independent 400-m^2 large forest relevés from the phytosociological database Sophy (Brisse et al. 1995). The original Braun-Blanquet scores were recoded according to the same scale as for the calibration data set. Among the 9830 relevés, *V. myrtillus* was found in 1513 relevés (Fig. 3a), with 754 relevés in class 1, 586 in class 2 and 173 in class 3. The 65 climatic variables presented in the previous section were also available for this data set. We computed a bio-indicator value of pH and C:N for each relevé, based on their floristic composition and on a unpublished catalogue of edaphic indicator values for forest plants species in France (Gégout et al. 2002; 2003). *V. myrtillus* was excluded from those bio-indicator computations in order to ensure independence between the response and the explanatory variables.

Proportional odds model

We used proportional-odds models to link *V. myrtillus* abundance to ecological factors (Bender & Benner 2000; Guisan & Harrell 2000; Guisan 2002), using the lrm function written by Frank Harrell Jr. in the S-Plus Design library. This model is a particular generalized linear model (GLM, see McCullagh & Nelder 1997) that allows the modelling of all classes of abundance giving the same coefficient for each selected ecological variable, and with a change only in the class specific intercept. A forward stepwise procedure was used to select the most relevant variables explaining *V. myrtillus* distribution and abundance. At each step, the most significant variable was kept (at the 0.001 level), based on a residual deviance test (McCullagh & Nelder 1997). Variables with their quadratic form were tested at each step to account for bell shaped response curves (ter Braak & Looman 1986). The stepwise procedure stopped when the incorporation of a supplementary variable (in its simple form or coupled with its quadratic form) did not lead to a significant reduction in residual deviance, at the 0.001 level (Coudun et al. 2006).

Model evaluation

Once the final proportional-odds model was computed and parameters were set for the equation between *V. myrtillus* presence and abundance, three sets of probabilities were computed for the 9830 evaluation relevés, corresponding to probabilities of presence of the species with a cover greater than 0% (Pred1), 5% (Pred2) and 50% (Pred3). These three sets of probabilities were compared with binary vectors describing observed abundance classes of *V. myrtillus* (Obs1, Obs2, Obs3, respectively). The first binary vector (Obs1), where 0 was given to observed absence plots (8317 relevés) and 1 was given to plots with observed scores 1, 2, 3 (1513 relevés with presence of the species with any cover), was compared with the vector of probabilities of cover greater than 0% (Pred1). For the second (Obs2) and third (Obs3) vectors, we attributed 1 only to plots with observed scores 2 and 3 (759 relevés with presence of the species with cover greater than 5%) or to plots with observed scores 3 (173 relevés with presence of the species with cover greater than 50%), respectively. The evaluation of each predicted set of probabilities against the corresponding constructed binary vector was performed using the Receiver operating characteristic (ROC) curve methodology (Fielding & Bell 1997; Manel et al. 2001). In each case, an optimal threshold value of probability was selected to transform the predicted probabilities into predicted binary vectors (0/1), allowing the derivation of three confusion matrices (Fielding & Bell 1997) and definition of synthetic measures of model quality: (1) global success (S, correct classification rate of 0s and 1s), (2) sensitivity (Sn, correct classification rate of 1s), (3) specificity (Sp, correct classification rate of 0s). Finally, the AUC (area under the ROC curve) was used to assess the predictive performance of the model for the evaluation set (Fielding & Bell 1997; Manel et al. 2001). All computations were performed with the S-Plus statistical package (Anon. 1999).

