# Vegetation ecology and diversity relationships in a riparian forest remnant of Western Greece 

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#### Abstract

The present study investigates vegetation differentiation in a riparian forest remnant dominated by Fraxinus angustifolia subsp. oxycarpa and Ulmus minor subsp. minor. Floristic data from 46 plots and soil data from 20 plots were collected from the study site in the area of Lesini (Western Greece). Dendrochronological analysis was conducted and forest structure was also investigated. Plot diversity was assessed for total floristic composition and species groups. Three vegetation units were distinguished, differentiating mainly along a soil texture gradient, with their floristic composition also affected by human disturbances. Total species, as well as species group diversity and evenness were differentiated along the main ecological gradient. The vegetation unit most affected by natural disturbance regimes is characterized by the highest diversity of riparian plant specialists and the lowest total species diversity. The vegetation units less affected by natural disturbances have increased forest species diversity. Human disturbances were found to increase total species diversity and evenness, as well as diversity of grassland and synanthropic species. With the exception of one vegetation unit, the forest lacks young individuals of the dominant tree species. This is a major problem for the persistence of the riparian forest, especially considering the reduction of annual precipitation in the wider area and the lower frequency and intensity of flood events. Conservation aspects in the view of anthropogenic pressures and natural disturbances are outlined.


Key words: alluvial forest vegetation, dendrochronology, Fraxinus angustifolia, Greece protected forest, riparian forest, Ulmus minor.

## INTRODUCTION

Riparian areas are considered the most productive and species-rich environments of many landscapes and riparian forests are among the most endangered habitat types in the Mediterranean (Looy \& Meire, 2009). Human-induced changes to river flow regimes and groundwater levels, together with the intensification of agricultural practices in the alluvial plain, cause a deterioration of the diversity of riparian landscapes (Dierschke, 1980; Décamps et al., 1988; Ward et al., 2002; Looy \& Meire, 2009, Zogaris et al., 2009).

[^0]Wet lowland forests are the prevailing alluvial vegetation in Europe. These forests exhibit a characteristic zonation with the distance from the river bed acting as the key factor. This distance actually depicts the frequency of floods and properties (e.g. texture and nutrient content) of the deposits (Ellenberg, 1988). They are restricted to large river systems, but have vanished widely due to hydrological regulations (Bohn et al., 2003; Dimopoulos \& Bergmeier, 2008). Hardwood alluvial forests occur at altitudes liable to flooding, usually at the edges of flood plains, where floods are rare and soil is very fertile because of the fine texture and nutrient rich deposits fertilizing these areas (Ellenberg, 1988).

Mediterranean alluvial hardwood forests consist of long-living tree species, one of which is the narrow leaved ash, Fraxinus angustifolia subsp. oxycarpa. These forests have an important ecological function in the landscape as they are characterised by high growth and regeneration capacity, exercise a positive influence on the mesoclimate of the valley plains, offer protection against the drying effects of wind to the neighbouring open fields, protect banks and soils against water erosion, slow down run-off during flooding and help accelerate water retreat after flooding events (Doyle, 1990; Sagers \& Lyon, 1997; Hughes et al., 2001; Micheli et al., 2004). River straightening and water level regulation, barrage construction, alluvial plain drainage, and cultivation of non-native woody plants are some of the interventions affecting ecological functions of riparian forests (Bohn et al., 2003).

The severest threats to these forests still originate from changes in the water regime and especially the non-flooding by inundation water and the drawdown of the water level, due to the rivers arrangements. Hardwood riparian forests are very fragile ecosystems and must be considered the most threatened forest habitats in Greece (Dimopoulos \& Bergmeier, 2008).

Fraxinus angustifolia, a characteristic component of Mediterranean alluvial forest vegetation, is a thermophilous deciduous fast-growing tree that occurs in lowland and submontane areas (Tonon et al., 2001). The plant communities of Fraxinus angustifolia subsp. oxycarpa forests have been studied by few researchers in Greece and the eastern Meditteranean area (Raus, 1980; Szijj, 1983; Athanasiadis \& Drossos, 1992; Athanasiadis et al., 1996; Kutbay et al., 1998; Vasilopoulos et al., 2007).

The existing riparian forests are remnants of formerly much more extensive and widespread wetland forests. The few remnants of such forests in Greece are very small, suffer from impacts from adjacent agricultural areas, and are at the brink of extinction. They form part of the Directive 92/43/EEC habitat type 'Riparian mixed forests of Quercus robur, Ulmus laevis and Ulmus minor, Fraxinus excelsior or Fraxinus angustifolia along the great rivers' (91F0). The Balkanic subtype that occurs in Greece corresponds to the Leucojo-Fraxinetum angustifoliae (Dimopoulos \& Bergmeier, 2008).

The study area is the natural monument of Lesini, which is an important riparian Fraxinus angustifolia subsp. oxycarpa forest relict and constitutes a habitat island surrounded by agricultural land. The existing forest is remnant of formerly much more extensive
and widespread wetland forests. The few remaining stands are very small and suffer from impacts from adjacent agricultural areas (Dimopoulos \& Bergmeier, 2008).

