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Population ecology of yew (*Taxus baccata* L.) in the Central Apennines: spatial patterns and their relevance for conservation strategies

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Abstract Understanding the ecological mechanisms that allow a species to transition from an occasional understory component to the dominant type in the forest canopy is essential for predicting future shifts in the distribution of species. We investigated this issue with regard to yew, also because mature yew trees have been reported to inhibit self-regeneration and seedling survival, prompting concerns for the long-term preservation of the species. Our objectives were (a) to quantify spatial patterns of yew (*Taxus baccata* L.) populations near the southern limit of the species' ecological distribution, (b) to determine the relationships between yew presence and topographic gradients, and (c) to answer the question of how yew regeneration is affected by such patterns and relationships. We analyzed three extensive yew populations (90–165 ha, including 3–12 thousand established individuals) that mostly occupy the understory of beech forests located in protected areas of the central Apennines (Italy). Overall, the realized niche of yew (either as established trees, saplings, or seedlings) followed the expected bell-shaped curve of a species response to an environmental gradient. Yew was mainly found at 1,000–1,600 m elevation on mesic exposures (north and west) and intermediate slopes (30–60%). Geostatistical analysis revealed that yew occurred in patches, as shown by variogram ranges of 40–110 m for yew tree basal area and regeneration abundance. Yew regeneration over the landscape was directly related to basal area of yew trees. At local scales ($\sim$10 m), presence of established trees favored regeneration in relatively less developed stands, whereas high density of mature yews suppressed regeneration. Healthy yew populations in beech forests had a minimum size of 0.5–3 ha. As yew density increased within these patches, regeneration dropped, so that yew conservation cannot be limited to presently occurring populations, despite the longevity and potential for vegetative reproduction of the species. Disturbance from grazing and wildfire was also found to impact yew survival. Long-term existence of yew in the Italian Apennines depends on maintaining and expanding old-growth beech forests that incorporate yew patches, and have a minimum continuous cover equivalent to a relatively undisturbed regime (10–50 ha).

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Introduction

Shifts in the ecological distribution of species, especially at their latitudinal or altitudinal extremes, are considered spatial fingerprints of climate change on biotic communities (Lenoir et al. 2008). Understanding the mechanisms that determine the geographical distribution of a species, and/or that allow a species to transition from an occasional understory component to the dominant type in the forest canopy (or viceversa), is therefore needed to predict future changes in ecosystem composition and function. As an example, the current distribution of yew (*Taxus baccata* L.) in the Italian Apennines, near its southernmost limit, is overall quite limited, both for its geographical range and for its population size, although in the past it was considerably greater, as shown by palinological, archival, and toponomastic studies (Giacomini and Fenaroli 1958; Marchesoni 1959; Salbitano 1988; Spada 2003). Almost two millennia ago, the ancient Greek botanist Dioscorides wrote in his book *De Materia Medica* that yew is similar to white fir (*Abies alba* Mill.) in terms of its needles and its size, thereby suggesting that in those times yew trees were on average considerably larger than today. Current yew populations in the Apennines are concentrated in remote localities and/or in conditions that have marginal value for human uses, such as steep slopes and rocky terrain (Paule et al. 1993). Individuals occur mostly as shrubs or as trees with polycormic stems, while tall, monocormic yew trees are rare. On the other hand, lush yew populations can still be found in regions with climate similar to the Apennines, but with considerably less anthropic disturbance (Spada 2003).

Yew size can be impressive with reported stem diameters exceeding 5 m, and heights up to 30 m (Büsgen et al. 1929; Paule et al. 1993; Thomas and Polwart 2003). This limit is apparently surpassed on mountains of northern Iran (Lesani 1999), and in the Hosta Reserve, a protected forest on the Russian coast of the Black Sea, where yew height may reach 40 m (Earle 2001). Yew is also supposed to live for more than a millennium (Bebber and Corona 1986; Larson et al. 2000; Molisch 1938), although in reality dendrochronological studies to date have proved a maximum longevity of about five centuries (Biondi 1992). As a long-lived, shade-tolerant species, yew is favored by lack of disturbance (such as wildfire), and is adapted to a range of edaphic conditions (Brzeziecki and Kienast 1994; Thomas and Polwart 2003). According to Leuthold (1998), yew occupies a peculiar role of “triple intermediate species.” In a typical ecological succession, yew is intermediate between pioneer and climax species; in a sociological sense, yew is mostly co-dominant in the lower canopy, half way between the overstory and the understory; in a morphophysiological sense it is intermediate between broadleaf and needle species.

Yew disappearance from many areas has been attributed primarily to anthropic factors rather than climatic change or reduced ecological fitness (Thomas and Polwart 2003). In fact, habitat fragmentation—which is a typical consequence of human activities—negatively impacts yew pollination and fitness because formation of viable seeds requires that individuals of both sexes co-exist on the landscape (yew is a dioeceous species). Land use changes are also likely to have contributed to shrinking yew habitat, through logging of old-growth stands, often in combination with grazing and burning. Such activities have transformed the forest landscape and affected vegetation dynamics, especially of shade-tolerant and late-successional species such as yew (Busing et al. 1995; Kwit et al. 2004). Hence, yew conservation should be viewed in the framework used for species threatened by human impacts (overexploitation, habitat loss and depletion, extinction cascades) that have reduced the abundance and range sizes of previously common species (Gaston and Fuller 2008).

While yew survival over geologic eras can be viewed as a product of adaptive strategies (Hageneder 2007), its decline over the last millennia is considered a widespread phenomenon, occurring over the entire biogeographical range of the species, hence causing concern for its preservation (Paule et al. 1993). Human impacts on yew populations provide an example of the intricate web of connections that determine species distribution and abundance. Since prehistoric times, yew wood has been valued for its strength and flexibility, which found many applications for building instruments and weapons (Hageneder 2007; Paule et al. 1993). In the Neolithic period, about 3000 BC, yew was intensely utilized, so much so that the archaeological site of Horgen Scheller (Switzerland) appears to have specialized in the production and trading of yew artifacts (Favre and Jacomet 1998); the impact of many human generations on such forest resources seems to have caused a gradual reduction in yew and white fir wood. Besides manufacturing and tool making, yew was also employed in phytotherapy, as a food supplement for domestic animals, and in religious ceremonies by multiple ancient cultures on separate continents (Voliotis 1986; Rikhari et al. 1998; Tirmenstein 2002; Schirone et al. 2003).

Clearly, there has been a change in attitude toward yew, considering that this species used to be planted mostly near cemeteries, and often considered a nuisance by foresters and mountain villagers (Hageneder 2007). Now yew is considered an indicator of healthy forest ecosystems, and also used in medical research because of compounds (such as taxol) with curative properties (Thomas and Polwart 2003). Concern for yew preservation has prompted the European Union (EU) to establish a priority habitat defined as "Apennine beech forests with *Taxus* and *Ilex*" (*9210; regulation 92/43). Support for conservation, restoration, and rehabilitation of this habitat was then provided through the LIFE program, which is EU's financial instrument for supporting environmental conservation projects (http://ec.europa.eu/environment/life/).

In recent years, several studies have expanded our knowledge of yew biology and ecology, but the circumstances under which this species develops from being an occasional component of woodland to becoming the dominant canopy species remain poorly understood (Thomas and Polwart 2003). Previous research indicated that yew recruitment was driven by factors at the micro-habitat scale (~ 100 m^2), but sapling establishment differed considerably between sites, suggesting that landscape factors such as topography (altitude, aspect, and slope), vegetation (canopy cover), and disturbance caused differences in germination and survival (García et al. 2005b). On the other hand, some studies have suggested that mature yew trees can prevent successful yew regeneration (Hulme 1996; Iszkulo and Boratynski 2006; Watt 1926). Hence, ecological pathways leading to the formation of pure yew forest stands are not well understood, and the limited number of such stands still remaining makes this task even more difficult. Landscape-level studies of forests where yew currently thrives are then critical for understanding how heterogeneous yew patches should be maintained. A similar argument was recently put forth for holly (*Ilex* sp.) populations (Arrieta and Suárez 2006).

Yew ecology at the southern limit of its distribution often relies on studies (e.g., Dhar et al. 2007; Svenning and Magård 1999) performed in areas geographically and biologically distant from those where they are applied. This, in part, depends on the fact that woodlands dominated by *Taxus baccata* L. are largely restricted to southern England and western Ireland (Perrin et al. 2006; Watt 1926). We have, however, been able to identify areas in the central Apennines that are particularly suitable for obtaining accurate information on spatially explicit mechanisms of yew regeneration and establishment. Our objectives were (a) to analyze size distribution of yew and beech populations at the study sites, (b) to quantify spatial patterns of yew (*Taxus baccata* L.) populations near the southern limit of the species' ecological distribution, (c) to determine the relationships between yew presence and topographic gradients, and (d) to answer the question of how yew regeneration is affected by such patterns and relationships. This project was aimed at understanding the mechanisms responsible for shrinking yew populations, thereby providing a guide for its preservation, while at the same time addressing the larger issue of the processes that control species distribution and abundance over periods of time (i.e., decades to centuries) that are relevant for assessing the impact of future climatic change. We aimed at quantitatively representing spatial relationships between ecological parameters and geographical gradients (elevation, slope, and exposure), together with the relationships between regeneration and presence of mature individuals, using an approach that could account for both micro- and macro-habitat differences in areas near the southern limit of yew distribution.

Materials and methods

Study area

Study sites were located within montane forests of the central Apennines dominated by European beech (*Fagus sylvatica* L.) that are currently managed as

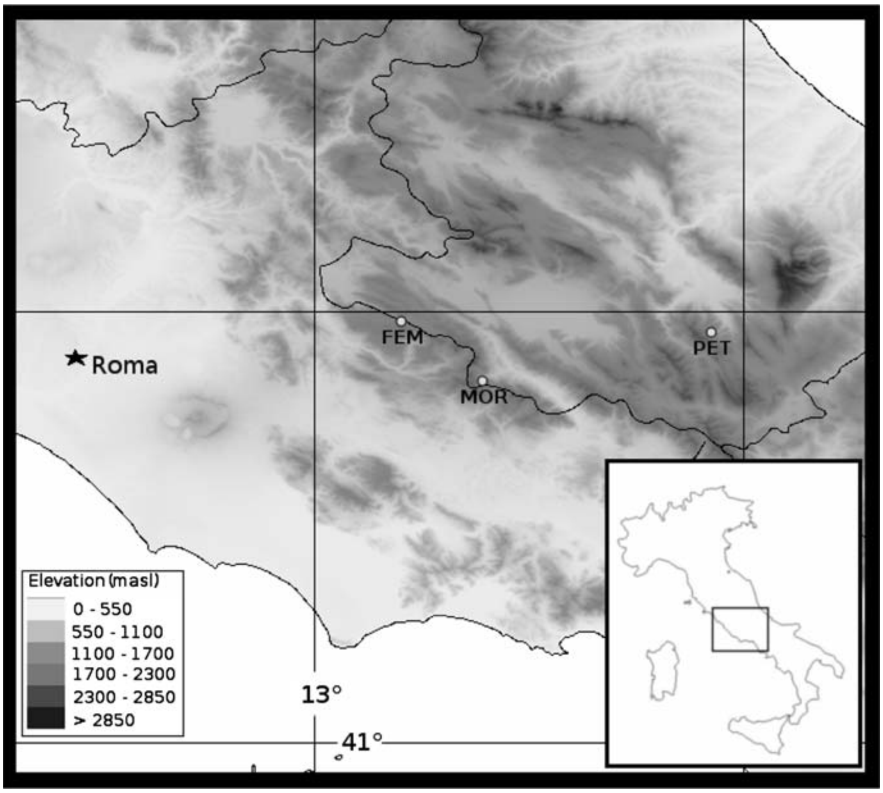

Fig. 1 Map showing the location of the three yew (*Taxus baccata* L.) populations (*small circles*), together with terrain elevation (*shading*)

protected areas ("Riserve Regionali"; Fig. 1). Although human impacts have ranged from selective logging of beech and yew to introduction of livestock, the strongest anthropic pressure at our study sites was truly restricted to the period when mechanized equipment became commonly available (1950s to 1970s in this region), because shortly thereafter these areas became protected, while in earlier times they were scarcely populated and isolated from communication routes (Presutti Saba 2005). Climate regime at the study areas (defined using data compiled over 1° × 1° grid cells, Brunetti et al. 2006) can be described as Mediterranean montane (oro-Mediterranean) with cold snowy winters and precipitation minima during summer. At the geographic baricenter (41°55′12″N, 13°30′36″E, 1,325 m asl) mean annual temperature was 8.1°C, and mean total annual precipitation was 1,500 mm (June–August: 206 mm). Yew normally occurred as an understory species below the beech canopy, so that forest stands were defined as EU Conservation Habitat n. 9210*, "Apennines beech forest with *Taxus* and *Ilex*."

