

A multiple approach for the evaluation of the spatial distribution and dynamics of a forest habitat: the case of Apennine beech forests with *Taxus baccata* and *Ilex aquifolium*

Luca Scarnati · Fabio Attorre · Michele De Sanctis · Alessio Farcomeni ·
Fabio Francesconi · Marco Mancini · Franco Bruno

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Abstract An approach integrating phytosociological and stand structure surveys with the predictive modelling of species distribution was applied to analyse the spatial distribution and dynamics of the Apennine beech forests with *Taxus* and *Ilex*, a high conservation priority forest habitat in Europe. The homogeneity of the habitat was tested through a Mann–Whitney test between beech woods with *Taxus* and those with *Ilex* with respect to climatic, topographic, structural and environmental parameters: the former have proven to be more microthermic, mesophilous and characterised by a closer canopy. Five statistical models were compared to analyse the relationship between bioclimatic parameters and *Taxus* and *Ilex* spatial distribution: Regression Tree Analysis, the most efficient model, has shown that the distribution of *Taxus* is influenced by precipitation variables, while *Ilex* is mainly influenced by temperature variables. This model highlighted that *Ilex* has a potential area that surrounds, at lower altitudes, that of *Taxus*. A stepwise multiple regression analysis has been applied to identify the factors influencing the regeneration of the two species: beside climatic parameters, *Taxus* regeneration is negatively influenced by soil nitrate concentration (an indicator of livestock disturbance) while *Ilex* is negatively influenced by beech forest cover. Traditional management practices seem to have an effect on the regeneration of the two species: frequent cuts favour the regeneration of *Ilex*, reducing the forest cover and allowing more light penetration, while *Taxus*, less resistant to grazing livestock, is confined to more inaccessible places. The multiple approach has proven to be useful for the elaboration of two differentiated conservation strategies for the two beech forest types.

Keywords Apennine beech forests · *Ilex aquifolium* · Regeneration ·
Potential areas · Regression models · *Taxus baccata*

L. Scarnati · F. Attorre (✉) · M. De Sanctis · F. Francesconi · M. Mancini · F. Bruno
Plant Biology Department, University of Rome Sapienza, P.le A. Moro, 5 00185 Rome, Italy
e-mail: fabio.attorre@uniroma1.it

A. Farcomeni
Department of Experimental Medicine – Statistics Unit, University of Rome Sapienza, P.le A. Moro,
5 00185 Rome, Italy

Introduction

In Italy the beech forests with *Ilex aquifolium* and *Taxus baccata* are distributed in the Apennines, mainly in the centre-south, with isolated fragments in Sicily, usually above 900 m of altitude. In particularly humid conditions they can also be found at 500 m. *Taxus* and *Ilex*, relicts of the Cenozoic flora, characterised by warm–humid climatic conditions, survived the glaciations of the Quaternary period in refugia areas, and may have followed *Fagus* in the successive postglacial expansion (Magri et al. 2006). This process, possibly characterised by long-range dispersion events, determined their current fragmented presence and reduced consistency (Spada 2001). Both the species are linked to humid climatic conditions and have low resistance to intense cold (Siniscalco and Montacchini 1989). Less abundant in other habitats, they probably own their presence to the ability to adapt to local conditions and to their reproductive strategies. This is true especially for *Taxus*: asexual reproduction and sex variations of adults in case of need (Paule et al. 1993; Thomas and Polwart 2003).

Such peculiarities ensured that the habitat “Beech forests of the Apennine with *Taxus* and *Ilex*” was considered, within the Habitat Directive (92-43/ECC), among those with a high conservation priority. The growing interest for the implementation of the Natura 2000 network with the activation of monitoring programmes and conservation actions of forest habitats, has brought to the attention of the scientific community the need to analyze their ecological characteristics and the factors that influence their dynamism and spatial distribution.

The aim of this work is to study the climatic, topographic, structural and environmental parameters influencing the spatial distribution and dynamics of the habitat. This was done by integrating traditional phytosociological and stand structure surveys (Closset-Kopp et al. 2006) with the predictive modelling of species distribution (Guisan and Zimmermann 2000) in order to support the elaboration of conservation strategies.

Study area

The study area is located in central Italy (Fig. 1), between the Tyrrhenian and the Adriatic sea, with an average distance between the two seas of approximately 180 km. It extends for about 28,000 km² with a very variable morphology, which includes sandy coasts and the high summits of the Apennines (the highest peak is the Gran Sasso, 2,912 m of altitude). The average total annual precipitation is 1,030 mm and the annual average temperature is 12.8°C.