It constitutes part of the site "GR2310001: Acheloos river delta, Messolonghi-Aitoliko lagoons and Evinos river estuaries" belonging to the European Natura 2000 network of protected areas and part of the zone III of the site "Messolonghi lagoons" designated under the Ramsar Convention. The Fraxinus - Ulmus forest of Lesini is considered unique in Greece (Dafis et al., 1996). It is one of the 51 natural Greek monuments and one of the 16 Greek biogenetic reserves (Dafis et al., 1996). Since 1985, some management measures have been taken by the Hellenic Ministry of Agriculture and the Forestry Service of Messolonghi, to preserve this relict forest. However, the vitality and regeneration tendency of Lesini Ash Forest have been considered problematic due to the absence of natural regeneration; a condition which is certainly a threatening parameter for the forest's survival.

The main objectives of this research were to investigate: a) the vegetation differentiation within Lesini Ash Forest and the ecological factors governing this differentiation, $b$ ) floristic diversity issues of the distinguished plant communities, and c) the forest structural characteristics and their relations to the floristic differentiation of the plant communities and the plant diversity they possess.

## MATERIALS AND METHODS

## Study area

The Fraxinus angustifolia subsp. oxycarpa - Ulmus minor subsp. minor forest is located in Western Greece approximately 3 km NW of the village Lesini and covers an area of 46 ha (Fig. 1). The altitude varies from 1 m to 10 m a.s.l. The climate is Meditteranean warm with dry summer and mild winter and belongs to the Csa type according to Koeppen classification. According to Mavrommatis (1980), the area belongs to the sub-humid bioclimatic level with mild winters and a 5-month dry period (Kladis, 2009). The bioclimatic "character" is intense meso-Meditteranean and the number of days of biological drought varies annually between 75 and $100(75<x<100)$. The vegetation of the wider area belongs to the formation of holm oak (Quercion ilicis). The substrate of the site is alluvium.

At the beginning of the 20th century, the former swamps of Lesini were still characterized by a widespread shallow lake during winter flooding. The first


FIG. 1. Geographical location of Lesini ash forest and position of the 46 sample plots in the studied area. Numbers of vegetation units correspond to those in Table 1.
attempts to transform part of this land for agricultural purposes, using draining works, were undertaken in 1930 (Vött et al., 2003, 2007). The existing forest is remnant of formerly much more extensive and widespread wetland forests almost reaching Acheloos river delta and was characterized as a natural monument in 1985. The absence of any regeneration in the forest and the great intensity of goat grazing have been underlined by Szijj (1983). Since 1985, some rather ineffective management measures have been taken to preserve this relict forest mainly by more drainage, grazing and logging.

## Vegetation and soil data

Field data were collected from September 2007 to May 2009. In total, forty-six plots were sampled, each plot having an area of $200 \mathrm{~m}^{2}$ (Fig. 1). All vascular plant species observed in each plot were recorded and their cover was estimated using the modified BraunBlanquet scale (Barkman et al., 1964).

Species nomenclature follows Flora Hellenica (Strid \& Tan, 1997, 2002), Med-Checklist (Greuter et
al., 1984-1989), and Flora Europaea (Tutin et al., 19681980, 1993).

Soil samples were collected in late spring 2008 from twelve profiles representing the whole range of ecological conditions and vegetation communities occurring in the study area. From each soil profile two samples were taken representing the soil depths 0-30 and $30-60 \mathrm{~cm}$ (humus layer and surface litter were excluded), and the following parameters were measured: acidity (determined electrometrically in a $1: 1$ soil-water slurry), organic matter content (wet oxidation method; Nelson \& Sommers, 1982), particle size distribution (hygrometer method; Bouyoucos, 1962) and $\mathrm{CaCO}_{3}$ content (Bernard's calcimeter method).

## Data Analysis

## 1. Stand Structure Analysis

In each vegetation plot, the diameter at breast height (DBH) and height of Fraxinus angustifolia subsp. oxycarpa and Ulmus minor subsp. minor trees with DBH over 4 cm were recorded. Tree basal area was calcu-
lated using the formula: Basal area $=\left(\pi \times \mathrm{DBH}^{2}\right) / 4$ (Husch et al., 1982). The basal area per plot was found by calculating the sum of the basal areas of all trees within the plot area. The basal area per ha $\left(\mathrm{m}^{2} \mathrm{ha}^{-1}\right)$ of $F$. angustifolia subsp. oxycarpa and the co-dominant U. minor subsp. minor, was estimated by multiplying the mean basal area $\left(\mathrm{m}^{2}\right)$ per plot $\left(200 \mathrm{~m}^{2}\right)$ by $50(200$ $\left.\mathrm{m}^{2} \times 50=10,000 \mathrm{~m}^{2}=1 \mathrm{ha}\right)$. To calculate the density per ha ( $\mathrm{N} \mathrm{ha}^{-1}$ ) of $F$. angustifolia subsp. oxycarpa and U. minor subsp. minor, the mean density (trees per sample plot) per plot ( $200 \mathrm{~m}^{2}$ ) was multiplied by 50 . To quantify the variation of height and diameter distribution, the standard deviation in relation to mean values was calculated. Neumann \& Starlinger (2001) noticed that this simple measure performs quite well for tree size diversity.

Furthermore, the Cox Index of clumping (Neumann \& Starlinger, 2001; MacElhinny, 2002) was calculated to investigate the patterns of dominant tree species spatial distribution. The Cox Index can reveal if individuals of a species are clustered, regular or randomly distributed.