The yew population of Pettorano sul Gizio (PET; 41°57′06″N, 13°55′54″E) is located within the Riserva Naturale Regionale "Monte Genzana—Alto Gizio," in L'Aquila Province, Abruzzi Region. Elevation ranges from 1,000 to 1,500 m asl, geological substrate is mostly calcareous, and topography is highly variable with rock outcrops up to 2–3 m high. At lower elevations, the beech forest used to be managed as coppice with standards (last logged in the 1950s), while at higher elevations the beech forest is uneven aged and less disturbed. Co-occurring tree species, at this site as well as the other two study areas, include maples (*Acer platanoides* L. and *A. pseudoplatanus* L.), ash (*Fraxinus excelsior* L.), lindens (*Tilia* spp.), and hop-hornbeam (*Ostrya carpinifolia* Scop.).

The Morino site (MOR; 41°50′20″N, 13°24′04″E) is located within L'Aquila Province too, but in a different protected area, the "Riserva Naturale Zompo Lo Schioppo." At this site we focused on the largest and most structured yew population, whose location is appropriately called "Tassiti" ("tasso" is the Italian word for yew), on the northern slopes of Monte Ferrera, between 1,100 and 1,500 m asl. Geological substrate is mostly calcareous, but topography is less variable than at the PET site. Vegetation is dominated by a mature beech forest with the oldest trees reaching 200–250 years.

The yew population at Femmina Morta (FEM; 41°58′43″N, 13°12′07″E) was the largest one we studied. It is located within the Rome Province, Latium Region, in the "Parco Naturale Regionale dei Monti Simbruini." Elevation ranges from 1,200 to 1,650 m asl, geologic substrate is calcareous, and topography varies with elongated rock outcrops and carsic formations where yew appears to concentrate. Vegetation is dominated by a beech forest characterized by even-aged groups (up to 100–150 years of age), and by a history of irregular and patchy timber harvesting.

Field surveys

In September–December 2003, we quantified forest structure at the study areas using randomly located circular plots with a 10-m radius. A total of 15 plots were located at MOR, 15 at PET, and 20 at FEM. Within each plot, we measured (a) stem diameter at breast height (DBH) for all trees (defined by DBH $\geq$3 cm), (b) height of the tallest beech and yew tree, and (c) height of a randomly selected subset of healthy beech and yew trees. The beech subset consisted of 50 trees at PET, 57 at MOR, and 110 at FEM; the yew subset included 47 trees at PET, 52 at MOR, and 67 at FEM; height–DBH curves were then developed using a semi-logarithmic function. Regeneration, i.e., woody plants with DBH <3 cm, was also tallied by species, and subdivided into height classes. Seedlings (R0) had height <5 cm; saplings had height $\geq$5 cm, and were further subdivided into three height classes: 5–20 cm (R1), 20–100 cm (R2), and >100 cm (R3).

During January–June 2004, we measured the yew populations based on 10 × 10 m grid cells. Within each cell, we recorded yew established trees (ET) using a lower DBH threshold (DBH $\geq$1 cm) than in the circular plots because yew can begin pollination and fructification at lower sizes than beech (Svenning and Magård 1999). We did not quantify the amount of yew individuals by sex (Iszkuło 2001) because other studies had shown a well balanced ratio of male and female trees (Thomas and Polwart 2003), even in the Apennines (Schirone et al. 2003). Sapling (height $\geq$5 cm; DBH <1 cm; no height classes were used) abundance was defined by class: S0, no saplings; S1, or scarce (<10 saplings per cell, equivalent to <1,000 ha^{-1}); S2, or intermediate (between 10 and 25 saplings per cell, equivalent to 1,000–2,500 ha^{-1}); and S3, or abundant (>25 saplings per cell, equivalent to >2,500 ha^{-1}). Seedlings (height <5 cm) were also counted within each cell because seedling density is used as an indicator for monitoring ecosystem response to rehabilitation actions prescribed in the LIFE project (Project n. 03/NAT/000160).

Laboratory analyses

Forest structure was quantified for all woody species, and separately for yew, by means of size distributions by DBH class, height–DBH curves, and stand basal area (BA). Stature was calculated by averaging the height of the three tallest trees at each site. Geographical analyses were performed using ESRI ArcView software version 3.1. Topographic maps at 1:10,000 scale for the Latium and Abruzzi regions were digitized to produce a Digital Elevation Model (DEM). Cell coordinates, recorded in the field using a Global Positioning System (GPS) receiver, were then plotted on the DEM for each study area to quantify cell elevation, exposure, and slope. To summarize the data, we used the term "overall" for describing the entire area (including cells without yew) occupied by the yew population. The overall perimeter of yew distribution was drawn as a polygon that connected the outer cells with yew plants (regardless of their size). Mean cell density and mean cell basal area for yew trees (ET, DBH $\geq$1 cm) were computed using only grid cells containing yew. Numerical data analysis, including correlation (Pearson's sample coefficient r), was performed using the base R statistical software version 2.6.2 (R Development Core Team 2008). Ordinal logistic regression between yew sapling abundance class and yew basal area was calculated using the R package Design; χ^2 likelihood ratio test (LR) with one degree of freedom was performed to assess the model goodness-of-fit.

Environmental gradient analysis was based on 20 m classes for elevation, 5% classes for slope, and 15° classes for exposure. For each of those classes, we computed the number of cells with established yew trees (ET), the number of cells with yew regeneration (sapling abundance classes S1–S3 or just classes S2 and S3), the number of cells with both saplings (S) and established trees (ET), and the total basal area of yew trees (ET). Frequency distributions by environmental gradient were then smoothed using a 5-point moving average, and the goodness-of-fit was measured by the coefficient of determination

(R^2). Gradient data analyses and plots were performed using Microsoft Excel 2002.

Spatial patterns were further investigated using variograms to test for spatial dependence (Fortin and Dale 2005) in yew sapling abundance (S classes) and basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$). Besides univariate variograms, which are based on values of the same variable at different locations, we also used bivariate variograms (called cross-variograms), which consider values of two variables (in this case yew basal area and sapling abundance) at different locations to find how they co-vary spatially (Dimov et al. 2005). Unlike a variogram, a cross-variogram can take negative values (see Maestre et al. 2005) when an increase of one variable corresponds, on average, to a decrease of the other variable for a given separation distance. Sample variograms and cross-variograms were estimated using 10-m distance classes up to a maximum distance of 200 m. The coefficient of determination, R^2, was examined to determine how the model variogram fitted the sample variogram. Variogram parameters (nugget, range, and sill) computed from the fitted theoretical model were used for comparing variables and sites. The amount of spatial dependence (SPD; %) was obtained from the ratio between the sill and the sum of nugget and sill. The software package used for geostatistical analysis was GS^+ version 5.3b (Gamma Design Software, LLC, Plainwell, MI).

At the Morino (MOR) site it was possible to identify a "core" yew population, defined by cells with yew BA $\geq 30\ \mathrm{m}^2\ \mathrm{ha}^{-1}$ whose centers were at distances ≤ 20 m from each other. The perimeter of this core group was drawn in ESRI ArcView using a 45 m buffer to account for edge effects. The rest of the Morino yew population located north of the "core" was then considered a "subtotal" population. Separate structural and spatial analyses were performed on the "core" and "subtotal" yew subpopulations. Given the smaller spatial extent of the "core," variograms and cross-variograms for this subpopulation were estimated up to a maximum distance of 120 m.

Results

Stand structure from circular plots

Beech stands that included yew exhibited a DBH distribution typical of uneven-aged forests. After log-transformation, beech density declined almost linearly with increasing DBH class (Fig. 2). Diameter distribution by DBH classes, as well as height–DBH curves (Fig. 3a), reflected the different management histories at the three study sites. Pettorano (PET), where beechwoods were mostly managed in the past as coppice with standards, differed from the other two study areas, formerly managed as high forest. PET had the highest beech density (the numerous small stems are pollards) and the lowest beech basal area (Table 1). Maximum beech DBH and stature are lower at PET and higher at the other two sites.

In all stands yew occupied the forest understory, growing beneath beech trees (Fig. 3a). Yew accounts for 21% of tree density at MOR and for 32% at PET and FEM (Table 1); yew basal area amounts to 27, 14, and 12% of total tree basal area at MOR, FEM, and PET, respectively. Yew log-frequency distribution (Fig. 2) shows a linear decline at PET, and a nonlinear, but still monotonic, decline at FEM. At MOR, yew log-density first declines as DBH increases (until about 15–25 cm), but then rises to a secondary peak, corresponding to a DBH of 40–45 cm. Yew stems with DBH >20 cm were uncommon at PET suggesting a simplified yew population compared to the other two sites. MOR is characterized by the highest yew structural complexity with an appreciable presence of large yew trees (DBH >65 cm). There are no special site differences in the yew height–DBH curves (Fig. 3a). However, maximum yew height was 12 m at PET, 15 m at FEM, and 20 m at MOR.

A comparison between the height–DBH relationship observed at our study areas and that identified for another species (*Taxus brevifolia*) or for the same species in other areas (Fig. 3b) reveals an overall similarity. In particular, the *Taxus baccata* populations we studied, which are now characterized by a large proportion of damaged or irregular crowns (Fig. 1S supplemental material), closely followed the reported height–DBH curve for damaged *Taxus brevifolia* (Ishii et al. 2000).

Regeneration (i.e., seedlings, R0 and saplings, R1–R3, pooled together) was highly variable among plots at each site, and even more so at the Morino (MOR) study area, as shown by the higher standard error (Table 1). The greatest yew regeneration was found at the MOR site, and the smallest at PET. Regeneration at PET was slightly higher for yew than for beech (53 and 47% of total, respectively), while it

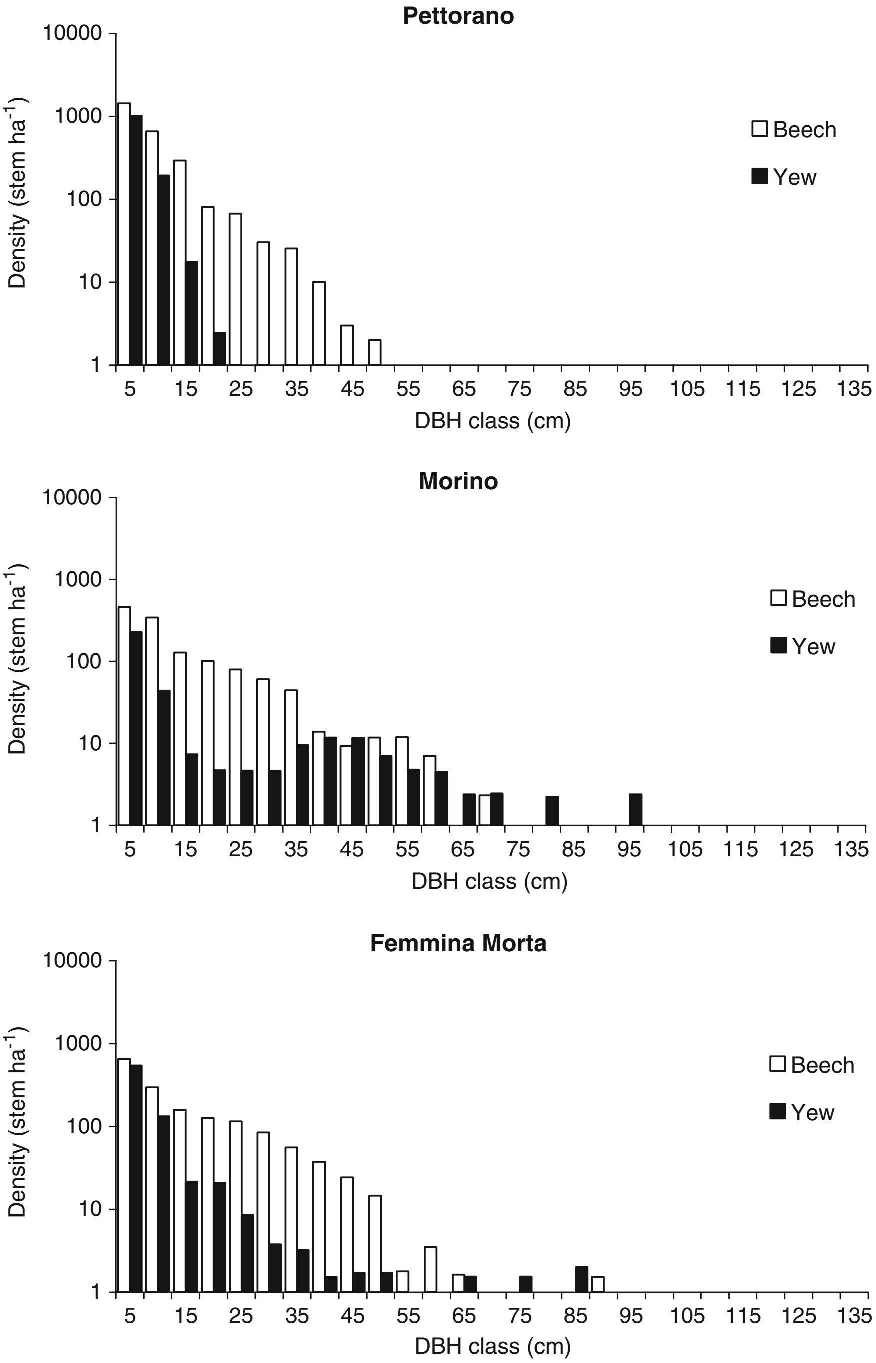

Fig. 2 Stem density (logarithmic scale) of beech and yew by DBH class. These values were computed from trees included in circular plots with a 10-m radius located at each study area. Every DBH class is 5-cm wide, except for the smallest one, which includes stems with $3 \leq \mathrm{DBH} \leq 7.5$ cm

was less for yew than for beech at the other two sites (MOR: 41 vs. 59% of total; FEM: 34 vs. 66%). At MOR and PET, yew seedlings were more abundant than at FEM, so that at MOR and PET density of yew seedlings exceeded density of beech seedlings.