Methods

Data set

Using bibliographical information and indications of the staff of the protected areas, we identified all the locations of beech woods with presence of *Taxus* and *Ilex*. In these areas 108 sample plots, with 15 m of radius, were identified by GPS coordinates (Fig. 1). We then proceeded to carry out dendrometric, phytosociological and regeneration surveys. To carry out dendrometric surveys we measured, with a caliper, the diameter at breast height

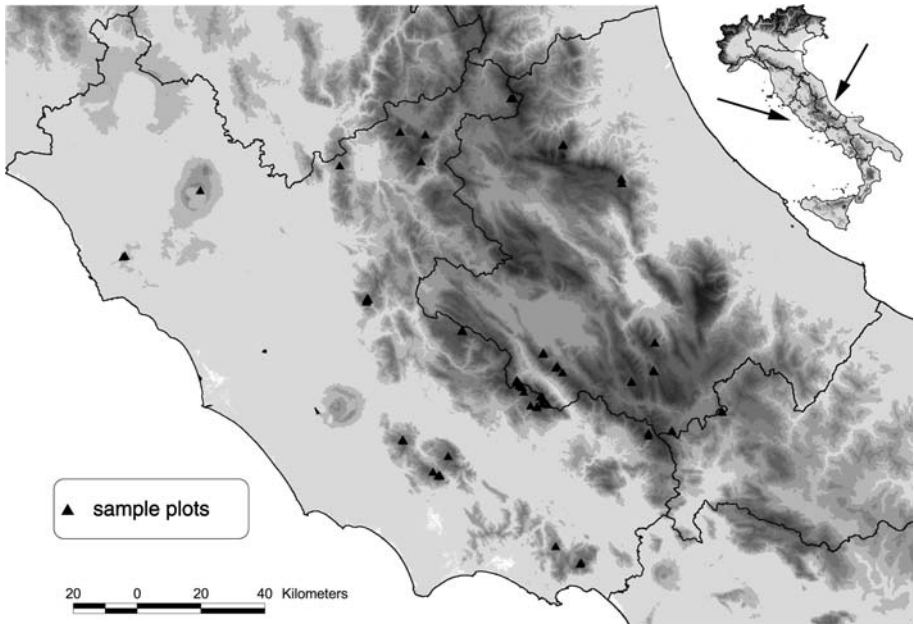


Fig. 1 Study area and sample plots

(1.30 m) of all the trees with a diameter equal or bigger than 2.5 cm, using 5 cm diametrical classes.

The phytosociological surveys, carried out using the Braun Blanquet scale were used to obtain, through the software Turboveg 2.37, the average values of the Ellenberg indicators (Ellenberg et al. 1991), updated for Italy by Pignatti (2005). These indicator values describe the ecological optima for the species along ecological gradients using an ordinal scale applied on several environmental parameters such as light, temperature, continentality, soil moisture, pH and nitrogen content. The average values of these indicators are considered good predictors of the environmental conditions that characterise the forest habitats, particularly for mature woodlands, whose composition is mainly influenced by the environmental regime (Dzwonko 2001; Naaf and Wulf 2007).

The regeneration surveys were done by measuring the heights of all the individuals with a diameter at breast height of less than 2.5 cm and higher than 20 cm (in order to distinguish sproutings from seedlings). In this way, an index of Regeneration expressed in cm of regeneration per hectare was obtained (Bianchi and Paci 2008).

Climatic data

For our study, we used climatic maps in GRID format with a spatial resolution of 500 m. These maps were obtained by interpolating precipitation and temperature data recorded in 300 meteorological stations and calculating the average data for the 1960–1990 period (see Attorre et al. 2007a for technical details). Climatic variables were chosen among those believed to be more meaningful for their influence on the growth and distribution of tree species and considered representative of others more directly related to them, like the

number of growing degree days or actual evapotranspiration (Huntley et al. 1995; Thuiller et al. 2003). We used:

- Annual mean temperature
- Minimum temperature of the coldest month (January)
- Maximum temperature of the hottest month (July)
- Summer precipitation
- Winter precipitation
- Total annual precipitation
- Mi (moisture index)

The moisture index was calculated with the following formula: $Mi = P/ETp$, where P = mean annual precipitation, ETp = potential evapotranspiration.