To assess the age structure of $F$. angustifolia subsp. oxycarpa trees in the forest, a dendrochronological investigation was conducted. Fifteen trees were selected, to represent all available diameter classes. To investigate the effects of light stress on ash tree growth dominant trees with little to no shade on their canopy from neighbouring trees were selected together with a smaller number of non dominant (subcanopy) trees that appeared to be strongly shaded. At least two cores were taken from opposite sides of each tree with a 5 mm increment corer (Suunto, Finland) at breast height ( DBH ), ca. 1.3 m from the ground; the diameter of each sampled tree at this height was recorded. When more than one core per tree side was available, the one reaching closest to the pith was used. Cores were mounted on channelled wood holders, air dried and sanded in the laboratory (with 120 P and 400 P sand paper). The age of cores containing the pith was determined by counting the number of tree-rings from bark to pith. The number of missing rings in cores that failed to hit the pith was estimated by assuming homocentric circles of tree rings.

## 2. Vegetation Data Analysis

Vegetation data were entered into the TURBOVEG vs. 2 database system (Hennekens \& Schaminée, 2001) and then imported to the JUICE software (Ti-
chý, 2002) for data analysis. Plots were classified using cluster analysis with the relative Euclidean distance and the Ward's method of clustering. Species occurring in one only plot, were omitted and species recorded in different layers were merged into one layer. Species cover values were square-root transformed before the analysis.

Differential species were determined using the algorithm of Tsiripidis et al. (2009). Only the species found differentiating (positively or negatively) all the vegetation units were considered as differential.

For the ecological interpretation of floristic differentiation between the distinguished vegetation units, Detrended Correspondence Analysis (DCA) was applied. DCA is considered as an appropriate analysis of community compositional data, even in the case of short environmental gradients (e.g. between 2 and 3 s.d.) (ter Braak \& Šmilauer, 2002; Lepš \& Šmilauer, 2003). Before DCA analysis, species cover values were transformed into square-root values. Furthermore, in the DCA, several variables were used as passive explanatory ones aiming to aid interpretation and exploration of floristic diversity differentiation and stand structure issues within the data set.

Floristic diversity of plots was assessed by calculating the Shannon $\left(\mathrm{H}^{\prime}\right)$ and Simpson (D) indices and the corresponding evenness measures ( $\mathrm{J}^{\prime}$ and $\mathrm{E}_{1 / \mathrm{D}}$ ). The reciprocal (1/D) expression of the Simpson's index was applied. The Shannon index stresses the species richness component, whilst the Simpson index emphasises dominance as opposed to the richness (Nagendra, 2002; Magurran, 2004). Measures of evenness remove the effect of species richness (Neumann \& Starlinger, 2001; Magurran, 2004). Diversity and evenness indices were calculated using the total floristic composition of the plots and the subgroups of the species in each plot. These subgroups were formed according to the vegetation units (types) in which the species preferably occur. The idea of the preferable occurrence of species in certain vegetation units or, in other words, the fidelity of species to certain vegetation units, is a fundamental concept of the phytosociological or Braun-Blanquet approach of vegetation classification (e.g. Braun-Blanquet, 1932; Westhoff \& van der Maarel, 1978; Dierschke, 1994; Chytrý et al., 2002; van der Maarel, 2005). According to this fidelity concept, species are considered as diagnostic of certain vegetation units. Here the species were classified according to the phytosociological class for which they are considered as diagnostic according to Muci-
na (1997) and secondarily to Horvat et al. (1974). To simplify the species classification scheme and avoid having species groups with very few members, the final species groups reflected the vegetation types (e.g. temperate forest vegetation, synanthropic vegetation) in which the species preferably occur. This was done by using the grouping of phytosociological classes to vegetation types according to Mucina (1997). For each vegetation type and plot the above-mentioned diversity and evenness indices were calculated.

In addition to the diversity and evenness indices, stand structure characteristics per plot were used as passive variables in the DCA. Stand structure characteristics concerned tree layer cover (T-C), shrub layer cover (S-C), sum of tree and shrub layers cover (WC), maximum tree (or shrub when no tree layer exists) height (V-H), maximum tree diameter at breast height ( mDBH ), maximum height and diameter at breast height of $U$. minor or $F$. angustifolia trees (UH, U-DBH, F-H and F-DBH, respectively) and total basal area per plot of $U$. minor or $F$. angustifolia trees as well as of both species together (U-BA, F-BA and BA, respectively). Furthermore, geographical coordinates ( X and Y ) of each plot were used as explanatory variables. The latter were calculated as the distances in meters in the north and east direction from the southern and westernmost plot of the study area. The use of coordinates was aiming to account for any spatial structured ecological differentiation, especially regarding the hydrological regime.

The non-parametric Spearman's rho correlation coefficient between the explanatory variables and the plot scores on the first two DCA axes was calculated. Furthermore, to explore the existence of any significant relationships between species diversity and stand structure characteristics the same correlation coefficient was calculated between the diversity and evenness indices and the stand characteristics per plot.

The correlation of soil analyses results with the corresponding DCA plots scores was calculated using Spearman's rho correlation coefficient to explore soil property differentiation among plots.

Finally, the values of the diversity and evenness indices of the plots belonging to different vegetation units were compared using the Mann-Whitney U test. In addition, the following tree size measurements were compared between the vegetation units also using the Mann-Whitney U test: tree height and DBH, height and DBH of $F$. angustifolia trees and height and DBH of $U$. minor trees. In these comparisons, the total number of measured trees per vegetation unit
was used. To deal with the problem of multiple comparisons in the Mann-Whitney U tests, $p$ values were adjusted using the Bonferroni correction.

DCA was applied using CANOCO ver. 4.5 software (ter Braak \& Šmilauer, 2002), classification of plots was done using PC-ORD ver. 5 software (MacCune \& Mefford, 1999), and correlation coefficients and Mann-Whitney U tests were calculated using SPSS ver. 15 (Chicago, USA).