Results

The final model linking the cover/abundance of *Vaccinium myrtillus* to environmental variables was composed of mean annual temperature (T), soil pH (pH) and C:N ratio (C:N):

$$\ln\left(\frac{p}{1-p}\right) = \alpha + 1.3039 \cdot T - 0.1357 \cdot T^2 - 2.3796 \cdot pH + 0.138 \cdot pH^2 + 0.1328 \cdot C/N \quad (1)$$

where p is the probability of presence of *V. myrtillus* with cover greater than 0%, 5% and 50%, with three corresponding values for α:
p(cover> 0%): $\alpha = 3.4747$
p(cover > 5%): $\alpha = 2.4209$
p(cover > 50%): $\alpha = 0.4004$

V. myrtillus thus has a preference for colder environments ($T < 6$ °C, Fig. 2a), acidic sites (pH < 4, Fig. 2b) and low nitrogen nutrition habitats (C:N > 30, Fig. 2c). In these favourable environments, the model predicts high covers of *V. myrtillus* (at least a value of 0.5 for the probability of cover greater than 50%).

The model also predicts high probability of presence (at least a value of 0.5 for the probability of cover greater than 0%) on calcareous forest sites (pH > 7) with $T < 6$ °C and C:$N > 20$ (poor nitrogen nutrition conditions). The presence of *V. myrtillus* in high elevation and calcareous sites is poorly known but is observed on some sites in the high Jura and northern Alps (Bornes and Chartreuse).

The inclusion of soil pH and C:N shows that soil conditions act as a local filter to predict species distribution. The inverse bell shaped response of *V. myrtillus* to pH allows a strong decrease of probabilities between pH values of 3.0 and 5.5, but also a certain stability between pH values of 5.5 and 8.5 which allows a non-zero prediction of presence in calcareous environments.

Our model was highly predictive for each of the three abundance classes (Table 2) with high AUC values. The prediction maps were also very similar to the observation data (Fig. 3).

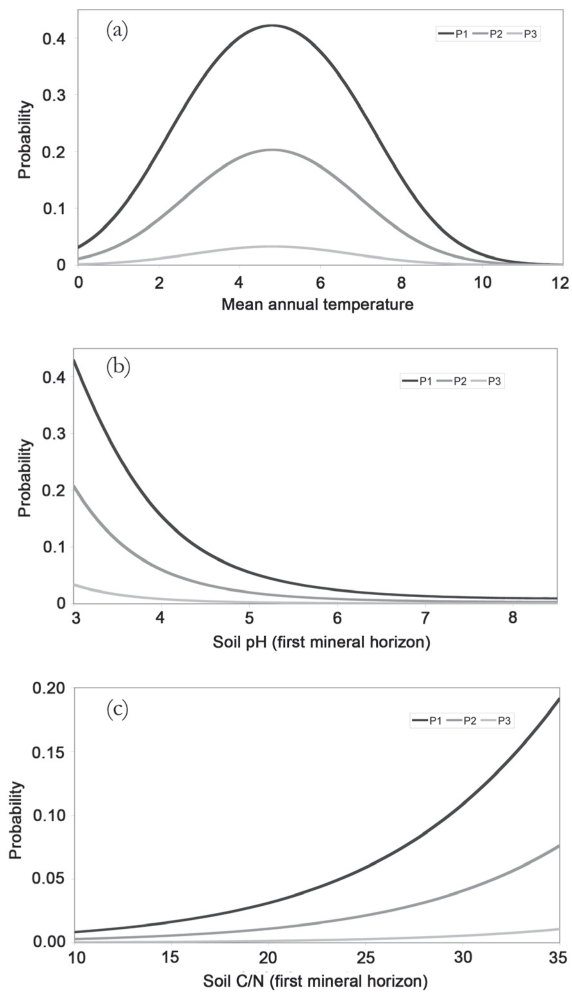

Fig. 2. Predicted probability of presence of *Vaccinium myrtillus* with cover greater than 0% (P1, black upper line), 5% (P2, dark grey intermediate line) and 50% (P3, light grey lower line), based on the computed three-variable model. To compute each graph, the other variables were set to the mean value of the calibration data set, i.e. 9.8 °C for T, 6 for soil pH and 18 for soil C:N ratio.

Table 2. Summary statistics on the model evaluation, based on the 9830 forest sites extracted from Sophy. S, Sn and Sp are the global success, sensitivity and specificity (in %), respectively. See Fielding & Bell (1997) and Manel et al. (2001) for further information on these measures. Numbers in brackets show the same statistics for a climatic model with only mean annual temperature as a predictor variable.