Data analysis

Comparison of beech wood types

Since in almost all the plots we found either *Ilex* (55 plots) or *Taxus* (45) and very rarely both at the same time (10), we carried out the Mann–Whitney test, using the software package R (R Development Core Team 2007), comparing the median of each variable, so as to find which factors differ meaningfully between the beech woods with *Taxus* and those with *Ilex*. The multiplicity of the tests was done taking into account and controlling the False Discovery Rate at 5% through the procedure of Benjamini and Hochberg (1995). Controlling the False Discovery Rate guaranteed that, in average, a maximum of 5% of the variables considered meaningfully different, are false positives (Farcomeni 2007). Together with climatic, topographical and Ellenberg indicators the following structural parameters were used to analyze the difference between the two beech types: plants per hectare, basal area and diameter of the mean basal area, Shannon index applied to diametrical classes, Vertical Evenness index and Gini coefficient. The Vertical Evenness index (Neumann and Starlinger 2001) was calculated by stratifying the trees into four layers (limits at 80, 50, and 20% of maximum height on the plot), estimating their crown projection area, and then applying the Shannon formula to the resulting proportions. The Gini coefficient (Weiner and Solbrig 1984) is a measure of the diversity and the heterogeneity of the distribution of the tree individuals among the diametrical classes. The Gini coefficient is obtained from the following formula:

$$G = \frac{\sum_{i=1}^n \sum_{j=1}^n |d_i - d_j|}{2n(n-1)\bar{d}}$$

where n is the number of trees measured within each stand. G has a minimum value of 0 when all individuals are equal, and a theoretical maximum of 1 in an infinite population in which all individuals except one have a value of 0.

Moreover, to examine the differences between pooled dbh-distributions the histogram of the number of beech individuals and that of cumulative dbh-distributions in each size class were obtained. This latter is known as Lorenz curve (Weiner and Solbrig 1984), where tree individuals are ranked from the smallest to the largest so that the cumulative percentage of the diameters for each cumulative percentage of number of trees is plotted (in this case 5, 10, 20, 30, 40, 50, 60, 70, 80 and 90%). If all individuals are equal with respect

to the diameter, the result should be a diagonal line from the origin to the upper right corner. Any inequality results in a curve below the diagonal.

Regression models and potential distribution

In the last years several models have proven to be useful to predict the distribution of presence/absence and abundance of tree species (Iverson and Prasad 1998, 2002; Vayssières et al. 2000; Thuiller 2003; Segurado and Araújo 2004; Attorre et al. 2008; Benito Garzón et al. 2008; Hidalgo et al. 2008) so that they are now considered a useful tool for the conservation and the management of forest habitats. As a measure of abundance for *Taxus* and *Ilex* the Importance Value (IV) was calculated based equally on relative basal area and the number of stems contained within each plot, with a maximum value of 200 in monotypic stands. For each plot the values of the climate variables were extracted from the GIS climatic maps. The relationship between the spatial distribution of the IV and the climatic variables was analysed using the software packages SPSS 15.0 and R, through Multiple Linear Regression applied on the normalized response, Generalized Additive Models (Hastie and Tibshirani 1990), Support Vector Regression (Smola and Scholkopf 2004), Multivariate Adaptive Regression Splines (Friedman 1991) and Regression Tree Analysis (Iverson and Prasad 1998; 2002; Iverson et al. 1999). For the latter method we compared two kinds of regression trees: the C&RT (Breiman et al. 1984) and the exhaustive CHAID (Biggs et al. 1991). The regression and the GAM are linear models that keep simple, hence with good generalization properties, the model (although the GAM method takes on an arbitrary effect for each covariate), the SVR and the MARS are instead non-linear models that produce models that are generally better adapted to the observed data. The observations used for the analyses consisted in the presences observed, and also in pseudo-absences. Pseudo-absence data (Zaniewski et al. 2002; Engler et al. 2004) were generated with the same case–control method as in Attorre et al. (2007b). Pseudo-absences were generated because the use of presence data only would have determined over-optimistic predictions of the potential distribution.

A 10-fold cross validation was carried out for all the methods, confronting the values observed and those predicted on the test set. The best method was the Regression Tree Analysis and this was confirmed by the classification accuracy, that is the proportion of presences correctly predicted on the test set.

The regression trees, thus, obtained were used to identify the climatic variables that influence the spatial distribution of the species. The regression tree analysis divides the data in subsets based on a single predictive variable, proceeding successively for every subset created and realizing an output constituted by a tree with nodes and terminal branches, for which the average values of IV and the percentage of the sample represented in the subset are indicated.

The decision trees were used to estimate the expected values of IV of the species for all the cells of 500 m of resolution so as to enable the production of maps of the potential distribution for the two species.

Regeneration analysis

A multiple regression analysis was applied using the software package SPSS 15.0 in order to identify the factors influencing the regeneration of *Taxus* and *Ilex*. The Regeneration index was used as dependent variable, and climatic, topographical, structural variables and

the Ellenberg indicators were used as independent variables. For each regression a subset of predictors was selected using a stepwise method.

Results

The Mann–Whitney test (Table 1) shows a clear difference between the beech woods with *Taxus* and those with *Ilex*. In particular, beech woods with *Taxus* are characterised by:

- lower minimum, maximum and mean temperatures and more humid climatic conditions;
- higher altitude, steeper slopes and greater distance from the coast;
- denser and less stratified beech wood;
- greater quantity of light and higher soil pH and water content, and lower nitrogen content.