## RESULTS

## Vegetation classification

Cluster analysis resulted in the distinction of three vegetation units (Table 1). The criterion for deciding the final number of clusters was the distinction of those which can be clearly differentiated floristically and interpreted ecologically.

The first vegetation unit comprises eight plots and is differentiated by the species Mentha aquatica, $L y$ copus europaeus, Iris pseudacorus, Polypogon monspeliensis, Conyza bonariensis, Apium nodiflorum and Carex remota. Three of the differential species are diagnostic of the Phragmito-Magnocaricetea, which is a class of fresh-water marshes and fens. The soil in this vegetation unit has higher moisture values compared to the other two units. Furthermore, it has higher percentages of clay and organic matter, and lower of sand and $\mathrm{CaCO}_{3}$ content (Table 2).

The second vegetation unit includes 15 plots. It is mainly negatively differentiated from the other two units and presents floristic affinities with both the first and third vegetation units. The two soil profiles sampled in this unit indicate that its soils are relatively richer in sand and poorer in clay than unit 1 (Table 2).

The third vegetation unit comprises 23 plots and is differentiated by the species Galium aparine, Hedera helix, Tamus communis and Vicia grandiflora. Apart from G. aparine which is nitrophilous preferentially occurring in synanthropic vegetation, the other species are diagnostic of temperate forests. The soil in this unit has high pH values (7.67-8.15), is richer in sand and $\mathrm{CaCO}_{3}$ and poorer in clay and organic matter than the first vegetation unit (Table 2).

## Ordination and diversity

In the DCA diagram of the plots (Fig. 2) the three vegetation units are discriminated along the first axis. The first and second DCA axes have lengths equal

TABLE 1. Differential species table of the 46 plots sampled at the Lesini area (West Greece). Second column presents the constancy of taxa in the table. Species cover values $m$, $a$ and $b$ correspond to the $2 \mathrm{~m}, 2 \mathrm{a}$ and 2 b of the modified Braun-Blanquet scale. Companion species occurring in five or less plots were omitted


TABLE 1. continues

| Vegetation unit | 1 | 2 | 3 |
| :---: | :---: | :---: | :---: |
| Plot number | 43123433 | 112111122191273 | 24444142332534328232316 |
|  | 52803654 | 951763043412 | 60142288693795071 |
| Prunella vulgaris | $13 . .$. | r + . + 1. +a 1 a | . 1 . . . 1. |
| Carex spicata | 12.1 ba 1 | a $\mathrm{ra}+\mathrm{a}$ | 1 . . 1 . . . . . . . 1 |
| Torilis nodosa | 1211 | $11+1$ | $1+++1.1$ |
| Quercus coccifera | 9 | +r r | . . . . r . . r . r . . . . . . . . r |
| Lathyrus hirsutus | $8 . .+r$ | 1...+ | 111 |
| Plantago major | $81+.+$ | + r | r . . . . . . . . . . . . r |
| Vicia sativa | 8 | . $1+$. + . . . 1 | . 1 a $1+$. |
| Agrostis stolonifera | 7 | . . . 1 . a | +11.1 |
| Avena sterilis | 7 | . m. . . . . . 1 | . 11 .+. . . 1 . 1 |
| Notobasis syriaca | 7 | 1 | . a $1 .+$. . . . . . b . . . . . . . . b |
| Rumex pulcher subsp. pulcher | 7 | . 1 | . a 1 . . . . . 111 |
| Sisymbrium officinale | 7 |  | . + . 1.1 |
| Vicia lutea | 7 . + + | + r . . . . + . . . | + |
| Vitis vinifera subsp. sylvestris | 6 .....+ | r . . . a . . . . . . | . + . |
| Convolvulus arvensis | 6 | . a b | . 11 a . . . . . 1 |
| Cynosurus elegans | 6 | +. . . . 1 | . 11 . . |
| Verbena officinalis | 6 . . . 1 | . .+1 | $1 .+$ |