	AUC	S	Sn	Sp
Class 1 (cover > 0%)	**0.89** (0.79)	**81** (68)	**82** (80)	**81** (65)
Class 2 (cover > 5%)	**0.90** (0.77)	**80** (63)	**85** (81)	**80** (62)
Class 3 (cover > 50%)	**0.90** (0.80)	**74** (66)	**94** (88)	**73** (59)

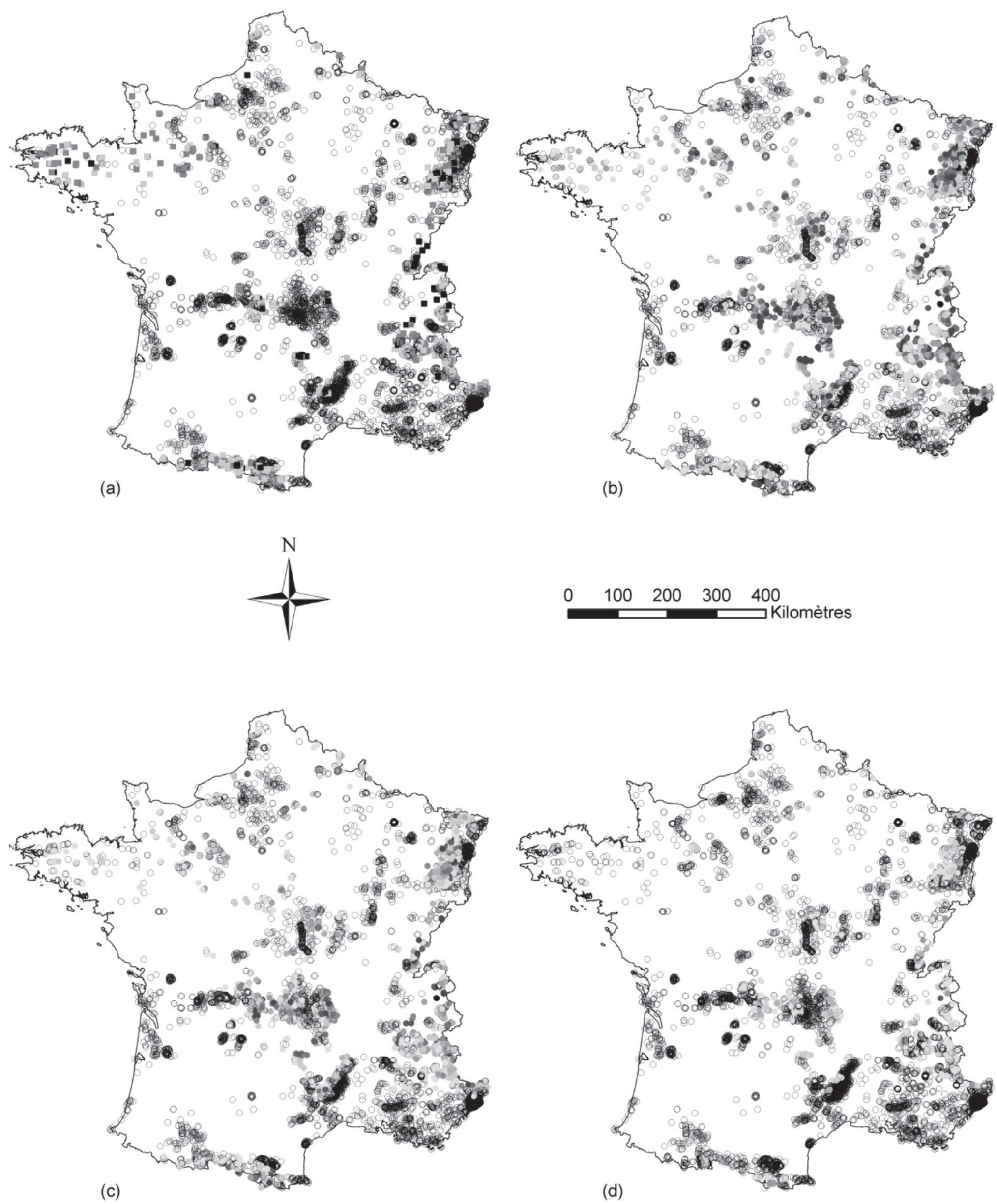

Fig. 3. (**a**) Geographic location of the 9830 evaluation forest relevés used in this study, with indication on absence (open points) and abundance (presence with cover < 5% = light grey squares, cover between 5% and 50% = dark grey squares, cover > 50% = black squares) of *Vaccinium myrtillus* in the evaluation data set extracted from Sophy. (**b**) Probabilities of presence of the species with cover greater than 0%; (**c**) ibid. > 5%; (**d**) ibid. > 50 %. The scale is from grey points for low probabilities to black for high probabilities.

Discussion

Vaccinium myrtillus can form extensive patches that lead potentially to high cover scores in the plots. The species develops rhizomes with centrifugal growth that allow a vegetative development of irregular circular patches from three to ten meters in diameter (Flower-Ellis 1971). Low scores of abundance in plots mean that there are only small patches or individuals while high cover scores mean large or joint patches over the plot. A random selection of plots, with heterogeneous sizes and random spatial distribution of patches, can explain the distribution of the different scores for given environmental conditions. The model chosen to predict *V. myrtillus* abundance assumes the same optimum for all the cover thresholds. A link between the sizes of patches and the values of gradients could modify the optima positions of the different classes of abundance implying different coefficients for the variables in abundance models. The potential variability of abundance optima could be explored with a very extensive dataset which would limit the random variability of optimum due to the low number of occurrences of high abundance values (Coudun & Gégout 2006).

V. myrtillus showed a reaction to both types of environmental factors: nutrition (either mineral or nitrogen) and climate. The species prefers cold environments and 'poor' soil resources (low pH and high C:N ratios). Acidic mountains (Vosges and Massif central) are the most favourable regions in France with highest abundance scores predicted while calcareous flat areas are highly unfavourable for *V. myrtillus*.