Yew regeneration at MOR and FEM was not correlated with the overstory structure, i.e., tree density and basal area either by species or total (Table 1S supplemental material). On the other hand, at PET we found a direct relationship between yew regeneration and yew overstory (Table 1S supplemental material). To better understand how these relationships varied at multiple spatial scales, from microhabitat to population (García et al. 2005b), we

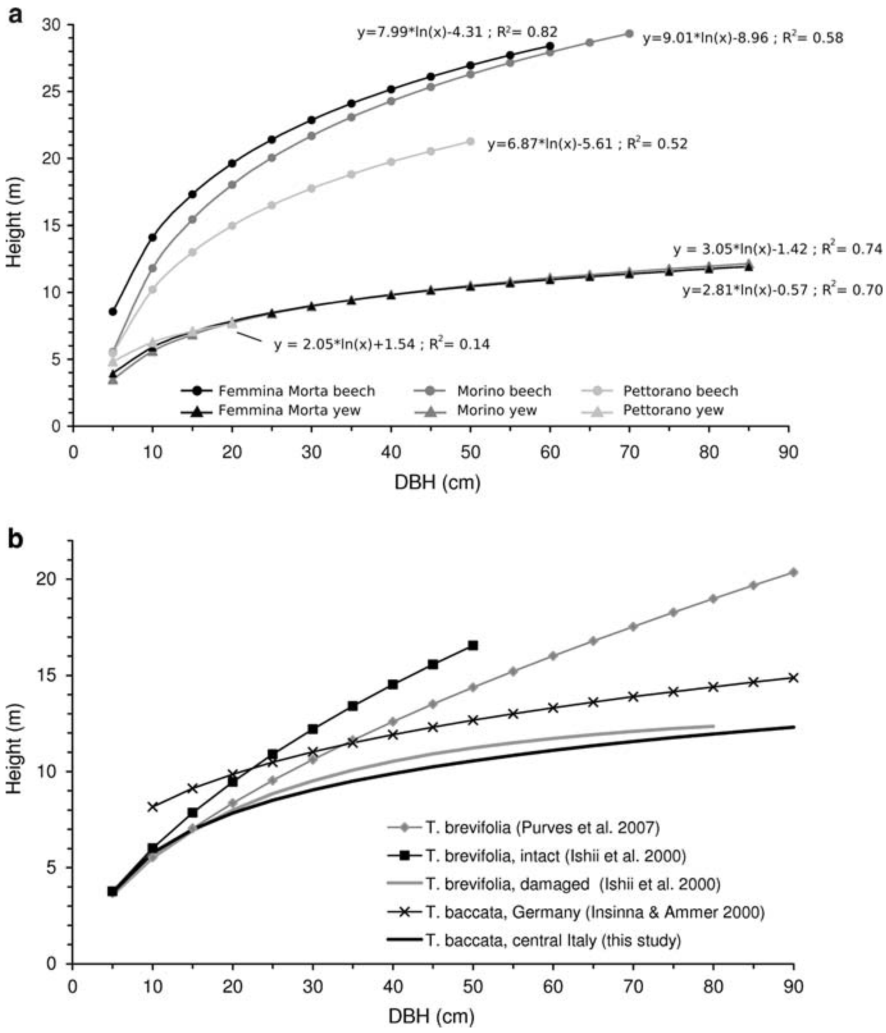

Fig. 3 **a** Height vs. DBH curves of beech and yew computed from the circular plots at the three study areas. **b** Height vs. DBH curve for yew at Morino and Femmina Morta (*solid black line*) compared to curves developed for the same species or for other *Taxus* species in different studies

then performed a more detailed yew population analysis.

Yew population structure from grid cells

The three study areas are characterized by extensive yew populations, the largest one at FEM and the smallest one at PET (Table 2 and Fig. 4a–c). The number of established yew trees (ET) varies from 3,079 at MOR (total basal area of 94 m^2), 8,974 at PET (total basal area of 26 m^2), and 12,838 at FEM (total basal area of 116 m^2). The PET site has the highest overall ET density and the lowest basal area (Table 2), whereas MOR has the lowest density but the highest basal area; at FEM both density and total basal area are in intermediate positions.

Yew density in grid cells occupied by yew trees is higher at FEM than at PET, contrary to yew density computed from all cells. Maximum yew density does not exceed 4,000 stem ha^{-1} at MOR, while it reaches 7,000 stem ha^{-1} at PET and FEM. At all sites, grid cells with yew (either as trees, saplings, or seedlings) correspond to 9–11% of the overall number of cells (Table 3). At PET only 0.03% of all grid cells had total yew basal area >30 m^2 ha^{-1} (Table 3), and 95% of all grid cells with ET have yew basal area <10 m^2 ha^{-1}. At MOR and FEM yew basal area in a single grid cell may be as high as 200 m^2 ha^{-1}, but 80% of all grid cells with ET at MOR, and 65% at FEM, has yew basal area <10 m^2 ha^{-1}.

Census data, expressed as log-frequency size distributions by DBH class for cells containing

Table 1 Abundance (mean ± SE) of beech and yew established trees (DBH ≥3 cm) and regeneration (seedlings and saplings, DBH <3 cm) computed from the circular plots at each study area

Site	Code	Species	Established trees				Regeneration				
			Density (N ha^{-1})	Basal area (m^2 ha^{-1})	Stature (m)	D_s (cm)	Density of seedlings + saplings (N ha^{-1})	Density by height (h) class (N ha^{-1})			
								R0[a] (h < 5 cm)	R1 (5 < h<20 cm)	R2 (20 < h<100 cm)	R3 (h > 100 cm)
Pettorano	PET	Beech	2,611 ± 376	25.16 ± 1.30	24	40	344 ± 89	45 ± 18	130 ± 47	57 ± 32	112 ± 26
		Yew	1,232 ± 225	3.42 ± 0.78	10	14	385 ± 70	142 ± 31	57 ± 15	50 ± 15	136 ± 31
Morino	MOR	Beech	1,272 ± 171	32.61 ± 2.47	33	56	1,118 ± 293	105 ± 49	434 ± 141	225 ± 139	355 ± 127
		Yew	348 ± 66	12.22 ± 4.80	14	75	761 ± 224	351 ± 102	124 ± 49	135 ± 52	151 ± 54
Femmina Morta	FEM	Beech	1,579 ± 152	41.19 ± 2.49	34	52	1,058 ± 204	113 ± 72	59 ± 28	99 ± 43	788 ± 171
		Yew	745 ± 131	6.68 ± 2.09	14	74	550 ± 81	45 ± 15	103 ± 31	172 ± 22	231 ± 49

N Number, *Stature* mean height of the three tallest trees at the site, D_s mean diameter at breast height of trees used to calculate stature

[a] Seedlings belong to this height class

established yew trees (Fig. 5), agreed with circular plot data (not shown). Still, census data better quantified the range of variability because they captured the largest individuals, as shown by greater frequency of large trees (compare Fig. 5a to Fig. 2). The range of DBH was greatest at MOR, where yew DBH reached 135 cm; at FEM yew DBH did not extend beyond the 95 cm class, and at PET it did not exceed the 35 cm one. At MOR the distribution of basal area by size (DBH) class was roughly bell-shaped with a wide peak corresponding to the 60–70 cm DBH classes (Fig. 5a). At PET and FEM, however, basal area was concentrated in the lower size classes, so that the frequency distribution was strongly skewed.

At the Morino (MOR) site, the "core" group (Fig. 4b) occupied an overall area of 6.28 ha characterized by the highest yew basal area we measured (about 37 m^2 ha^{-1} considering cells containing yew). The "subtotal" group (overall area: about 100 ha) included the fairly continuous yew stands located north of the "core" group (Fig. 4b) with quite lower basal area (8 m^2 ha^{-1} using cells containing yew). The area sum of these two groups was less than the overall MOR population (124 ha) because it did not include its southernmost portion. Density of established yew trees (ET) was not very different in the "core" and "subtotal" groups (375 and 408 stems ha^{-1}, respectively), although the density (number per ha) of cells with ET in the "core" group was almost thrice that in the "subtotal" group (Table 3b). Cells with high yew basal area (≥30 m^2 ha^{-1}) were separated by a greater distance in the "subtotal" group than in the "core" one, as expected given the definition of "core" group. Medium–large yew trees were more abundant in the "core" group, as reflected in the basal area distribution (Fig. 5b), with 46% of total BA included in the 60–70 cm DBH classes, and 74% in the 50–80 cm ones.

Although overall yew basal area at a site was directly related ($r = 0.99$, $P = 0.02$) to the number of grid cells that contained yew regeneration, this relationship became more complex when viewed on a cell-by-cell basis. At the three sites, most grid cells containing regeneration include low numbers of saplings (more than 85% of cells at MOR and FEM, and almost all at PET, fall in class 1). At MOR and FEM grid cells that contain both established trees (ET) and regeneration (saplings and seedlings) are

Table 2 Demographic attributes of the three yew populations, obtained from the census of 10 × 10 m grid cells

Demographic attribute	Pettorano (PET)	Morino (MOR)	Femmina Morta (FEM)
Number of established trees	8,974	3,079	12,838
Overall area covered (ha)	90	124	165
Overall ET density (stem ha^{-1})	100	25	78
Overall basal area (m^2 ha^{-1})	0.29	0.76	0.70
Mean cell ET density (stem ha^{-1})	974	394	1,162
Mean cell basal area (m^2 ha^{-1})	2.88	12.07	10.51

Overall population density and basal area were computed considering all cells (including those without yew) inside the perimeter occupied by the yew population (see Materials and methods). Mean cell density and mean cell basal area were computed using only grid cells containing yew trees (trees: DBH ≥1 cm)

about 64 and 62%, respectively, of all cells that include yew regeneration, but at PET this proportion is much higher (92%). When present, seedlings were usually not too dense, with values of 250 ± 310 ha^{-1} at PET, 530 ± 280 ha^{-1} at FEM, and 450 ± 380 ha^{-1} at MOR (see Table 1 for a comparison with plot-based data).

Grid cells with no yew saplings (S0) were often characterized by higher yew basal area than those with saplings, especially when comparing PET vs. FEM and MOR-core vs. MOR-subtotal (Fig. 2S supplemental material). Logistic regression results were statistically significant and illustrated the likelihood of yew regeneration with increasing yew basal area (Fig. 6). At the PET site, which is characterized by smaller yew individuals (Tables 2 and 3a; Figs. 2 and 5), increasing yew basal area corresponded to a greater chance of abundant saplings (Fig. 6a; logistic regression LR = 54.23, $P < 0.001$). At MOR and FEM, where more cells had abundant saplings (S2 and S3; Table 3a), increasing yew basal area was inversely related to regeneration (FEM: Fig. 6b; logistic regression LR = 105.97, $P < 0.001$; MOR: logistic regression LR = 11.11, $P < 0.001$). At MOR, the “core” group was characterized by a higher density of grid cells containing yew regeneration (Table 3b), but by a low presence of grid cells with abundant yew saplings (S3 was absent and S2 occurred in 4% of grid cells with saplings). While the “core” yew sapling abundance was negatively related to yew basal area (Fig. 6b; logistic regression LR = 35.99, $P < 0.001$), the “subtotal” yew sapling abundance and basal area were positively related (Fig. 6a; logistic regression LR = 9.65, $P < 0.01$).