Compagnions: Daucus carota 11 (r), 24 (r), 26 (r), 31 (+), 32 (1), Ficus carica 12 (+), 25 (+), 36 (b), 44 (+), 46 (a), Juncus inflexus 18 (1), 19 (a), $20(\mathrm{a}), 22(+), 33(+)$, Medicago arabica $1(+), 3(\mathrm{a}), 6(\mathrm{~m}), 11(+), 28(\mathrm{a})$, Silybum marianum $3(1), 8$ (1), $28(+), 31(1), 37(1)$, Celtis australis $6(\mathrm{r}), 12(+), 33(\mathrm{r}), 44$ (r), Juncus acutus 15 (a), $31(+), 33(+), 35(\mathrm{a})$, Prunus species $1(+), 2(+), 26(\mathrm{r}), 31(\mathrm{r})$, Urtica pilulifera $1(+), 34(+), 43(+), 46(+)$, Alopecurus utriculatus $15(1), 19(+), 20(\mathrm{r})$, Carex pendula 11 (r), 37 (r), 44 (r), Delphinium staphisagria 27 (r), 39 (r), 40 (+), Euphorbia platyphyllos 18 (1), 43 (a), 44 (1), Laurus nobilis $5(\mathrm{r}), 25(+), 44(3)$, Lolium multiflorum $7(1), 18(+), 22(+)$, Mercurialis annua $1(\mathrm{~b}), 25(\mathrm{r}), 27(\mathrm{r})$, Sherardia arvensis $2(+), 12(\mathrm{r}), 25(\mathrm{r})$, Stellaria neglecta $1(\mathrm{a}), 2(+), 7(1)$, Tilia tomentosa $10(\mathrm{r}), 33(\mathrm{r}), 46(+)$, Verbascum blattaria $7(+)$, $37(+), 43(+)$, Anagallis arvensis $7(1), 8(+)$, Bromus hordeaceus $26(+), 40(1)$, Crepis neglecta subsp. corymbosa $16(1), 44$ (1), Lamium bifidum subsp. bifidum 5 (r), 7 (1), Olea europaea subsp. oleaster 4 (+), 5 (r), Paliurus spina-christi 6 (a), 39 (a), Populus alba 5 (4), 42 (3), Ranunculus muricatus 1 (+), 6 (1), Teucrium scordium subsp. scordioides 31 (1), 35 (+), Trifolium squamosum 17 (1), 19 (1), Urospermum picroides 9 (1), 26 (1)
to 2.585 and 2.121 and eigenvalues equal to 0.315 and 0.169 , respectively. The first two DCA axes account for $16.6 \%$ (first axis $10.8 \%$ and second axis $5.8 \%$ ) of the total species data variance (total inertia: 2.91). The first axis reflects the soil moisture content and soil texture of the second soil layer, as well as the nutrient content, soil acidity and $\mathrm{CaCO}_{3}$ content of both soil layers (Table 2). Specifically, plots with soils richer in moisture and organic matter, having less sand content, lower pH and $\mathrm{CaCO}_{3}$ content, appear on the right part of the first axis, where the plots of the first vegetation unit are located. The second axis does not contribute to the discrimination of the vegetation units and presents a significant correlation with organic matter content (positive) and pH (negative) (Table 3). On the basis of its correlation with the diversity and evenness indices it appears to reflect the
degree of disturbance. Plots X and Y coordinates present significant correlations with the DCA axes (Table 2) and from the distribution of the vegetation units in the study area (Fig. 1) a spatial differentiation is revealed. Specifically, plots of the first vegetation unit are mainly confined to the western part of the study area, presenting a linear distribution, probably because of this unit's dependence on the streams crossing the study area. Plots of the second vegetation unit are located in the southeastern part of the study area.

In Table 3 the Spearman's rho correlation coefficients of the passive explanatory variables with the first two DCA axes are given (see also Fig. 2B). Most explanatory variables present significant correlations with the first two DCA axes. The first axis is positively correlated with fresh-water species diversity and

TABLE 2. Minimum, median and maximum values of soil variables per vegetation unit (vegetation units are indicated by the numbers 1, 2 and 3). The last two columns present the Spearman's rho correlation coefficients (one and two asterisks indicate significant correlation at the 0.05 and 0.01 probability level, respectively) of soil variables with the first and second DCA axes (AX1 and AX2, respectively). SH: soil humidity (\%), $\mathrm{Sa}, \mathrm{Si}$ and Cl : sand, silt and Clay (\%), O.M.: organic matter content (\%) and $\mathrm{CaCO}_{3}$ : calcium carbonate content (\%)

|  | Veget. unit | 1 | Minimum | 3 | 1 | $\begin{gathered} 2 \\ \text { Median } \end{gathered}$ | Maximum |  |  |  |  | AX2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $1{ }^{\text {st }}$ | SH | 0.50 | 0.00 | 0.00 | 17.20 | 0.00 | 0.00 | 19.50 | 0.00 | 4.20 | 0.40 | 0.43 |
| layer | pH | 7.31 | 7.67 | 7.67 | 7.72 | 7.70 | 7.92 | 7.84 | 7.73 | 8.15 | -0.75** | -0.65* |
|  | Sa | 22.00 | 32.00 | 26.00 | 27.00 | 37.00 | 32.60 | 38.20 | 42.00 | 42.00 | -0.30 | 0.18 |
|  | Si | 5.00 | 6.00 | 5.00 | 6.00 | 8.00 | 7.00 | 8.00 | 10.00 | 9.00 | 0.03 | 0.28 |
|  | Cl | 54.80 | 52.00 | 54.00 | 67.00 | 55.00 | 58.40 | 73.00 | 58.00 | 69.00 | 0.17 | -0.25 |
|  | O.M. | 5.66 | 3.53 | 3.53 | 7.07 | 4.56 | 4.24 | 9.90 | 5.66 | 4.95 | 0.81** | 0.58* |
|  | $\mathrm{CaCO}_{3}$ | 8.61 | 10.25 | 22.14 | 10.60 | 12.80 | 22.72 | 11.89 | 15.38 | 26.65 | -0.66* | -0.09 |
| $2^{\text {nd }}$ | SH | 4.00 | 0.00 | 0.00 | 28.40 | 0.75 | 0.50 | 41.10 | 1.50 | 6.20 | 0.70* | 0.33 |
| layer | pH | 7.31 | 7.68 | 7.83 | 7.70 | 7.69 | 7.89 | 7.90 | 7.70 | 8.05 | -0.64* | -0.61* |
|  | Sa | 14.00 | 24.00 | 18.00 | 16.80 | 26.00 | 29.60 | 21.20 | 28.00 | 32.00 | -0.61* | 0.12 |
|  | Si | 6.00 | 6.00 | 4.00 | 7.00 | 6.00 | 5.00 | 10.00 | 6.00 | 10.00 | 0.49 | -0.11 |
|  | Cl | 68.80 | 66.00 | 60.40 | 76.20 | 68.00 | 64.00 | 78.00 | 70.00 | 78.00 | 0.38 | -0.14 |
|  | O.M. | 2.62 | 1.41 | 1.20 | 5.66 | 2.12 | 2.12 | 7.07 | 2.83 | 2.12 | 0.82** | 0.38 |
|  | $\mathrm{CaCO}_{3}$ | 7.79 | 13.33 | 22.55 | 14.76 | 15.89 | 24.60 | 24.19 | 18.45 | 27.10 | -0.64* | -0.21 |