The species is predicted to be abundant (with cover greater than 50%) only in the mountainous areas (Fig. 3d), which is confirmed by observational data (Fig. 3a). The preference of *V. myrtillus* for cold mean temperatures in France can be related with its circumboreal distribution (Ritchie 1956). It would be interesting to investigate if the species' altitudinal preferences of temperature, observed in the southern part of its distribution could be related to its latitudinal range of preference.

We observed a decrease of the probability of occurrence and dominance of *V. myrtillus* with increasing nutrient concentrations (increase pH and nitrogen availability) that is consistent with the decrease of its biomass for high nitrogen concentrations (Chapin et al. 1986; Mäkipää 1999). *V. myrtillus* biomass is weakly affected by nitrogen additions (Mäkipää 1999), contrary to some of its competitors such as *Deschampsia flexuosa* or *Agrostis capillaris* (Hester et al. 1991). A low response to nutrient enrichment both under increasing competition from other plant species and under decreasing stress conditions (Callaway et al. 2002; Maestre et al. 2005), may explain that, nevertheless, improving nutritional conditions lead to a decrease in frequency and cover probability.

Some studies show a clear effect of light conditions on the development of *V. myrtillus* (Hester et al. 1991; Atlegrim & Sjoberg 1996). These conditions act at a local scale with the openness of forests stands but do not affect distribution maps elaborated at the country scale. Taking this factor into account should improve the efficiency of the models and local predictions of *V. myrtillus* abundance that open new perspectives of efficient modelling at various geographical scales.

High cover of *V. myrtillus* is a major determinant for the conservation of the endangered bird species *Tetrao urogallus* (capercaillie; Storch 1993; Selas 2000; Baines et al. 2004). *V. myrtillus* represents an important dimension of *Tetrao urogallus* habitat and nutritional resources. Models predicting occurrences, as well as abundance, of *V. myrtillus* are important to assess favourable areas for conservation of endangered species.