The pooled dbh-distributions for beech woods with *Taxus* and those with *Ilex*, were descending with an inverse-J shape, typical of uneven-aged stands (Fig. 2). Significant differences were found by applying the Mann–Whitney test to each diameter class. In particular, beech woods with *Taxus* showed a higher number of individuals for the classes from 5 cm to 25 cm, and a lower one for the 80 and 85 cm classes. The shape of the two curves was not significantly different, as demonstrated by the Mann–Whitney test on dbh cumulative percentage classes of the Lorenz curves (Fig. 3). This was also confirmed by the values of the Gini coefficient, since the relationship between the Gini coefficient and the Lorenz curve is that the fraction of the area below the diagonal, that is between the Lorenz curve and the diagonal, is the Gini coefficient.

The tree diagrams for *Taxus* and *Ilex* produced by RTA are shown in Fig. 4. The tree diagrams proved to be a useful way to highlight the interactions between environmental variables and species distribution (Iverson and Prasad 1998; Vayssières et al. 2000, Thuiller et al. 2003). The terminal nodes of the data set indicate the average IV value for the relatively homogeneous subset. *Taxus* is influenced by annual and summer precipitations, preferring minimal thresholds of total annual precipitations of 1,092 mm (Fig. 4a), while *Ilex* is influenced mainly by temperature variables, with an optimum of mean annual temperature between 10.07 and 10.41°C, above which it can be found only in areas characterized by winter precipitations higher than 475 mm and below only in areas with a minimum temperature higher than -0.8°C (Fig. 4b).

The Fig. 5 shows the potential distribution of *Taxus* and *Ilex* abundance and the overlapping areas between them (see also summary in Table 2). *Ilex* has a wider potential area of distribution (558,450 ha) than *Taxus* (436,500 ha), with an overlapping area of 167,500 ha. *Ilex* is less common on the eastern Adriatic side, because the mean temperatures there are lower than on the Tyrrhenian side, in lower altitude (mean altitude is around 1,000 m), and adjacent—nearly always in a concentric way—to *Taxus*, which is situated at higher altitude (mean altitude of 1,300 m).

According to the results of the multiple regression analysis (Table 3) the regeneration of *Taxus* is influenced:

- positively by the total annual precipitations;
- negatively by the nitrogen content as expressed by the relative Ellenberg indicator.

Table 1 Comparison between beech woods with *Taxus* and those with *Ilex*

Parameters	<i>Taxus baccata</i>					Significant	<i>Ilex aquifolium</i>				
	Min	Max	Mean	S.D.	Median		Min	Max	Mean	S.D.	
<i>Climate</i>											
Minimum temperature of the coldest month (°C)	-3.80	1.67	-1.99	1.35	-1.90	1	0.10	3.6	-0.36	2.09	
Maximum temperature of the hottest month (°C)	19.70	24.34	22.36	1.42	22.50	1	23.98	26.59	23.66	1.67	
Annual mean temperature (°C)	6.50	11.50	8.36	1.23	8.75	1	10.40	13.50	9.96	1.76	
Winter precipitation (mm)	229	516	414	72.23	475	0	475	520	447	62.06	
Summer precipitation (mm)	144	250	188	34.33	204	1	153	250	166	41.89	
Total precipitation TOT (mm)	1,022	1,641	1,365	164.76	1,414	1	1,380	1,589	1,340	174.17	
Moisture index [Mi]	1.1	1.7	1.4	0.17	1.40	1	1.20	1.7	1.2	0.20	
<i>Topography</i>											
Percentage of rock	5	50	15	12.85	10	0	10	60	12	11.85	
Continentality (km)	28	95	65	3.65	60	1	40	85	43	5.26	
Slope (%)	5	30	20.1	6.47	20	1	15	30	15	5.86	
Altitude (m)	1,010	1,625	1,358	159.08	1,380	1	1,050	1,450	1,110	245.15	
<i>Structure</i>											
Diameter of mean basal area (cm)	7.79	36.60	19.94	7.01	19.03	1	27.46	55.89	27.36	13.30	
Tree number/ha	168	4,745	1,360	1,033	910	1	520	3,662	919	852.90	
Basal area (cm ² /ha)	7.69	65.14	33.58	12.08	32.22	0	28.22	73.70	33.84	15.00	
Vertical Evenness index	0.34	0.94	0.61	0.15	0.50	1	0.58	0.68	0.51	0.11	
Gini coefficient	0.12	0.50	0.35	0.09	0.37	0	0.34	0.57	0.33	0.11	
Shannon index	0.67	2.16	1.57	0.36	1.60	0	1.73	2.42	1.66	0.41	
<i>Ellenberg indicators</i>											
Light	2.7	3.9	3.3	0.27	3.3	1	3.65	4.5	3.6	0.37	
Temperature	4.8	5.9	5.2	0.25	5.2	1	5.3	6.4	5.36	0.35	
Continentality	2.1	3.0	2.5	0.23	2.4	0	2.4	3.1	2.4	0.22	