TABLE 3. Spearman's rho correlation coefficients of explanatory variables with the samples scores on the first two DCA axes (one and two asterisks indicate significant correlation at the 0.05 and 0.01 probability level, respectively). Abbreviations: D, H, R (used after the dash together with the abbreviations All, FV, GV, MV, SV and WV): Simpson and Shannon diversity indices, and species richness, respectively; E, J (used after the dash together with the abbreviations All, FV, GV, MV, SV and WV): Simpson and Shannon evenness indices, respectively; All: total floristic composition; FV: forest vegetation; GV: grassland vegetation; MV: Mediterranean vegetation; SV: synanthropic vegetation, WV: fresh-water vegetation; for the rest abbreviations see Vegetation Data Analysis section (Material and Methods)

| Variable | AX1 | AX2 | Variable | AX1 | AX2 |
| :---: | :--- | :---: | :---: | :---: | :---: |
| All-D | $-0.45^{* *}$ | $-0.45^{* *}$ | SV-H | $-0.31^{*}$ | $-0.32^{*}$ |
| All-E | $-0.51^{* *}$ | -0.20 | SV-J | 0.28 | 0.11 |
| All-H | $-0.32^{*}$ | $-0.51^{* *}$ | SV-R | $-0.44^{* *}$ | $-0.40^{* *}$ |
| All-J | $-0.39^{* *}$ | $-0.52^{* *}$ | WV-D | $0.71^{* *}$ | 0.05 |
| All-R | -0.05 | $-0.34^{*}$ | WV-E | $0.46^{* *}$ | -0.03 |
| FV-D | $-0.63^{* *}$ | 0.15 | WV-H | $0.64^{* *}$ | 0.12 |
| FV-E | -0.12 | -0.18 | WV-J | $0.64^{* *}$ | 0.12 |
| FV-H | $-0.64^{* *}$ | 0.19 | WV-R | $0.71^{* *}$ | 0.04 |
| FV-J | $-0.54^{* *}$ | -0.15 | T-C | 0.10 | $0.46^{* *}$ |
| FV-R | $-0.56^{* *}$ | $0.32^{*}$ | S-C | -0.22 | 0.12 |
| GV-D | $0.41^{* *}$ | $-0.33^{*}$ | W-C | -0.02 | $0.37^{*}$ |
| GV-E | -0.17 | 0.14 | V-H | 0.06 | 0.29 |
| GV-H | $0.41^{* *}$ | $-0.33^{*}$ | mDBH | 0.08 | 0.21 |
| GV-J | 0.05 | 0.04 | U-H | $-0.57^{* *}$ | -0.21 |
| GV-R | $0.41^{* *}$ | $-0.35^{*}$ | U-DBH | $-0.57^{* *}$ | -0.22 |
| MV-D | $-0.34^{*}$ | 0.01 | F-H | 0.19 | $0.35^{*}$ |
| MV-E | -0.01 | -0.27 | F-DBH | 0.19 | 0.27 |
| MV-H | $-0.38^{* *}$ | 0.08 | BA | 0.18 | $0.32^{*}$ |
| MV-J | $-0.34^{*}$ | -0.02 | F-BA | $0.34^{*}$ | $0.40^{* *}$ |
| MV-R | -0.28 | 0.09 | U-BA | $-0.42^{* *}$ | -0.10 |
| SV-D | -0.21 | -0.20 | X | -0.23 | $-0.36^{*}$ |
| SV-E | $0.41^{* *}$ | $0.34^{*}$ | Y | $-0.42^{* *}$ | $-0.37^{*}$ |




FIG. 2. Ordination diagram of plot scores and differentialdominant species scores on the first two DCA axes (A) and of the explanatory variables passively projected in the ordination space of plots (B). Vegetation unit 1: stars, Vegetation unit 2: boxes, Vegetation unit 3: rhombs.

TABLE 4. Minimum, median and maximum values of diversity and evenness indices per vegetation unit. Asterisks indicate significantly different diversity or evenness values between the vegetation units according to the Mann-Whitney $\mathbf{U}$ test ( $p$ $\leq 0.016$; adjusted after the Bonferroni correction for multiple comparisons). Abbreviations as in Table 3

negatively correlated with forest and Mediterranean species diversity. Grassland species diversity is positively related with the first axis and negatively with the second, while synanthropic species diversity and total floristic diversity of the plots are negatively correlated with both axes. Interestingly the evenness measures show similar trends (correlations) with the diversity indices for the total floristic composition of the plots and certain species groups (fresh-water, forest and Mediterranean vegetation), while some other species groups (grassland vegetation) are not significantly correlated with any DCA axis or they show a completely opposite trend (synanthropic vegetation). In general, a lower proportion of evenness measures show significant correlation with DCA axes compared with the diversity indices and species richness. The latter presents similar trends with the diversity indices.