Gradient analyses

Yew population structure followed irregular bell-shaped patterns in relation to gradients of elevation, aspect, and slope at all study areas (Fig. 7). The smoothing applied to the raw frequency distributions usually had high R^2 (0.8–0.9), with the exception of abundant regeneration (S2 + S3 = sapling classes 2 and 3), which often showed much lower R^2 values, especially at PET, where most grid cells fell in class 1 (Fig. 3S supplemental material).

The number of grid cells containing yew established trees (ET), as well as yew basal area, reached a peak for higher elevations at FEM than at the other two sites (Fig. 7). At each site, the elevation range occupied by yew was similar (about 400–500 m), but the actual elevation and the optimum (peak) varied according to longitude, increasing from east to west. Maxima at PET were reached at approximately 1,150–1,250 m asl for ET, and 1,250 for BA; at MOR they corresponded to about 1,300 m asl, being slightly less for ET and slightly more for BA; at FEM both ET and BA peaked at about the same elevation, roughly 1,470 m asl. At MOR and FEM the changes in sapling abundance (S) with elevation followed those of ET (and, to a slightly lower extent, those of BA). At PET, on the other hand, the number of cells with saplings (S) was consistently less than those with ET, so that sapling abundance followed more closely the BA curve. At MOR, and to some extent also at FEM, the greatest frequency of cells with abundant regeneration (sapling classes S2 + S3) was found about 50–100 m higher in elevation than the greatest frequency of cells with established trees (Fig. 3S supplemental material). This pattern also

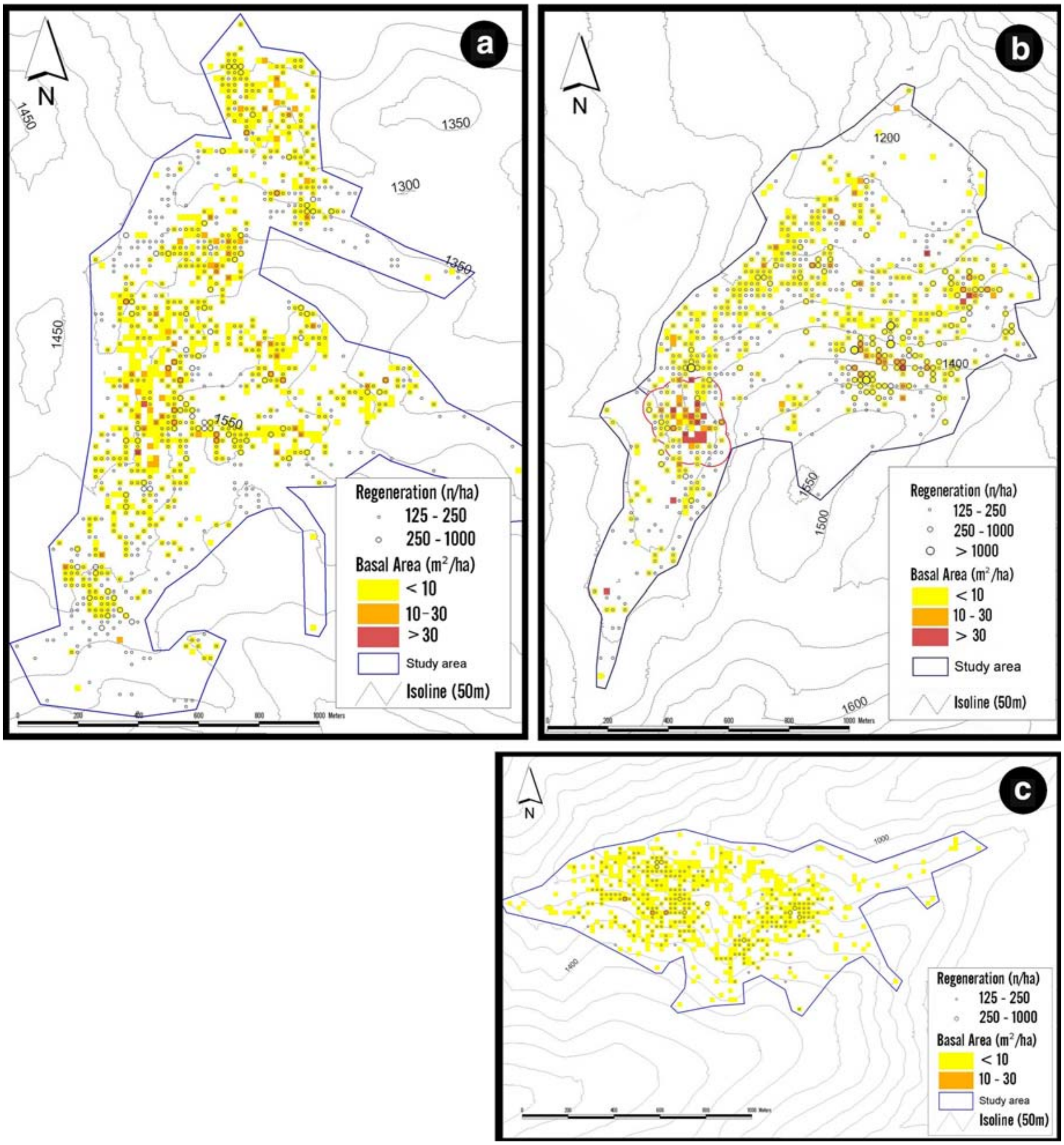

Fig. 4 Census maps of the yew population at **a** Femmina Morta (FEM), **b** Morino (MOR; the "core" group is the nucleus delineated inside the population perimeter, while the "subtotal" group includes stands to the north and east of the "core" group), and **c** Pettorano (PET). Basal area and regeneration were summarized by aggregating data collected on 10 × 10 m cells into 20 × 20 m cells. Also, to compute total regeneration in each 20 × 20 m cell, the number of yew seedlings was added to the central value of the sapling abundance class

occurred in the distribution of yew maximum DBH and height with respect to elevation (data not shown).

With regard to terrain slope, the highest density of grid cells containing yew established trees (ET), showing the greatest regeneration (S), and having the largest basal area (BA), were found on steeper slopes going from west to east across central Italy (Fig. 7). At PET the peak was reached around 70%, at MOR it was 40–50% (closer to 60% for BA), and at FEM it was 30–40%. Therefore, changes in sapling

Table 3 (a) Summary of grid cells that included yew at the three study areas. (b) The same summary at the Morino site for the "core" and "subtotal" yew populations (see text for details on the definition and area of these groups)

	Variable	N cells with yew	Overall cell density (N ha^{-1})	Mean cell distance (m)
(a) Site				
PETTORANO	Entire population[a]	948	10.50	13.9
MORINO	Entire population[a]	1,119	8.87	15.6
FEMMINA MORTA	Entire population[a]	1,511	9.15	14.3
PETTORANO	Established trees	921	10.21	14.0
MORINO	Established trees	782	6.29	17.8
FEMMINA MORTA	Established trees	1,105	6.69	15.4
PETTORANO	BA $\geq 30\ m^2\ ha^{-1}$	3	0.03	101.3
MORINO	BA $\geq 30\ m^2\ ha^{-1}$	100	0.80	34.5
FEMMINA MORTA	BA $\geq 30\ m^2\ ha^{-1}$	93	0.56	45.2
PETTORANO	Saplings (S1 + S2 + S3)	345	3.83	18.5
MORINO	Saplings (S1 + S2 + S3)	885	7.12	17.2
FEMMINA MORTA	Saplings (S1 + S2 + S3)	1,083	6.56	16.6
PETTORANO	Abundant saplings (S2 + S3)	5	0.06	130.2
MORINO	Abundant saplings (S2 + S3)	106	0.85	31.5
FEMMINA MORTA	Abundant saplings (S2 + S3)	73	0.44	35.0
PETTORANO	Seedlings	47	0.51	30.5
MORINO	Seedlings	225	1.81	27.5
FEMMINA MORTA	Seedlings	126	0.76	31.2
(b) MORINO				
Core	Entire population[a]	132	21.02	11.0
Subtotal	Entire population[a]	891	7.16	15.7
Core	Established trees	102	16.24	12.3
Subtotal	Established trees	626	6.27	17.8
Core	BA $\geq 30\ m^2\ ha^{-1}$	43	6.85	13.7
Subtotal	BA $\geq 30\ m^2\ ha^{-1}$	48	0.48	50.1
Core	Saplings (S1 + S2 + S3)	91	14.49	13.7
Subtotal	Saplings (S1 + S2 + S3)	711	7.12	17.1
Core	Abundant saplings (S2 + S3)	4	0.64	88.7
Subtotal	Abundant saplings (S2 + S3)	99	0.99	28.6
Core	Seedlings	70	11.15	13.1
Subtotal	Seedlings	118	1.18	33.6

N number, *BA* basal area, *S1, S2, S3*, sapling abundance classes, *mean distance* mean first nearest neighbor distance (considering cell centers)

[a] Cells with the presence of established trees, saplings and/or seedlings

abundance (S) with slope at the three sites mimicked those of tree density (ET).

At the three study areas, yew stands on northern exposures were characterized by the highest density of established trees (ET) and by the greatest regeneration (S; Fig. 7). The range of terrain aspects occupied by yew was small at PET (from NW to NE), became wider at MOR (from W to E), and even more so at FEM (from SW to SE), thereby showing the same east-to-west increase that was found for elevation. The maxima of ET were relatively narrow at PET and MOR, while FEM showed a broad plateau rather than a peak. The maximum height (H max) of yew was found on northern exposures at PET, it was about the same from west to east exposures (but dropped off quickly for southern exposures) at MOR,

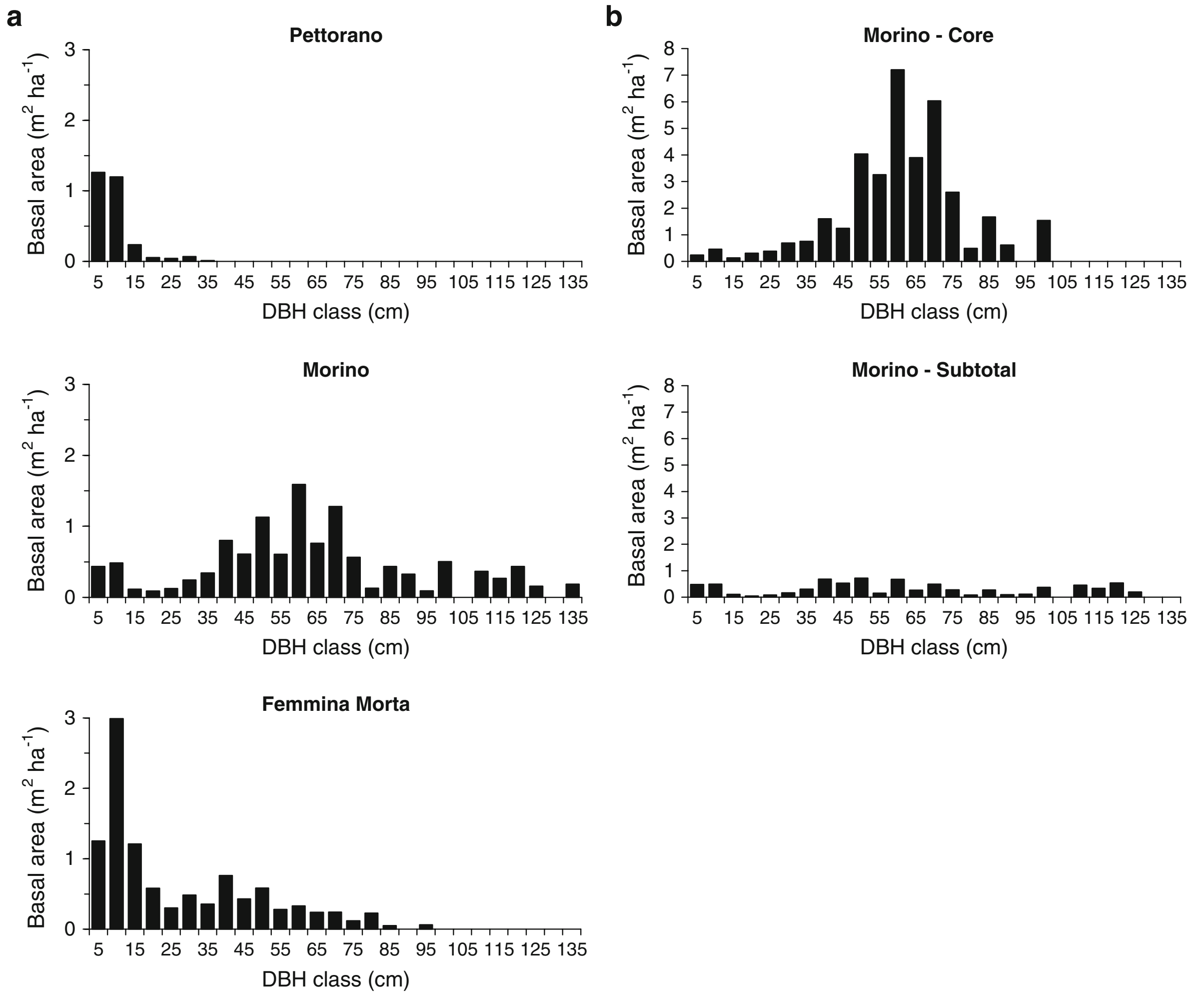

Fig. 5 **a** Basal area of yew by DBH class at the three sites. These values were computed from the yew population census on a 10 × 10 m grid, and were referred to the total area of grid cells containing established trees (ET). Every DBH class is 5-cm wide, except for the smallest one, which includes stems with 1 ≤ DBH ≤ 7.5 cm. **b** Basal area of yew by DBH class at the Morino site: comparison between "core" and "subtotal" populations (the definition is provided in the text, and their location is shown in Fig. 4b)

and it changed slightly with exposure at FEM (data not shown). At PET, basal area showed a peak similar to ET (i.e., for northern exposures), but at the other two sites yew basal area reached a maximum on western exposures. Most regeneration at MOR and PET was located on north-facing slopes; at FEM regeneration occurred over a greater range of aspects, from northwest to northeast.