This study confirms, for an acidophilous species, that nutritional factors improve plant species distribution models (Coudun et al. 2006), in terms of prediction of both presence and abundance. Soil conditions allow the prediction of areas with high and low densities of populations inside the species geographical range. Spatial distribution models including climate and soil conditions contribute to the explanation of spatial variability of plant biodiversity at the regional scale.

Acknowledgements. The authors wish to thank Bertrand Martinez for his technical help in editing Figs. 1 and 3. EcoPlant was financed with research grants from the French Institute of Forestry, Agricultural and Environmental Engineering (ENGREF), the French Ministry of Agriculture (DERF) and the Agency for the Environment and Energy Management (ADEME). Christophe Coudun worked as a post-doctoral research associate for the Centre for Terrestrial Carbon Dynamics (CTCD) during this study.

References

Anon. 1999. *S-Plus 2000: programmer's guide*. MathSoft, Inc., Seattle, WA, US.

Araújo, M.B. & Guisan, A. 2006. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* 33: 1677-1688.

Atlegrim, O. & Sjoberg, K. 1996. Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvests in uneven-aged boreal *Picea abies* forests. *For. Ecol. Manage*. 86: 39-50.

Austin, M.P. 1999. The potential contribution of vegetation ecology to biodiversity research. *Ecography* 22: 465-484.

Austin, M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Model.* 157: 101-118.

Baines, D., Moss, R. & Dugan, D. 2004. Capercaillie breeding success in relation to forest habitat and predator abundance. *J. Appl. Ecol.* 41: 59-71.

Bender, R. & Benner, A. 2000. Calculating ordinal regression models in SAS and S-Plus. *Biometretical J.* 42: 677-699.

Benichou, P. & Le Breton, O. 1987. Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. *La Météorologie* 7: 23-34.

Braun-Blanquet, J. 1932. *Plant sociology, the study of plant communities*. McGraw Hill, New York, NY, US.

Brisse, H., de Ruffray, P., Grandjouan, G. & Hoff, M. 1995. European Vegetation Survey. The phytosociological database "SOPHY". Part 1. Calibration of indicator plants. Part 2. Socio-ecological classification of the relevés. *Annali di Botanica* 53: 177-223.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124: 255-279.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. 1995. Spatial variation in abundance. *Ecology* 76: 2028-2043.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.L., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., & Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-848.

Chapin, F.S. III, Vitousek, P.M. & Van Cleve, K. 1986. The nature of nutrient limitation in plant communities. *Am. Nat*. 127: 48-58.

Coudun, Ch. 2005. *Approche quantitative de la réponse écologique des espèces végétales forestières à l'échelle de la France*. Ph.D. Thesis, French Institute of Forestry, Agricultural and Environmental Engineering, Nancy, FR.

Coudun, Ch. & Gégout, J.-C. 2006. The derivation of species response curves with Gaussian logistic regression models is sensitive to sampling intensity and curve characteristics. *Ecol. Model*. 199: 164-175.

Coudun, Ch., Gégout, J.-C., Piedallu, Ch. & Rameau, J.-C. 2006. Soil nutritional factors improve plant species distribution models: an illustration with *Acer campestre* (L.) in France. *J. Biogeogr.* 33: 1750-1763.

de Ruffray, P. 1980. *Caractérisation climatique de deux espèces spontanées à petits fruits: le framboisier (Rubus idaeus L.) et la myrtille (Vaccinium myrtillus L.)*. Productions spontanées, INRA (French National Institute for Agricultural Research), Colmar, FR.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobot*. 18: 1-248.

Fielding, A.H. & Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Envir. Conserv.* 24: 38-49.

Flower-Ellis, J.G.K. 1971. *Age structure and dynamics in stands of bilberry (Vaccinium myrtillus L.)*. Ph.D. Thesis, Royal College of Forestry, Stockholm, SE.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R. & Lawton, J.H. 2000. Abundance-occupancy relationships. *J. Appl. Ecol*. 37: 39-59.