In Table 4 the minimum, median and maximum values of diversity and evenness measures are given for each vegetation unit. Significant differences between the vegetation units were found (Mann-Whitney U test; $p \leq 0.016$ ) mainly for the diversity and evenness indices of the temperate forest and fresh-water species. Diversity of the temperate forest species was found to increase from the first to the second and
then to the third vegetation unit, while the diversity and evenness (according to Shannon indices) of the fresh-water species were found to be significantly higher in the first vegetation unit. Furthermore, total floristic diversity and evenness (according to Simpson indices) were found to be significantly lower in the first unit than the third. Finally, synanthropic species richness was found significantly higher in the third vegetation unit and the diversity and species richness of the grassland species was higher in the second unit.

## Stand structure

Fraxinus angustifolia subsp. oxycarpa and Ulmus minor subsp. minor are respectively the dominant and codominant species of the investigated riparian forest stands. The basic statistic results for 300 trunks located in the sample plots are presented in Table 5 and the stand characteristics related to the number of $F$. angustifolia subsp. oxycarpa and $U$. minor subsp. minor individuals in different classes of height and DBH are given in Figures 3 and 4.

The Cox Index of clumping values is $7.24,10.62$ and 0.52 , for the first, second and third vegetation unit, respectively, thus indicating a clustered horizontal distribution of Fraxinus trees for the first two vegetation units and a regular distribution for the third.

TABLE 5. Fraxinus angustifolia subsp. oxycarpa and Ulmus minor subsp. minor stand characteristics in the study area (DBH $>4 \mathrm{~cm}$ )

| Species | DBH (cm) |  | Height (m) |  | Basal area | Density |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Mean | s.d. | Mean | s.d. | $\left(\mathbf{m}^{\mathbf{2}} \mathbf{h a}^{\mathbf{- 1})}\right.$ | $\left(\mathbf{N o ~ h a}^{\mathbf{- 1})}\right.$ |
| Fraxinus | 35.14 | 7.4 | 14.9 | 7.4 | 8.16 | 250 |
| Ulmus | 36.1 | 24.7 | 17.1 | 6.9 | 7.41 | 50 |
| Fraxinus \& Ulmus | 35.2 | 28.6 | 15.1 | 7.3 | 8.08 | 300 |

TABLE 6. Minimum, median and maximum values of tree height, diameter at breast height (DBH), height and DBH of Fraxinus angustifolia trees (Height-Fraxinus and DBH-Fraxinus, respectively) and height and DBH of Ulmus minor subsp. minor trees (Height-Ulmus and DBH-Ulmus, respectively) per vegetation unit ( ${ }^{*} p \leq 0.016,{ }^{* *} p \leq 0.05$ )

| Veget. <br> unit | $\mathbf{1}$ | $\mathbf{2}$ <br> Minimum | $\mathbf{3}$ | $\mathbf{1}$ | $\mathbf{2}$ <br> Median | $\mathbf{3}$ | $\mathbf{1}$ | $\mathbf{2}$ <br> Maximum | $\mathbf{3}$ | $\mathbf{1} \boldsymbol{v s} \mathbf{2}$ | $\mathbf{1} \boldsymbol{v s} \mathbf{3}$ | $\mathbf{2} \boldsymbol{v} \mathbf{3}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Height $(\mathrm{m})$ | 3.50 | 5.50 | 8.00 | 11.00 | 10.00 | 22.00 | 31.00 | 32.00 | 30.00 |  | $*$ | $*$ |
| DBH $(\mathrm{cm})$ | 5.40 | 5.70 | 23.50 | 16.35 | 13.81 | 56.05 | 104.40 | 101.90 | 107.60 |  | $*$ | $*$ |
| Height-Fraxinus | 3.50 | 5.50 | 8.00 | 11.00 | 10.50 | 22.00 | 31.00 | 32.00 | 29.00 |  | $*$ | $*$ |
| DBH-Fraxinus | 5.40 | 5.70 | 33.10 | 16.35 | 15.20 | 62.10 | 104.40 | 101.90 | 107.60 | $*$ | $*$ |  |
| Height-Ulmus |  | 6.50 | 13.00 |  | 9.50 | 22.00 |  | 22.00 | 30.00 |  | $* *$ |  |
| DBH-Ulmus |  | 5.70 | 23.50 |  | 11.10 | 42.00 |  | 88.80 | 90.70 |  | $* *$ |  |

The Mann-Whitney U test concerning tree characteristics (Table 6) revealed that the third vegetation unit has a significantly higher DBH and height for $F$. angustifolia and $U$. minor trees than the first and second units. In other words the first two vegetation units are covered by $F$. angustifolia and/or $U$. minor trees of low height and DBH, while the third unit has taller, mature trees. It should be noted that the first vegetation unit does not host Ulmus trees.

Thus, for dendrochronological analysis ash trees (shaded and non-shaded) of the third vegetation unit were more suitable for assessing the age for the for-
est's most mature tree stands (Fig. 5). Naturally shaded trees were found to grow slower per year and are older than their non-shaded counterparts for the same DBH. Results are based on fitted logarithmic curves (for not strongly shaded trees $r^{2}=0.24, P=0.12$, $\mathrm{n}=11$, while for shaded tress $r^{2}=0.93, P=0.04, \mathrm{n}=4$ ). As the majority of ash trees in the third vegetation unit are of 40-100 cm DBH (Fig. 4), their average age should be 60-75 years (80-120 years under strong light stress conditions). The third vegetation unit has the lowest soil moisture and nutrient content (Table 2) most likely leading to reduced wood productivity


FIG. 3. Number of individuals $\left(\mathrm{N} \mathrm{ha}^{-1}\right)$ per tree height distribution class for the three vegetation units. Black bars refer to Fraxinus angustifolia subsp. oxycarpa trees and white bars to Ulmus minor subsp. minor trees.