Table 1 continued

Parameters	<i>Taxus baccata</i>					Significant	<i>Ilex aquifolium</i>				
	Min	Max	Mean	S.D.	Median		Min	Max	Mean	S.D.	
Soil moisture	4.0	5.0	5.0	0.17	5.0	1	4.2	5.0	4.8	0.19	
pH	2.3	7.3	6.6	0.79	6.8	1	2.3	7.1	5.7	0.96	
Nitrogen content	4.0	6.7	5.5	0.74	5.9	1	4.9	6.6	6.09	0.42	

FDR-adjusted P -values are computed. If the FDR-adjusted P -value is lower than 0.05, the difference was statistically meaningful and 1 was reported in the “Significant” column, zero otherwise

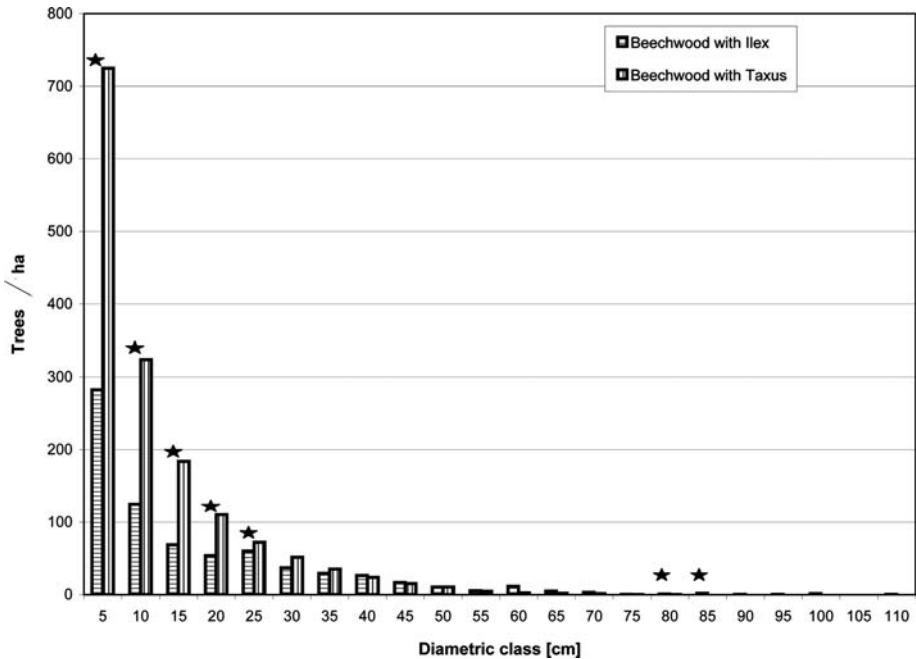


Fig. 2 Pooled dbh-distributions of trees in beech woods with *Taxus* and those with *Ilex*. Significant differences between the stand categories are marked with asterisks (Mann–Whitney test, $P < 0.05$)

The regeneration of *Ilex* (Table 4) is influenced:

- positively by the maximum temperature;
- negatively by the annual precipitations;
- negatively by the basal area per hectare of the beech wood.

Discussion

The elaboration of appropriate conservation measures of a forest habitat should be based on the knowledge of its dynamic. This can be achieved by integrating the information obtained by traditional investigation techniques, such as phytosociological analysis and forest inventory, with the insights from spatial distribution models. In this way, the forest habitat dynamic, defined by species composition and structure, can be analysed within the framework of its environmental niche and projected into geographic space, providing a spatial prediction of the most suitable areas. By applying this approach to a specific case, we discovered that the forest habitat “Apennine beech forests with *Taxus baccata* and *Ilex aquifolium*” as defined by the Habitat Directive can be separated into two habitats. In fact, *Taxus* and *Ilex* occupy, inside the Apennine beech forests, two different ecological niches. In particular, as it is shown by the Mann–Withney test on climatic and environmental variables (Table 1) and by the RTA (Fig. 4), *Taxus* needs higher climatic and edaphic humidity. This differentiation is also well expressed by the maps of their potential distribution, where *Ilex* potential area surrounds, at lower altitudes, that of *Taxus*, with only