Gégout, J.-C. 2001. Création d'une base de données phytoécologiques pour déterminer l'autécologie des espèces de la Flore Forestière de France. *Rev. For. Fr.* 53: 397-403.

Gégout, J.-C., Coudun, Ch., Brisse, H. & Bergès, L. 2002. *Comportement écologique des espèces forestières vis-à-vis du climat et du sol en France: application à l'évaluation des charges critiques d'acidité et d'azote*. Tech. Rep. French Institute of Forestry, Agricultural and Environmental Engineering, Nancy, FR.

Gégout, J.-C., Hervé, J.-C., Houllier, F. & Pierrat, J.-C. 2003. Prediction of forest soil nutrient status using vegetation. *J. Veg. Sci*. 14: 55-62.

Gégout, J.-C., Coudun, Ch., Bailly, G. & Jabiol, B. 2005. Eco-Plant: a forest site database linking floristic data with soil and climate variables. *J. Veg. Sci*. 16: 257-260.

Guisan, A. 2002. Semi-quantitative models for predicting the spatial distribution of plant species. In: Scott, J.M., Heglund, P.J., Samson, F., Haufler, J., Morrison, M., Raphael, M. & Wall, B. (eds.) *Predicting species occurrences: issues of accuracy and scale*, pp. 315-326. Island Press, Covelo, CA, US.

Guisan, A. & Harrell, F.E. Jr. 2000. Ordinal response regression models in ecology. *J. Veg. Sci*. 11: 617-626.

Guisan, A., Edwards, T.C. Jr. & Hastie, T.J. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Model*. 157: 89-100.

Guisan, A., Lehmann, A., Ferrier, S., Austin, M.P., Overton, J.McC., Aspinall, R.J. & Hastie, T.J. 2006. Making better biogeographical predictions of species' distributions. *J. Appl. Ecol*. 43: 386-392.

Hester, A.J., Miles, J., & Gimingham, C.H. 1991. Succession from heather moorland to birch woodland. II. Growth and competition between *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Agrostis capillaris*. *J. Ecol*. 79: 317-328.

Holt, R.D., Lawton, J.H., Gaston, K.J. & Blackburn, T.M. 1997. On the relationship between range size and local abundance: back to basics. *Oikos* 78: 183-190.

Ihalainen, M. & Pukkala, T. 2001. Modelling cowberry (*Vaccinium vitis-idaea*) and bilberry (*Vaccinium myrtillus*) yields from mineral soils and peatlands on the basis of visual field estimates. *Silva Fennica* 35: 329-340.

Ihalainen, M., Alho, J., Kolehmainen, O. & Pukkala, T. 2002. Expert models for bilberry and cowberry yields in Finnish forests. *For. Ecol. Manage*. 157: 15-22.

Ihalainen, M., Salo, K. & Pukkala, T. 2003. Empirical prediction models for *Vaccinium myrtillus* and *V. vitis-idaea* berry yields in North Karelia, Finland. *Silva Fennica* 37: 95-108.

Ihalainen, M., Pukkala, T. & Saastamoinen, O. 2005. Regional expert models for bilberry and cowberry yields in Finland. *Boreal Environ. Res*. 10: 145-158.

James, F.C. & McCulloch, C.E. 2002. Predicting species presence and abundance. In: Scott, J.M., Heglund, P.J., Samson, F., Haufler, J., Morrison, M., Raphael, M. & Wall, B. (eds.) *Predicting species occurrences: issues of accuracy and scale*, pp. 461-465. Island Press, Covelo, CA, US.

Jones, M.T., Niemi, G.J., Hanowski, J.M. & Regal, R.R. 2002. Poisson regression: a better approach to modelling abundance data? In: Scott, J.M., Heglund, P.J., Samson, F., Haufler, J., Morrison, M., Raphael, M. & Wall, B. (eds) *Predicting species occurrences: issues of accuracy and scale*, pp. 411-418. Island Press, Covelo, CA, US.