Spatial patterns

Mean distance between the centers of grid cells with certain properties was 14–18 m for yew trees and sapling presence, and about 30 m for seedlings (Table 3a). High density of yew (BA $\geq$30 m^2 ha^{-1}) and greater number of saplings (class $\geq$2) occur more frequently, and over shorter distances, at MOR and FEM than at PET. Within the Morino (MOR) site, the "subtotal" group usually resembles the overall population with regard to mean distance between the centers of grid cells with specific features (Table 3b). The "core" group, on the other hand, shows a reduction in such mean distance, except for sapling abundance (class $\geq$2), for which it becomes considerably longer.

For variogram analysis, the nugget plus spherical model was usually chosen to represent spatial

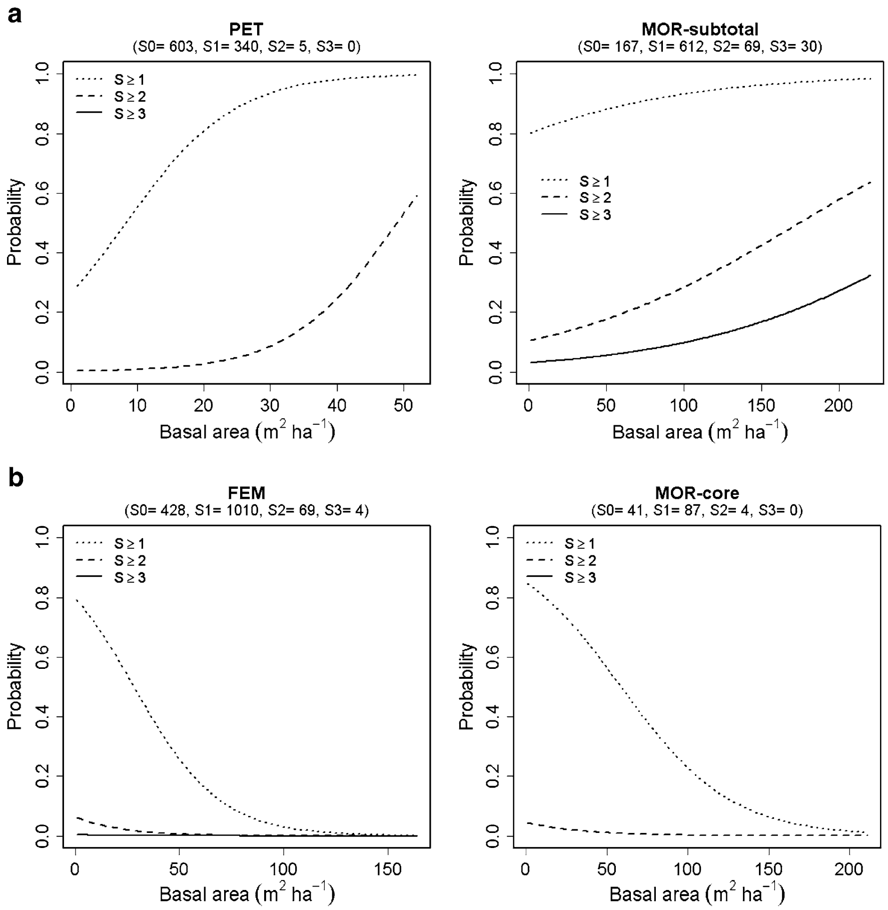

Fig. 6 Predicted probability of yew sapling abundance class (S) given yew basal area (data from 10 × 10 m cells) based on ordinal logistic regression. **a** Direct relationship between yew basal area and regeneration. **b** Inverse relationship between yew basal area and regeneration

continuity of yew BA and sapling abundance (Figs. 8 and 9), based on the R^2 value of the model fit to the sample omni-directional variogram (Table 4). The amount of spatial dependence (SPD) indicated by variogram models was always greater for yew basal area than for sapling abundance and reached a maximum at the MOR site. Within MOR, the “core” group had a much larger SPD for sapling abundance than anywhere else, suggesting that regeneration has occurred with greater spatial homogeneity. According to the estimated range parameters, MOR is characterized by smaller groups with similar BA than the other two sites. In addition, at MOR the similarity between yew BA extends over shorter distances than the similarity between sapling abundance, whereas the opposite pattern emerged at the other two sites (Table 4a, Figs. 8 and 9). In fact, the “core” group at MOR showed the longest range of spatial dependence for sapling abundance than any other site.

Sample cross-variograms between yew BA and sapling abundance were best fit by a spherical model at PET and FEM, although the spatial co-dependence of these two variables showed opposite patterns (Table 4b, Fig. 8). This result is in agreement with the opposite association (positive at PET and negative at FEM) that was found between yew basal area and yew regeneration. At MOR, on the other hand, the sample cross-variogram is U-shaped (Fig. 8), possibly due to the different spatial co-dependence observed in the “core” and “subtotal” groups (Table 4b, Fig. 9). In other words, the overall MOR cross-variogram may be dominated by the “core” pattern (decreasing) for shorter separation lags and by the “subtotal” pattern (increasing) for longer separation lags.

Discussion

Stand structure and regeneration

The yew populations considered in this study are characterized by a geographical extension, density,

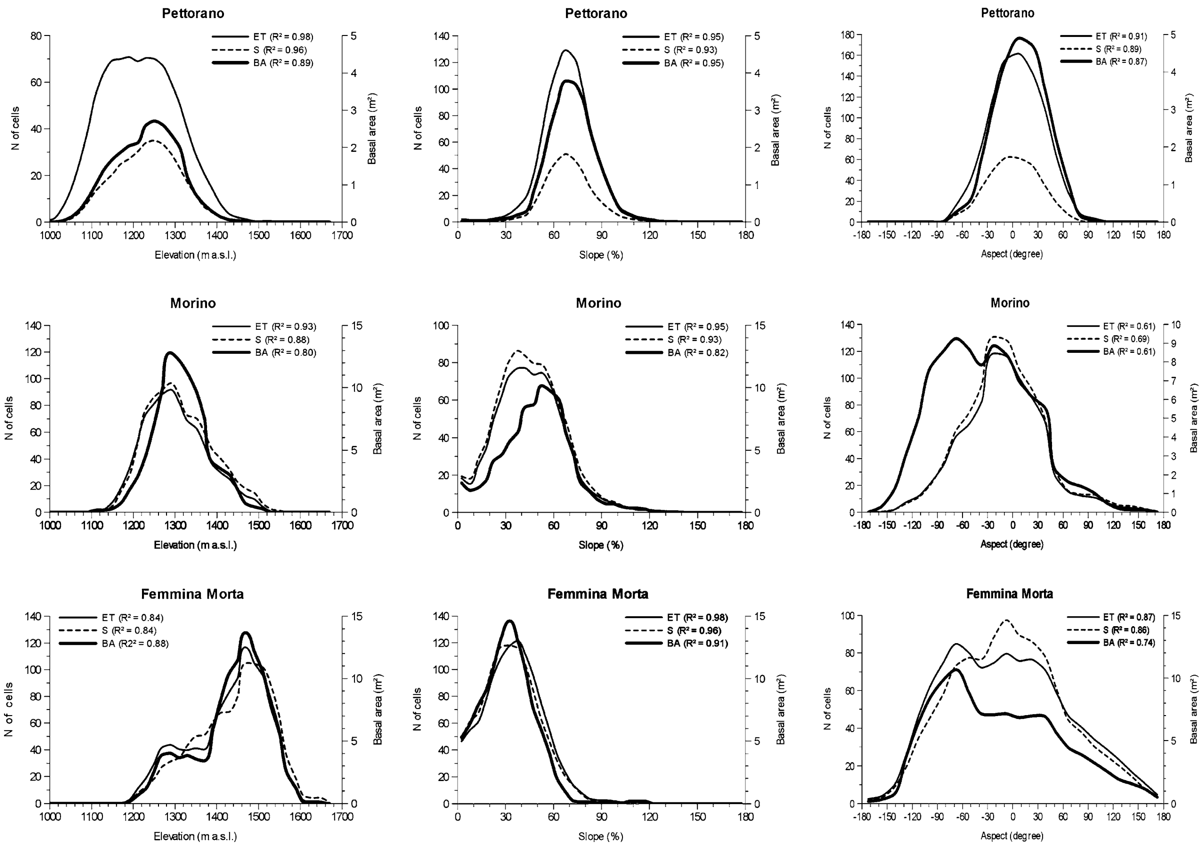

Fig. 7 Gradient analysis of yew population structure as a function of elevation, slope, and aspect. Graphs display the number of grid cells with established trees (ET), saplings (S: all abundance classes), abundant saplings (S2 + S3: classes 2 and 3), number of grid cells with both saplings (S) and established trees (ET), and total basal area (BA). R^2 coefficient of determination

and structural complexity that place them among the best yew populations in Europe (Hageneder 2007). In particular, two study areas (MOR and FEM) are occupied by yew trees, both isolated and in groups with remarkable size as either stem diameter or total height (for a comparison of yew dimensions see also Rikhari et al. 1998). The biggest yew individuals we encountered had flat crown tops, either because of truncation or dieback, and they also had hollow stems, as typical of the species (Moir 1999). Besides natural senescence, it is possible that these morphological characters have been selectively enhanced by past logging, which for economic reasons concentrated on individuals with regular crown and solid trunk. Furthermore, environmental stress (drought, snow accumulation, wind, and lightning) can directly affect old yew trees. Both past logging and environmental stress can also cause nearby trees to fall, further increasing the likelihood of leaving damaged yew trees on the landscape.

Taxus species are currently segregated in more than one continent of the northern hemisphere (Thomas and Polwart 2003), but they are all found mostly in the understory of mixed hardwood and/or conifer forests, either in Europe (Ellenberg 1988) or elsewhere in the world (Bolsinger and Jaramillo 1990; Rikhari et al. 2000). Further north in Europe, common yew was found to have limited regeneration within beech forests (Hulme 1996; Svenning and Magård 1999). At our study areas, regeneration is often abundant, especially considering past human disturbance, and overall yew regeneration resembles patterns observed near the southern margin of the species distribution (García et al. 2005a). We found no evidence of antagonism between yew and beech regeneration (Bailey and Liegel 1998; Dhar et al.