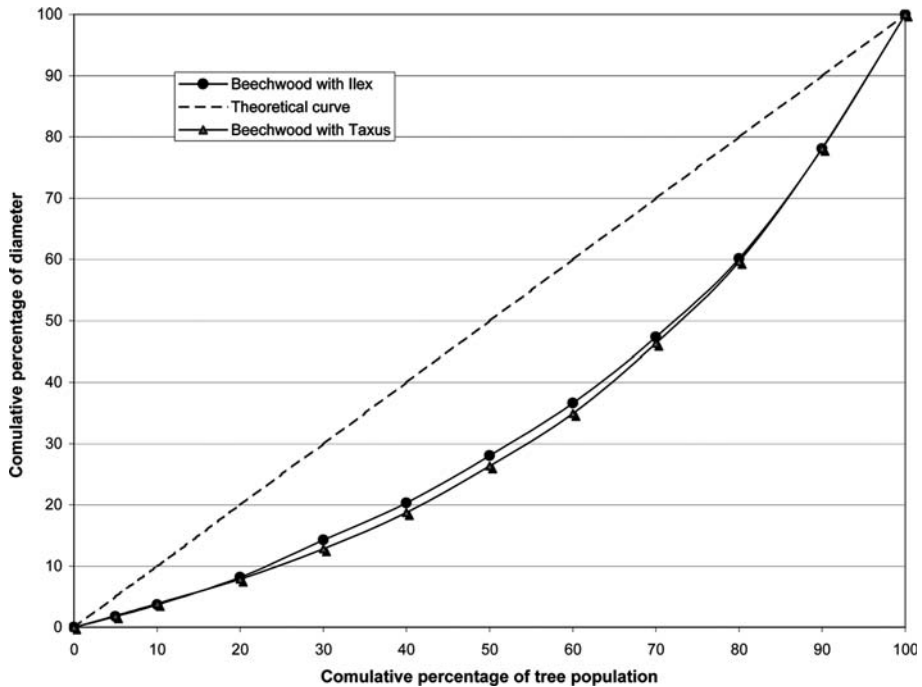


Fig. 3 Lorenz curves for beech woods with *Taxus* and those with *Ilex*. No statistical differences were identified at each cumulative percentage classes (Mann–Whitney test, $P < 0.05$)

a small overlapping area (Fig. 5c). This is generally due to the presence of *Taxus* at an altitude lower than its typical distribution, on slopes exposed towards the seas, which intercept the humid winds, thus causing a rainfall increase, able to compensate the higher temperatures. Differences also exist regarding the structure of the two beech woody types. In fact, on one side, the pooled dbh-distributions show a similar inverse-J shape suggesting in both cases viable beech populations (Fig. 2). And this similarity is also confirmed by the fact that the Lorenz curves, the Gini coefficient and the Shannon index do not statistically differ (Table 1). On the other side, beech woods with *Ilex* are characterised by greater light levels, as shown by the relative Ellenberg indicator: the lower density and the higher mean diameter of trees and Vertical Evenness index of beech woods with *Ilex* indicate structural conditions that allow more light to reach the forest floor (Table 1). This is probably due to higher disturbance caused by human activities favoured by their easier accessibility, lower altitude and less steep slopes. In these areas irregular cuts for civic uses—particular areas of forests where citizens are allowed to harvest timber for their own consumption (Feliziani 2006)—are more frequent. This factor seems to have an effect on the regeneration of *Ilex*. In fact, according to the results of the multiple regression analysis, beside climatic variables such as total precipitation and maximum temperature, *Ilex* is negatively influenced by the cover of the beech trees measured as basal area per hectare (Table 4). For this reason, it can be hypothesized that traditional practices favour the regeneration of *Ilex*, reducing forest cover and allowing higher penetration of light. *Taxus* regeneration, instead, is positively influenced by the total precipitation and negatively by the nitrogen content expressed by the relative Ellenberg indicator (Table 3). A high level of nitrogen content