Lehmann, A., Overton, J.McC. & Austin, M.P. 2002. Regression models for spatial prediction: their role for biodiversity and conservation. *Biodiv. Conserv.* 11: 2085-2092.

Maestre, F.T., Valladares, F. & Reynolds, J.F. 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *J. Ecol*. 93: 748-757.

Mäkipää, R. 1999. Response patterns of *Vaccinium myrtillus* and *V. vitis-idaea* along nutrient gradients in boreal forest. *J. Veg. Sci*. 10: 17-26.

Manel, S., Williams, H.C. & Ormerod, S.J. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *J. Appl. Ecol*. 38: 921-931.

Maurer, B.A. 2002. Predicting distribution and abundance: thinking within and between scales. In: Scott, J.M., Heglund, P.J., Samson, F., Haufler, J., Morrison, M., Raphael, M. & Wall, B. (eds.) *Predicting species occurrences:*

issues of accuracy and scale, pp. 411-418. Island Press, Covelo, CA, US.

McCullagh, P. & Nelder, J.A. 1997. *Generalized linear models*. Chapman & Hall, London, UK.

Moisen, G.G., Edwards, T.C. Jr. & Osborne, P.E. 2006. Further advances in predicting species distributions. *Ecol. Model.* 199: 129-131.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. Wiley, New York, NY, US.

Noest, V., van der Maarel, E., van der Meulen, F. & van der Laan, D. 1989. Optimum-transformation of plant species cover-abundance values. *Vegetatio* 83: 167-178.

Pearce, J. & Ferrier, S. 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biol. Conserv.* 98: 33-43.

Pinto, P. & Gégout, J.-C. 2005. Assessing the nutritional and climatic response of temperate tree species in the Vosges Mountains. *Ann. For. Sci.* 62: 1-10.

Potts, J.M. & Elith, J. 2006. Comparing species abundance models. *Ecol. Model.* 199: 153-163.

Rameau, J.-C., Mansion, D., Dumé, G., Timbal, J., Lecointe, A., Dupont, P. & Keller, R. 1989. *Flore forestière française. Guide écologique illustré. Tome 1: plaines et collines*. Institut pour le Développement Forestier, Paris, FR.

Rameau, J.-C., Mansion, D. & Dumé, G. 1993. *Flore forestière française. Guide écologique illustré. Tome 2 : montagnes*. Institut pour le Développement Forestier, Paris, FR.

Ritchie, J.C. 1956. *Vaccinium myrtillus* L. *J. Ecol.* 44: 291-299.

Scott, J.M., Heglund, P.J., Samson, F., Haufler, J., Morrison, M., Raphael, M. & Wall, B. 2002. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Covelo, CA, US.

Selas, V. 2000. Population dynamics of capercaillie *Tetrao urogallus* in relation to bilberry (*Vaccinium myrtillus*) production in southern Norway. *Wildl. Biol.* 6: 1-11.

Seynave, I., Gégout, J.-C., Hervé, J.-C., Dhôte, J.-F., Drapier, J., Bruno, E. & Dumé, G. 2005. *Picea abies* site index prediction by environmental factors and understorey vegetation: a two-scale approach based on survey databases. *Can. J. For. Res.* 35: 1669-1678.

Storch, I. 1993. Habitat selection by Capercaillie in summer and autumn – Is Bilberry important? *Oecologia* 95: 257-265.

ter Braak, C.J.F. & Looman, C.W.N. 1986. Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio* 65: 3-11.

Turc, L. 1961. Evaluation des besoins en eau d'irrigation et évaporation potentielle. *Ann. Agron.* 12: 13-49.

van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97-114.

Vincent, P.J. & Haworth, J.M. 1983. Poisson regression models of species abundance. *J. Biogeogr.* 10: 153-160.

Woodward, F.I. 1986. Ecophysiological studies on the shrub *Vaccinium myrtillus* L. taken from a wide altitudinal range. *Oecologia* 70: 580-586.

Received 6 February 2006;
Accepted 17 November 2006;
Co-ordinating Editor: R. Bekker.