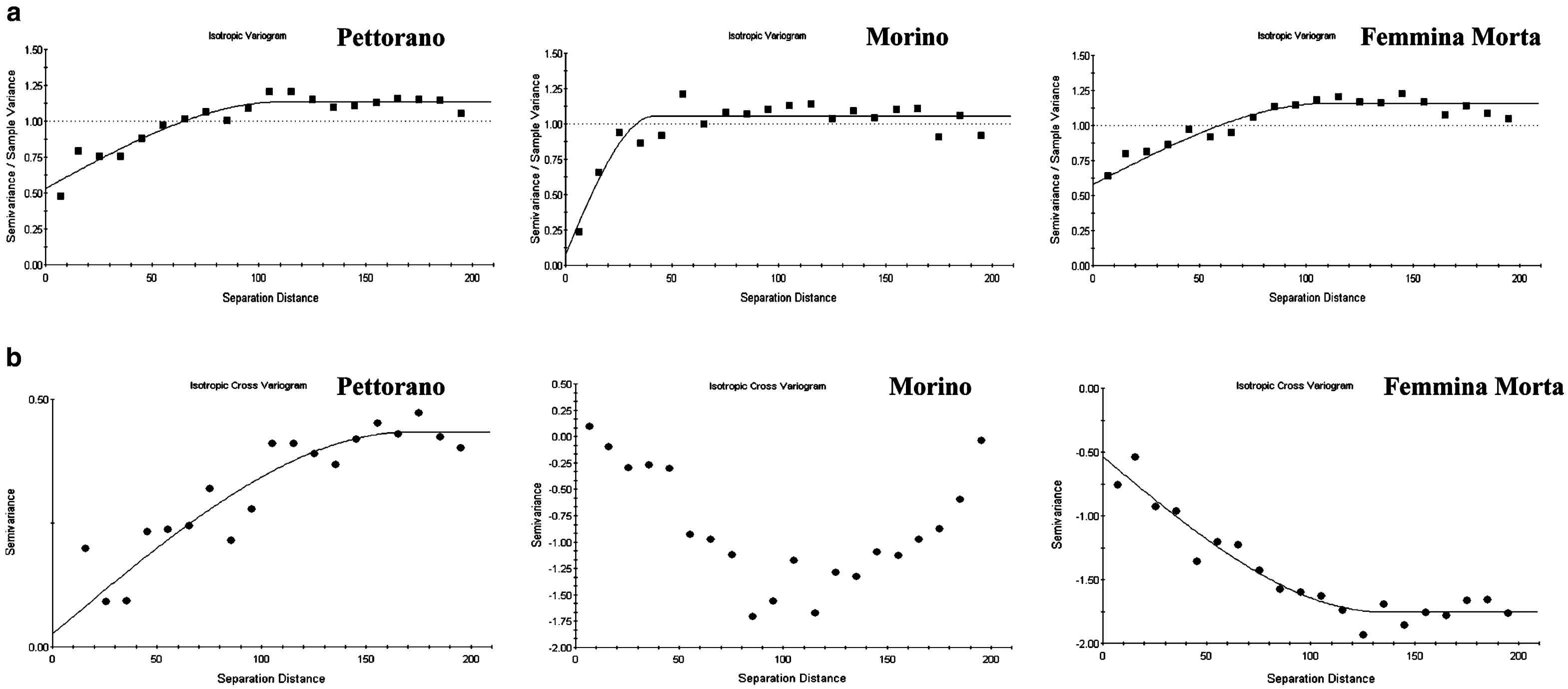

Fig. 8 Variograms computed from census data of the three yew populations. **a** Sample semivariograms (*filled circles*) and model fit (*line*) for basal area. **b** Cross-variograms between basal area and sapling abundance class

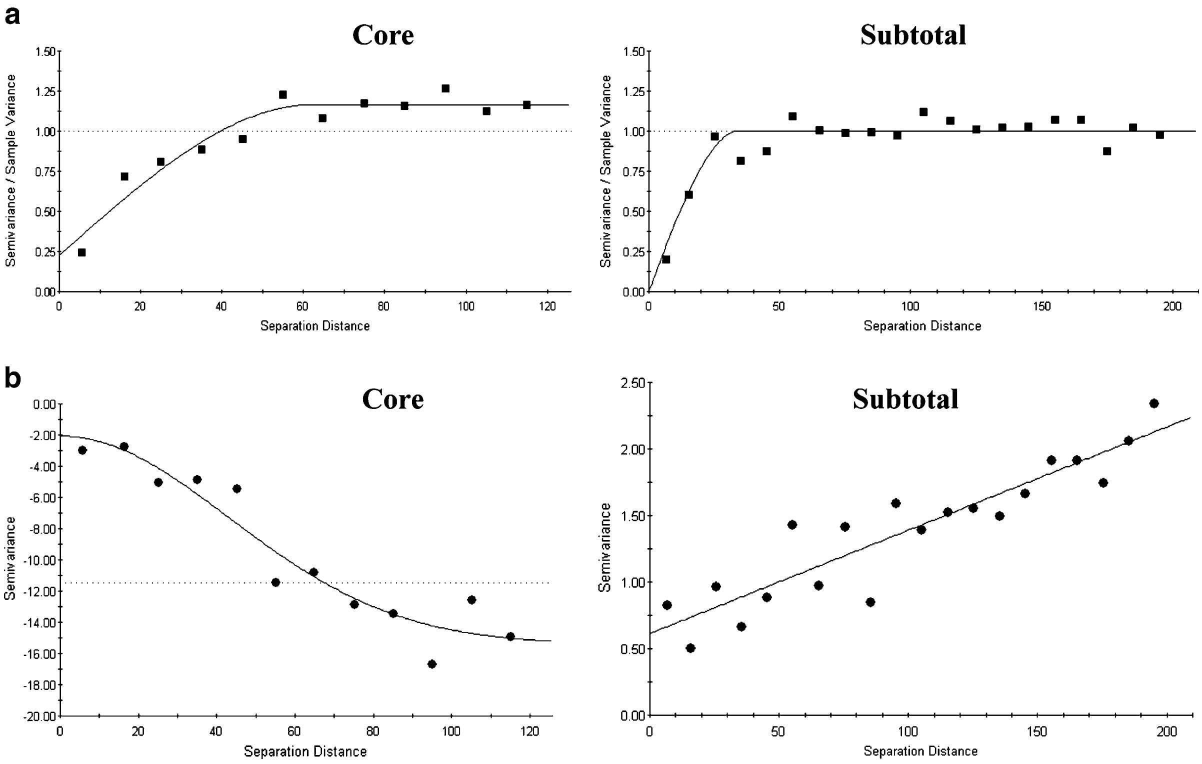

Fig. 9 Variograms computed from census data of the "core" and "subtotal" groups at the Morino site. **a** Sample semivariograms (*filled circles*) and model fit (*line*) for basal area. **b** Cross-variograms between basal area and sapling abundance class

2007). The beech forest at our study sites is therefore providing favorable conditions for yew survival, possibly in part because of niche partitioning between the deciduous overstory (beech) and the evergreen understory (yew; Perry 1994). The presence of healthy regeneration (i.e., considerable number of grid cells with class 2 and 3 of sapling abundance) at usually higher elevations than where adult trees are found (Fig. 7) can be interpreted as a re-expansion of yew into suitable areas. Because of this, and given the well-developed structure of at least some stands among the yew populations we studied, it is possible to argue that their current classification as "Apeninne beech forests with *Taxus* and *Ilex*" (*9210) is more a reflection of past human impacts than the potential vegetation in these areas. In other words, the habitat "Mediterranean *Taxus baccata* woods" (*9580) is currently restricted to Mediterranean islands (e.g., Sos Niberos in Sardinia or Madonie in Sicily), but it may truly extend to a larger portion of the Italian Apennines, as was also mentioned in the "Introduction."

The correlation we found between overall yew basal area and grid cells with yew regeneration is in agreement with what was found in the Cantabrian range of Asturias, Spain (García et al. 2005b). In terms of differences between our three study areas, the lower yew regeneration observed at PET is therefore mostly related to the lower seed production caused by a more rarefied adult yew population. However, the influence between stand structure and yew regeneration requires greater spatial detail to be unraveled in all its complexity. For instance, the relationship between BA and regeneration observed at the MOR site is opposite between the "core" and the "subtotal" group, indicating that high density of yew trees can locally become a limiting factor for yew regeneration (autoexclusion), while the presence of scattered yew trees or simply an increasing distance from a dense yew patch may favor yew regeneration.

Yew conservation has been primarily concerned with regeneration processes, given the lack of viable seedlings observed in multiple regions (Lewandowski et al. 1995; Hulme 1996; Kwit et al. 1998; Rikhari

Table 4 (a) Parameter estimates of models fit to the sample semi-variogram for basal area and sapling classes. (b) Parameter estimates of models fit to the sample cross-variograms between basal area and sapling classes

Site		Variable	Model	Nugget	Sill	Range (m)	SPD	R^2
(a)								
Pettorano		BA	Spherical	0.53	1.14	111	0.53	0.90
		S	Spherical	0.77	1.00	80	0.24	0.82
Morino	Total	BA	Spherical	0.08	1.05	41	0.92	0.83
		S	Spherical	0.56	0.86	80	0.35	0.86
	Subtotal	BA	Spherical	0.00	1.00	35	1.00	0.86
		S	Spherical	0.55	0.85	80	0.35	0.78
	Core	BA	Spherical	0.23	1.17	63	0.81	0.92
		S	Spherical	0.49	1.21	106	0.60	0.94
Femmina Morta		BA	Spherical	0.58	1.16	111	0.50	0.90
		S	Spherical	0.76	0.98	50	0.22	0.64
(b)								
Pettorano		BA-S	Spherical	0.03	0.43	171	0.94	0.87
Morino	Total	BA-S	(U-shape)	–	–	–	–	–
	Subtotal	BA-S	Linear	0.61	2.13	195	0.71	0.83
	Core	BA-S	Gaussian	−2.07	−15.40	61	0.87	0.92
Femmina Morta		BA-S	Spherical	−0.54	−1.75	135	0.69	0.93

SPD Spatial dependence, *BA* basal area, *S* sapling classes

et al. 1998; García et al. 2000; Rajewski et al. 2000). Lack of regeneration can be caused by low seed production (because of limited pollination, excessive crown shading, adverse climate, seed predation, etc.), difficulty in seedling establishment (thick litter, drought or frost, pathogens, etc.,), and/or grazing pressure (Lewandowski et al. 1995; Allison 1990, 1992; Di Fazio et al. 1997, 1998; Giertych 2000). A comparison of our results with published literature indicates that the average density of seedling at our sites can be described as medium to low (Rikhari et al. 1998; Dovčiak 2002; García and Obeso 2003; Kwit et al. 2004; Perrin et al. 2006), possibly because of the high accumulation of beech litter (Dhar et al. 2007). On the other hand, the sapling density and size range we found are similar to that of European yew populations with active and successful regeneration, suggesting that yew survival is not strictly controlled by seedling abundance and/or that seedling density is highly variable on relatively short time scales (Kwit et al. 2004; Dhar et al. 2007). Yew is also able to propagate through branch layering (Fig. 8b in Hageneder 2007) when snow accumulation causes the lowest branches to be buried in topsoil, and this phenomenon was sometime observed at our study sites.

Herbivory can affect yew regeneration, and in a previous LIFE-sponsored study we found that summertime open range grazing by cattle and goat, especially at the Morino site, negatively impacted yew regeneration (Piovesan et al. 2003). According to that study, in 1997–2001 abundance of yew saplings was reduced in the intermediate height class, and a similar impact was attributed to grazing for two yew populations in Austria (Dhar et al. 2007). Livestock often produce effects analogous to those derived from an overabundance of wild ungulates (Ammer 1996; Parks et al. 1998; Insinna and Ammer 2000; Saniga 2000; Mysterud and Østbye 2004). Repeated browsing, when it does not kill the plant, forces yew to assume a shrub form, or to develop an irregular crown, unless the individual tree has already reached a height greater than the maximum chewing level (Fig. 10). Besides causing changes in crown structure and plant form, grazing reduces overall yew growth (García et al. 2000), and may favor introduction of pathogens into the plant. At our study sites, a reduction in grazing pressure was obtained in 2003–2007 by establishing a number of watering places for cattle at locations further away from the yew populations, while at the same time improving the grass cover around these watering sites.

The fact that grazing can impact yew regeneration may seem to contradict the notion that yew had been eradicated by humans to protect livestock from poisoning themselves (Lieutaghi 1975; Ellenberg 1988). Yew is indeed resistant to herbivory, such as from defoliator arthropods, especially lepidopters (Daniewski et al. 1998; Lattin 1998). To date no study has considered how the concentration of venomous alcaloids (taxins) in foliage varies between yew populations, or if there is even a connection with endophytic fungi as was found in *Festuca rubra* (Bazely et al. 1997). However, the dose required for yew ingestion to become lethal varies greatly among domesticated animals with horses being the most susceptible ones (Cooper and Johnson 1984; Wilson et al. 2001). On the other hand, ruminants, such as cattle, are often able to feed on it without adverse consequences (Watt 1926; Paule et al. 1993; Rikhari et al. 1998; Tirmenstein 2002) suggesting that the digestive apparatus (monogastric vs. poligastric) does matter. From information contained in Latin texts (Voliotis 1986) and at archaeological sites, such as Horgen Scheller in Switzerland, where large stashes of yew branches have been found, it appears that humans have used yew as winter forage for their livestock since the Neolithic (Favre and Jacomet 1998). In conclusion, grazing impacts from wild or domesticated animals, and the pastoral activities connected with it, have played a role in shaping yew populations for a very long time, possibly even contributing to its disappearance from entire regions, such as Lithuanian forests (Navys 2000). Understanding the current (and future) role of livestock and wild ungulates is therefore essential for yew conservation.