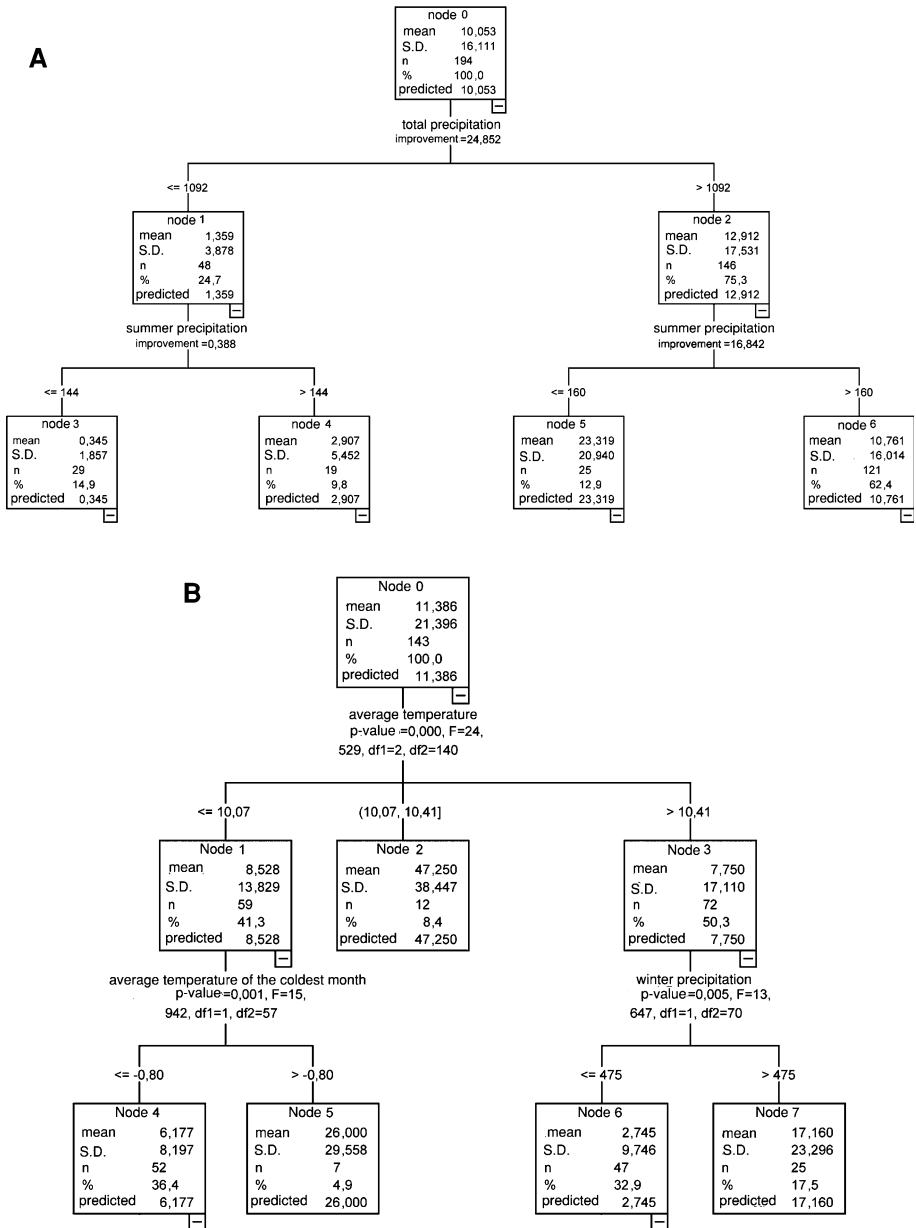


Fig. 4 Regression tree for **a** *Taxus* and **b** *Ilex*. The final predicted values are the mean values in the branches of the regression tree, which are chosen according to the characteristics of the sample plots considered sequentially from the root of the tree

determined the presence of competitive nitrophilous species such as *Rubus ulmifolius* and *Alliaria petiolata*. These species are favoured by disturbance caused by livestock, especially cows who can also directly influence *Taxus* regeneration by eating seedlings and sprouting. In fact, the toxicity of *Taxus* for the cows, referred by some authors (Paule et al.