Another factor to consider for yew regeneration is forest structure. In coniferous vegetation of the western USA, unaided stand development toward old-growth conditions has been recommended (Busing et al. 1995). Other authors, especially those focused on European beech ecosystems, have proposed to use selective cutting in order to reduce competition from overstory beech, thereby enhancing yew fruttification, regeneration, and growth (Hulme 1996; Svenning and Magård 1999; Dhar et al. 2007). In central Italy, yew regeneration is often greater where beech is managed as coppice than where it is managed as high forest (Di Cosmo 2004). In some cases, however, reduced shading of the ground may favor hardwood or grass regeneration more than yew (Iszkulo and Boratynski 2006). In a previous study on beech dendroecology in the Apennines, it was found that beech forests where yew is present are bioclimatically different from other beech forests (Piovesan et al. 2005a). In general, as also shown by our study, it is necessary to understand the impact of multiple environmental factors, either physical or biological, at multiple temporal and spatial scales, before determining the most suitable strategies for maintaining and improving yew regeneration.

Fig. 10 The effect of cattle browsing on yew crowns at the Morino site. Grazing impact is a function of tree height, as shown by the damaged crown of a small tree (on the *left*) versus damaged branches of taller trees (in the *center* and on the *right* of the picture). In the box: lateral shoot re-growth after grazing was excluded at the site

Environmental gradients

At our study sites, the realized niche of yew usually follows the expected unimodal, bell-shaped response curve to an environmental gradient (Austin 2002). In a few cases, especially with regard to elevation and aspect, we observed relatively large deviations (skewness and/or kurtosis) from this theoretical pattern, and, as discussed below, such deviations are most likely related to disturbance history and human impacts, possibly combined with changes in climate over time. In terms of elevation, the yew populations we studied in central Italy reach a maximum (1,400–1,650 m asl) that is similar to that found in the Pyrenees (Thomas and Polwart 2003). Usually yew regeneration and basal area curves culminate at the same elevations, but at the Morino site grid cells with abundant saplings are located higher than grid cells with the greatest basal area. Further research will be needed to determine if this difference is a result of an ongoing shift in the distribution of the species caused by changes in climate (Peñuelas and Boada 2003; Lenoir et al. 2008) or if it represents a return of the species to its potential habitat, given that yew diameter and height reach their peak at the same elevations as sapling abundance.

Although the elevation range occupied by yew at the three sites is practically constant (400–500 m), the maximum elevation decreases going from west to east. This could be related to air temperature, mediated by a greater impact of cold north-easterly winds during wintertime (Mennella 1967), which can increase the risk of late frosts and bring overall lower temperatures (Thomas and Polwart 2003). Yew resistance to freezing varies geographically: in Sweden foliar damage occurs at −35°C, but flowers can be damaged at −23°C, while in Austria foliar damage begins at −23°C, and in Great Britain March frost damages yew leaves at −13°C (and sometime at higher temperatures). Photosynthesis in yew can occur over a large range of air temperatures, with an optimum between 14 and 25°C, a summertime maximum of 38–41°C, a summertime minimum of −3 to −5°C, and a winter minimum of −8°C (Thomas and Polwart 2003; Hageneder 2007). From these values, it is clear that yew is adapted to relatively mild climates, and that in Mediterranean mountains it can begin growing relatively early (late winter to early spring), when other canopy species, such as beech, are still without leaves. The early start of yew growing season also allows for a reduced need of summertime photosynthesis, which would be difficult to achieve given the shading from overstory trees and the Mediterranean dry summers. Once the overstory canopy is fully developed, yew can still produce flowers and fruits even in low light conditions (Thomas and Polwart 2003).

Our research confirmed the yew preference for northern exposures. At two of our study areas (MOR and FEM), yew basal area was slightly greater on western exposures, whereas yew regeneration peaked on northern exposures at all three sites. In mountainous areas of Europe, yew tends to grow on north-western to north-eastern slopes in deciduous or mixed forests (Thomas and Polwart 2003). Since the central Apennines have experienced a drying trend over the past few decades (Piovesan et al. 2008), we argue that yew regeneration may have been favored by the cooler conditions found on northern exposures, whereas in the more distant past it established just as easily on western exposures. Although the lower evapotranspiration found on north-east to north-west exposures favors yew survival, it is also possible that its current distribution, even in terms of aspect, is in part a reflection of land use changes. At other sites in the Italian Apennines (e.g., Monte Terminillo), we have found yew populations on south-west exposures, especially near the elevational limit of the species (1,300–1,500 m). Another factor to be considered is the lower risk of wildfire usually associated with northern exposures. In fact, yew is particularly sensitive to fire damage (Halpern and Spies 1995; Tirmenstein 2002), given its thin bark and its lack of resprouting when the aboveground stems burn down. Yew reintroduction in burned areas requires seed dispersal from unburned yew stands, and is an extremely slow process (Halpern and Spies 1995). In Mediterranean mountains, yew is rarely found among woody species that recolonize old pastures, as it is instead the case in areas with an oceanic climate (Watt 1926). In beech and fir forests, which are considered the climax vegetation over a large portion of the Apennines, yew has survived also due to the lack of wildfires, and because it tolerates competition from overstory species (Ellenberg 1988; Pignatti 1998).

In terms of terrain slope, yew was found to prefer gentler slopes going from east to west across central Italy. This could be related to the milder temperatures found across such longitudinal gradient (for constant elevations), as was mentioned above. In fact, under a warmer climate, lower slope angles allow for reduced drought stress through greater persistence of snow pack and soil moisture. In general, snow accumulation, and persistence of snow pack until late spring, characterizes the areas occupied by the yew populations we studied. Snow is not only important for the hydrological balance of these Mediterranean mountains, and for reducing wildfire risk, but also for discouraging grazing by wild ungulates in fall and spring (Querrec and Filion 2008). In terms of regeneration, it is interesting to note that nearly flat terrain hampers yew establishment by favoring the accumulation of beech litter (Ellenberg 1988;

Dovčiak 2002; Dhar et al. 2007). At our study sites, yew also occurs in particularly rugged locations, with individuals that are relatively small but with signs of old age, which they may have acquired thanks to lack of human impacts and other disturbance factors (see Larson et al. 2000).

Spatial patterns

Overall, the type of autocorrelation structure we identified in the *Taxus baccata* populations of central Italy is similar to that observed for a population of *Taxus brevifolia* in North America (Chen et al. 2004). Spatial dependence in the attributes of a species distribution is usually associated with environmental conditions, competitive processes (Nanos et al. 2005), and/or dispersal mechanisms (Svenning and Skov 2002). In yew populations, spatial patterns could be related to breeding, which requires a considerable amount of pollination between neighboring males and females (Leinemann and Hattemer 2006). Since mean dispersal distance of yew pollen is about 140 m, several of our variogram range estimates could be conditioned by the presence of fertile individuals—of both sexes—located within pollination reach. This factor could be more limiting than seed dispersal, which is controlled by animals eating the fruits; it has been reported that yew seed clumps are mostly found near yew trees (García et al. 2007).

From the combination of variogram and cross-variogram models, one can infer that the presence of spatially homogeneous yew trees inhibits the establishment of yew regeneration within the group, but favors it in nearby areas. The direct relationship that exists at the PET site between yew basal area and regeneration becomes an inverse one at FEM, while at MOR it varies between the “core” group (inverse) and the “subtotal” group (direct). Therefore, yew populations that are less abundant, or without dense groups with large individuals, show a positive influence of established trees (ET) on regeneration, whereas in areas where yew ET presence is greater, and particularly over short distances (tens of meters), autoexclusive inhibition caused by shading and/or soil toxicity becomes prevalent (Iszkulo and Boratynski 2006; Dhar et al. 2007). The fact that yew regeneration decreases when density of yew trees is too high was already pointed out for central European ecosystems (Hulme 1996; Dovčiak 2002). A similar process has been identified in holly (*Ilex* sp.) populations (Arrieta and Suárez 2006), and it also resembles the phenomenon of reciprocal replacement often found in mixed European beech-silver fir forests (Dobrowolska 1998). With regard to yew, it is known that it can germinate at the lowest light levels among European trees, but it requires up to 10 times more illumination when it reaches the sapling stage (Iszkulo and Boratynski 2006). Because of this, the actual formation of yew “woods” might be dynamically related to the senescent phase of beech or beech-fir forests (Peterken 1996), which favors formation of overstory gaps that yew saplings can exploit (Hageneder 2007).

Conclusion

The yew populations we studied included much more than 500 healthy mature individuals, which is the minimum amount currently considered necessary to safeguard population genetic variability (USDA Forest Service 1992). From this premise, and the fact that yew is usually characterized by high intrapopulation biodiversity (Lewandowski et al. 1995; Lee et al. 2000), these Apennine populations ought to have maintained a varied genetic pool, hence they are not currently deemed at risk in this regard. The active regeneration observed at the study sites, in conjunction with the presence of a well structured adult population, suggests that climate, topography, and vegetation at the sites create conditions that favor yew survival (Rikhari et al. 1998; Carvalho et al. 1999). In fact, old-growth and late successional forests with pronounced vertical stratification usually provide the best environment for yew (USDA Forest Service 1992; Paule et al. 1993; Rikhari et al. 2000; Thomsen et al. 2005). Yew long-term survival becomes therefore intertwined with maintaining and restoring old-growth forest ecosystems, which also harbor other tree species whose distribution has been reduced in modern times by human impacts (Busing et al. 1995; Svenning and Skov 2002).

Fragmentation of yew populations is often the main driver for reduced fitness of the species. In our study, we found that viable yew groups had an approximate area of 0.5–3 ha, which in turn represents the minimum patch size for yew preservation over the landscape. In reality, for Apennine old-growth beech forests, the minimum area occupied by a yew stand should be consistent with a continuous shifting mosaic steady state (5–10 ha; Piovesan et al. 2005b). Existing yew groups should also become more and more connected as re-establishment of the species in its potential habitat continues. Since high yew density can hamper regeneration, conservation practices need to favor expansion at the boundary of dense yew nuclei, to promote edge regeneration and avoid the risk of reduced fruit production because of senescence.

Monitoring programs and targeted ecological studies, such as this one, are required to guarantee that local management decisions, including the hands-off approach proposed by Busing et al. (1995), rely on scientific information, especially considering the impact of future climatic changes on species distribution and abundance.

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References

Allison TD (1990) The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.). Part I: direct effect on pollen, ovule, and seed production. Oecologia 83:523–529. doi:10.1007/BF00317204

Allison TD (1992) The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.). Sex expression. Oecologia 89:223–228

Ammer C (1996) Impacts of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. For Ecol Manag 88:43–45

Arrieta S, Suárez F (2006) Marginal holly (*Ilex aquifolium* L.) populations in Mediterranean central Spain are constrained by a low-seedling recruitment. Flora 201:152–160

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol Model 157:101–118. doi:10.1016/S0304-3800(02)00205-3

Bailey JD, Liegel LH (1998) Pacific yew (*Taxus brevifolia* Nutt.) growth and site factors in western Oregon. Northwest Sci 72:283–292

Bazely DR, Vicari M, Emmerich S, Filip L, Lin D, Inman A (1997) Interactions between herbivores and endophyte-infected Festuca rubra from the Scottish island of St. Kilda, Benbecula and Rum. J Appl Ecol 34:847–860. doi:10.2307/2405276

Bebber A, Corona E (1986) Nota dendrocronologia su una trave di tasso (*Taxus baccata* L.). Dendrochronologia 4:115–124

Biondi F (1992) Development of a tree-ring network for the Italian Peninsula. Tree-Ring Bull 52:15–29

Bolsinger CL, Jaramillo AE (1990) *Taxus brevifolia* Nutt., Pacific yew. In: Burns RM, Honkala BH (eds) Silvics of North America: volume 1, conifers. US Department of Agriculture Forest Service, Washington, pp 573–579

Brunetti M, Maugeri M, Monti F, Nanni T (2006) Temperature and precipitation variability in Italy in the last two centuries from homogenised instrumental time series. Int J Climatol 26:345–381. doi:10.1002/joc.1251

Brzeziecki B, Kienast F (1994) Classifying the life-history strategies of trees on the basis of the Grimian model. For Ecol Manag 69:167–187

Büsgen M, Münch E, Thomson T (1929) The structure and life of forest trees. Chapman and Hall, London

Busing RT, Halpern CB, Spies TA (1995) Ecology of Pacific yew (*Taxus brevifolia*) in western Oregon and Washington. Conserv Biol 9:1199–1207. doi:10.1046/j.1523-1739.1995.9051199.x