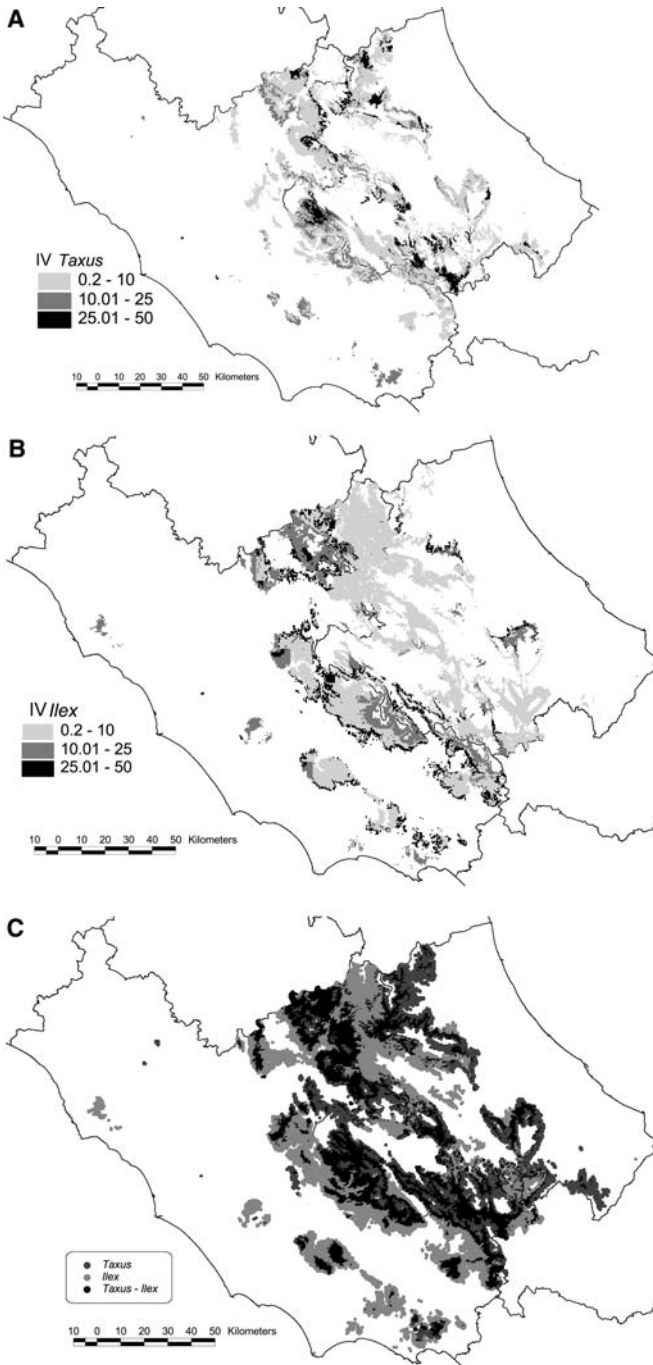


Fig. 5 Current potential distribution of **a** *Taxus* and **b** *Ilex* abundance measured as Importance Value and their overlapping areas (c)

Table 2 Potential areas and altitudinal distribution of *Taxus baccata* and *Ilex aquifolium*

	Potential area (ha)	Mean altitude (m)	Minimum altitude (m)	Maximum altitude (m)
<i>Taxus baccata</i>	436,500	1,300	900	1,750
<i>Ilex Aquifolium</i>	558,450	1,000	400	1,550
Overlapping area	167,500	1,200	950	1,500

Table 3 Model Summary of the stepwise multiple regression for *Taxus baccata* regeneration Index

	R	R square	Adjusted R square	Std. error of the estimate	
Regression	0.559	0.313	0.277	29,243.011	
	Unstandardized coefficients		Standardized coefficients	T	Sig.
	B	Std. error	Beta		
(Constant)	44,245.814	56,755.217		0.780	0.440
Nitrogen content	-20,052.876	6,318.598	-0.431	-3.174	0.003
Annual precipitation	65.777	29.592	0.302	2.223	0.032

Predictors: (constant), maximum temperature, total precipitation, basal area/ha

Table 4 Model Summary of the stepwise multiple regression for *Ilex aquifolium* regeneration Index

	R	R square	Adjusted R square	Std. error of the estimate	
Regression	0.794	0.632	0.591	20,028.874	
	Unstandardized coefficients		Standardized coefficients	T	Sig.
	B	Std. error	Beta		
(Constant)	-49,331.996	65,116.678		-0.758	0.445
Maximum temperature of the hottest month	8,348.282	2,191.403	0.450	3.810	0.001
Annual precipitation	-68.86	21.343	-0.382	-3.226	0.003
Basal area/ha	-901.079	240.787	-0.430	-3.742	0.001

Predictors: (constant), maximum temperature, annual precipitation, basal area/ha

1993), has not been recorded by us. *Taxus* can face these difficulties retreating to more inaccessible and steeper places and by means of asexual reproduction mechanisms such as, for example, the generation of stolons favoured by the weight of the dead beech leaves that push the low branches of *Taxus* into contact with the ground.

The observed ecological differences between beech woods with *Taxus* and those with *Ilex* and their effects in determining the spatial distribution and the regeneration of the two characteristic species required the elaboration of two differentiated strategies for conservation actions. In particular for *Taxus* two projects aimed at the construction of fences to protect its regeneration from livestock have already been implemented in the study area. For *Ilex*, which—thanks to its thorny leaves—is not affected by grazing, the introduction in forest management plans of indications for supporting traditional forest management practices, such as the civic use, or of programs for thinning the forest cover to maintain

gaps have been promoted. This in order to avoid the canopy closure, determined by the natural development into high forest, that can have a negative effect on the regeneration of *Ilex*. Only areas with high suitability for the two habitats inside protected areas have been chosen for implementing these conservation actions. In this way, the technical staff of the protected areas can be involved in the elaboration, implementation and monitoring processes. In conclusion, spatial models can be useful not only to define environmental niche of species and habitats but also to support the elaboration and the implementation of conservation measures. Spatial distribution models are gaining consensus as a useful tool for the conservation of biodiversity, but further efforts should be made to integrate it with other traditional investigation disciplines in order to further fill the blamed gap between modelers and practitioners.

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