Carvalho A, Rebelo A, Dias J (1999) Distribution and natural regeneration of yew trees in the national parks of Peneda-Gerês (Portugal) and Baixa Limia Serra-Xurès (Spain). Rev Biol Lisb 17:43–49

Chen J, Song B, Rudnicki M, Moeur M, Bible K, North M, Shaw CD, Franklin JF, Braun MD (2004) Spatial relationship of biomass and species distribution in a old-growth *Pseudotsuga-Tsuga* forest. For Sci 50:364–375

Cooper MR, Johnson AW (1984) Poisonous plants in Britain and their effects on animals and man. Her Majesty's Stationery Office, London

Daniewski W, Gumulka M, Anczewski W, Masnyk M, Bloszyk E, Gupta KK (1998) Why the yew tree (*Taxus baccata*) is not attacked by insects. Phytochemistry 49:1279–1282. doi:10.1016/S0031-9422(98)00102-2

Dhar A, Ruprecht H, Klumpp R, Vacik H (2007) Comparison of ecological condition and conservation status of English yew population in two Austrian gene conservation forests. J For Res 18:181–186. doi:10.1007/s11676-007-0037-5

Di Cosmo L (2004) Contributo alla conoscenza dell'ecologia del tasso (*Taxus baccata* L.). Ital For Mont 59:289–303

Di Fazio SP, Vance NC, Wilson MV (1997) Strobilus production and growth of Pacific yew under a range of overstory conditions in western Oregon. Can J Res 27:986–993. doi:10.1139/cjfr-27-7-986

Di Fazio SP, Wilson MV, Vance NC (1998) Factors limiting seed production of *Taxus brevifolia* (*Taxaceae*) in Western Oregon. Am J Bot 85:910–918. doi:10.2307/2446356

Dimov LD, Chambers JL, Lockhart BR (2005) Spatial continuity of tree attributes in bottomland hardwood forests. For Sci 51:532–540

Dobrowolska D (1998) Structure of silver fir (*Abies alba* Mill.) natural regeneration in the 'Jata' reserve in Poland. For Ecol Manag 110:237–247

Dovčiak M (2002) Population dynamics of the endangered English yew (*Taxus baccata* L.) and its management implications for biosphere reserves of the Western Carpathians. Mab UNESCO

Earle CJ (2001) *Taxus baccata* L. http://www.conifers.org

Ellenberg H (1988) Vegetation ecology of Central Europe. Cambridge University Press, Cambridge

Favre P, Jacomet S (1998) Branch wood from the lake shore settlements of Horgen Scheller, Switzerland: evidence for economic specialization in the late Neolithic period. Veg Hist Archaeobot 7:167–178. doi:10.1007/BF01374005

Fortin MJ, Dale MRT (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge

García D, Obeso JR (2003) Facilitation by herbivore-mediated nurse plants in a threatened tree, *Taxus baccata*: local effects and landscape level consistency. Ecography 26:739–750

García D, Zamora R, Hódar JA, Gómez JM, Castro J (2000) Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. Biol Conserv 95:31–38

García D, Obeso JR, Martinez I (2005a) Rodent seed predation promotes differential recruitment among bird-dispersed trees in temperate secondary forests. Oecologia 144:435–446

García D, Obeso JR, Martinez I (2005b) Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? J Ecol 93:693–704

García D, Martinez I, Obeso JR (2007) Seed transfer among bird-dispersed trees and its consequences for post-dispersal seed fate. Basic Appl Ecol 8:533–543

Gaston KJ, Fuller RA (2008) Commonness, population depletion and conservation biology. Trends Ecol Evol 23:14–19

Giacomini V, Fenaroli L (1958) Conosci L'Italia: La Flora. Touring Club Italiano, Milano

Giertych P (2000) Factors determining natural generation of yew (*Taxus baccata* L.) in the Kórnik Arboretum. Dendrobiology 45:31–40

Hageneder F (2007) Yew—a history. Stroud Publishing, Sutton

Halpern CB, Spies TA (1995) Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol Appl 5:913–934

Hulme PE (1996) Natural regeneration of yew (*Taxus baccata* L.): microsite, seed or herbivore limitation? J Ecol 84:853–861

Insinna P, Ammer C (2000) Investigations of yew (*Taxus baccata*) in the "Eibenwald bei Paterzell" nature conservation area. Forst Holz 55:136–140

Ishii H, Reynolds JH, Ford ED, Shaw DC (2000) Height growth and vertical development of an old-growth *Pseudotsuga-Tsuga* forest in southwestern Washington State U.S.A. Can J For Res 30:17–24

Iszkuło G (2001) The yew (*Taxus baccata* L.) of the Cisowy Jar reserve near Olecko. Dendrobiology 46:33–37

Iszkulo G, Boratynski A (2006) Analysis of the relationship between photosynthetic photon flux density and natural *Taxus baccata* seedlings occurrence. Acta Oecol 29:78–84

Kwit C, Schwartz MW, Platt WJ, Geaghan JP (1998) The distribution of tree species in steepheads of the Alapachicola River Bluffs, Florida. J Torrey Bot Soc 125:309–318

Kwit C, Horvitz CC, Platt WJ (2004) Conserving slow-growing, long-lived tree species: input from the demography of a rare understory conifer, *Taxus floridana*. Conserv Biol 18:432–443

Larson DW, Matthes U, Gerrath JA, Larson NWK, Gerrath JM, Nekola JC, Walker GL, Porembski S, Charlton A (2000) Evidence for the widespread occurrence of ancient forests on cliffs. J Biogeogr 27:319–331

Lattin JD (1998) A review of the insects and mites found on *Taxus* spp. with emphasis on western North America. USDA Forest Service, Pacific Northwest Research Station, Portland

Lee SW, Choi WY, Kim WW, Kim ZS (2000) Genetic variation of *Taxus cuspidata* Sieb. et Zucc. in Korea. Silvae Genet 49:124–130

Leinemann L, Hattemer HH (2006) Genetic variation and mating pattern in a stand of yew (*Taxus baccata* L.). Allg Forst Jagdzeitg 177:217–224

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771

Lesani MR (1999) Yew, *Taxus baccata* L. Research Institute of Forest and Rangeland, Islamic Republic of Iran, Iran

Leuthold C (1998) Die pflanzensoziologische und ökologische Stellung der Eibe (Taxus baccata L.) in der Schweiz—ein Beitrag zur Wesenscharakterisierung des "Ur-Baumes" Europas. Schweiz Z Forstwes 49:349–371

Lewandowski A, Burczyk J, Mejnartowicz L (1995) Genetic structure of English yew (*Taxus baccata* L.) in the Wierzchlas reserve: implications for genetic conservation. For Ecol Manag 73:221–227

Lieutaghi P (1975) Il Libro Degli Alberi e Degli Arbusti. Rizzoli Editore, Milano

Maestre FT, Rodríguez F, Bautista S, Cortina J, Bellot J (2005) Spatial associations and patterns of perennial vegetation in a semi-arid steppe: a multivariate geostatistics approach. Plant Ecol 179:133–147

Marchesoni V (1959) Importanza del fattore storico-climatico e dell'azione antropica nell'evoluzione della vegetazione forestale dell'Appennino umbro-marchigiano. Ann Accad Ital Sci For 8:327–343

Mennella C (1967) Il Clima d'Italia. Fratelli Conti Editori, Napoli

Moir AK (1999) The dendrochronological potential of modern yew (*Taxus baccata*) with special reference to yew from Hampton Court Palace, UK. New Phytol 144:479–488

Molisch H (1938) The longevity of plants. E.H. Fulling, New York

Mysterud A, Østbye E (2004) Roe deer (*Capreolus capreolus*) browsing pressure affects yew (*Taxus baccata*) recruitment within nature reserves in Norway. Biol Conserv 120:545–548

Nanos N, Pardo F, Nager JA, Pardos JA, Gil L (2005) Using multivariate factorial kriging for multiscale ordination: a case study. Can J For Res 35:2860–2874

Navys E (2000) English yew (*Taxus baccata* L.) in forests of Baltic States and the main reasons for its extinction from Lithuania. Balt For 6:41–46

Parks CG, Bednar L, Tiedemann AR (1998) Browsing ungulates—an important consideration in dieback and mortality of Pacific yew (*Taxus brevifolia*) in a Northeastern Oregon stand. Northwest Sci 72:190–197

Paule L, Gömöry D, Longauer R (1993) Present distribution and ecological conditions of the English yew (*Taxus baccata* L.) in Europe. In: International yew resources conference: yew (*Taxus*) conservation biology and interactions, Berkeley, CA, USA, pp 189–196

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). Glob Chang Biol 9:131–140

Perrin PM, Kelly DL, Mitchell FJG (2006) Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: natural regeneration and stand dynamics. For Ecol Manag 236:356–367

Perry DA (1994) Forest ecosystems. John Hopkins University Press, London

Peterken GF (1996) Natural woodland: ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge

Pignatti S (1998) I boschi d'Italia. UTET, Torino

Piovesan G, Hermanin L, Lozupone G, Palumbo M, Schirone B (2003) Considerazioni ecologico-selvicolturali per la ricomposizione e la riabilitazione delle tassete. Sherwood For Alberi Oggi 91:46–53

Piovesan G, Biondi F, Bernabei M, Di Filippo A, Schirone B (2005a) Spatial and altitudinal bioclimatic zones of the Italian peninsula identified from a beech (*Fagus sylvatica* L.) tree-ring network. Acta Oecol 27:197–210

Piovesan G, Di Filippo A, Alessandrini A, Biondi F, Schirone B (2005b) Structure, dynamics, and dendroecology of an old-growth *Fagus* forest in the Apennines. J Veg Sci 16:13–28

Piovesan G, Biondi F, Di Filippo A, Alessandrini A, Maugeri M (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. Glob Chang Biol 14:1265–1281

Presutti Saba E (2005) Monitoring and management of beech stands with yew (*Taxus baccata* L.) in the Central Appennines. Department of Environment and Forests, Università degli studi della Tuscia, Viterbo

Querrec L, Filion L (2008) White-tailed deer activity reconstructed from tree-rings in eastern boreal Canada. For Ecol Manag 255:234–244

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org. ISBN 3-900051-07-0

Rajewski M, Lange S, Hattemer HH (2000) Problem of reproduction in the genetic conservation of rare tree species: the example of common yew (*Taxus baccata* L.). For Snow Landsc Res 75:251–266

Rikhari HC, Palni LMS, Sharma AS, Nandi SK (1998) Himalayan yew: stand structure, canopy damage, regeneration and conservation strategy. Environ Conserv 25:334–341

Rikhari HC, Sharma AS, Nadeem M, Palni LMS (2000) The effect of disturbance levels, forest types and associates on the regeneration of *Taxus baccata*: lessons from the Central Himalaya. Curr Sci 79:88–90

Salbitano F (1988) Per uno studio delle modificazioni del paesaggio forestale: il caso del monte Catria. In: Andreoli B, Montanari M (eds) Il Bosco nel Medioevo. Clueb, Bologna, pp 287–301

Saniga M (2000) Structure, production and regeneration processes of English yew in the Plavno State Nature Reserve. J For Sci 46:76–90

Schirone B, Bellarosa R, Piovesan G (2003) Il Tasso: Un albero da Conoscere e Conservare. Cogestre Edizioni, Penne (PE)

Spada F (2003) Considerazioni sulla fitogeografia e sulla genesi delle comunità a *Taxus baccata* L.in Europa. In: Schirone B, Bellarosa R, Piovesan G (eds) Il Tasso: Un albero da Conoscere e Conservare. Cogestre Edizioni, Penne (PE), pp 13–34

Svenning JC, Magård E (1999) Population ecology and conservation status of the last natural population of English yew (*Taxus baccata*) in Denmark. Biol Conserv 88:173–182

Svenning JC, Skov F (2002) Mesoscale distribution of understorey plants in temperate forest (Kalø, Denmark): the importance of environment and dispersal. Plant Ecol 160:169–185

Thomas PA, Polwart A (2003) *Taxus baccata* L. J Ecol 91:489–524

Thomsen RP, Svenning JC, Balslev H (2005) Overstorey control of understorey species composition in a near-natural temperate broadleaved forest in Denmark. Plant Ecol 181:113–126

Tirmenstein DA (2002) *Taxus brevifolia*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Collins

USDA Forest Service (1992) An interim guide to the conservation and management of Pacific yew. USDA Forest Service, Pacific Northwest Region, Portland

Voliotis D (1986) Historical and environmental significance of the yew (*Taxus baccata* L.). Isr J Bot 35:47–52

Watt AS (1926) Yew communities of the south downs. J Ecol 14:282–316

Wilson CR, Sauer JM, Hooser SB (2001) Taxines: a review of the mechanism and toxicity of yew (*Taxus* spp.) alkaloids. Toxicon 39:175–185