FIG. 4. Number of individuals $\left(\mathrm{N} \mathrm{ha}^{-1}\right)$ per diameter (DBH) distribution class in vegetation units 1-3. Black bars refer to Fraxinus angustifolia subsp. oxycarpa trees and white bars to Ulmus minor subsp. minor trees.
compared to the other two units. Because of these slower growth rates the oldest tree stands would be expected in areas of the third vegetation unit at any given DBH. Hence, current ash tree stands in the forest of the lowest DBH $(4-20 \mathrm{~cm})$ cannot be more that 60 years old, while trees of the highest DBH $(120 \mathrm{~cm})$ cannot be over 150 years old (especially for non-shaded trees; Figs 4 and 5).

The Spearman's rho correlation coefficients between the stand structure characteristics per plot and the diversity and evenness indices given in Table 7 re-
veal: a) the negative correlation of tree and woody species cover as well as the total basal area per plot of Fraxinus trees or Fraxinus and Ulmus trees with the total floristic diversity and evenness measures, b) the negative correlation of tree and woody species cover with the evenness indices of forest vegetation species, c) the positive correlation of forest species diversity indices with shrub cover and d) the negative correlation of Ulmus tree height, DBH and basal area with synanthropic vegetation species evenness measures.

FIG. 5. Age estimation curves for Fraxinus angustifolia subsp. oxycarpa trees based on all available tree diameters (DBH).


TABLE 7. Spearman's rho correlation coefficients between diversity/evenness measures and stand characteristics per plot. For abbreviations see Table 3 and Vegetation Data Analysis section (Material and Methods), ${ }^{*} p<0.05,{ }^{* *} p<0.01$

| Variab. | T-C | S-C | W-C | V-H | mDBH | U-H | U-DBH | F-H | F-DBH | BA | F-BA | U-BA |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| All-D | -0.57 ** | 0.25 | -0.36* | -0.33* | -0.23 | 0.21 | 0.23 | -0.28 | -0.21 | $-0.44 * *$ | -0.41 | - 0.05 |
| All-E | -0.62 ** | 0.26 | -0.4 ** | -0.35* | -0.21 | 0.25 | 0.28 | -0.32* | -0.23 | $-0.4 * *$ | -0.4 ** | 0.03 |
| All-H | -0.49 ** | 0.19 | -0.31* | -0.29 | -0.21 | 0.16 | 0.17 | -0.22 | -0.18 | -0.43 ** | $-0.38^{* *}$ | - -0.09 |
| All-J | -0.63** | 0.15 | -0.47** | -0.39** | -0.3* | 0.19 | 0.21 | -0.32* | -0.29 | -0.52 ** | -0.49** | -0.05 |
| All-R | -0.08 | 0.13 | 0.08 | -0.05 | -0.08 | 0.01 | -0.01 | -0.02 | -0.04 | -0.16 | -0.11 | -0.14 |
| FV-D | -0.25 | 0.54** | 0.04 | -0.17 | -0.07 | 0.25 | 0.27 | -0.05 | 0.00 | -0.17 | -0.14 | 0.03 |
| FV-E | -0.65 ** | 0.08 | -0.55** | $-0.52^{* *}$ | -0.33* | 0.07 | 0.09 | $-0.38^{* *}$ | - -0.22 | -0.39** | -0.28 | -0.17 |
| FV-H | -0.16 | 0.55** | 0.13 | -0.13 | -0.06 | 0.23 | 0.25 | -0.02 | -0.01 | -0.16 | -0.14 | 0.03 |
| FV-J | -0.49** | 0.41** | -0.22 | -0.29* | -0.14 | 0.22 | 0.24 | -0.17 | -0.07 | -0.28 | -0.22 | -0.06 |
| FV-R | 0.22 | 0.44** | 0.43** | 0.16 | 0.10 | 0.27 | 0.28 | 0.14 | 0.04 | 0.07 | -0.01 | 0.25 |
| GV-D | 0.12 | -0.01 | 0.20 | 0.16 | 0.11 | -0.12 | -0.11 | 0.10 | 0.07 | 0.10 | 0.15 | -0.13 |
| GV-E | -0.17 | 0.02 | -0.10 | 0.05 | 0.16 | -0.05 | -0.03 | 0.07 | 0.14 | 0.09 | 0.09 | 0.02 |
| GV-H | 0.11 | 0.02 | 0.20 | 0.13 | 0.07 | -0.11 | -0.10 | 0.08 | 0.04 | 0.07 | 0.12 | -0.14 |
| GV-J | 0.08 | 0.08 | 0.18 | 0.14 | 0.18 | 0.04 | 0.05 | 0.12 | 0.11 | 0.22 | 0.18 | 0.13 |
| GV-R | 0.10 | 0.00 | 0.18 | 0.10 | 0.01 | -0.08 | -0.08 | 0.05 | -0.01 | 0.01 | 0.07 | -0.14 |
| MV-D | 0.29 | -0.06 | 0.17 | 0.22 | 0.11 | 0.18 | 0.18 | 0.16 | 0.12 | 0.09 | 0.05 | 0.15 |
| MV-E | 0.02 | 0.06 | -0.04 | -0.09 | 0.03 | -0.08 | -0.08 | -0.05 | 0.05 | -0.09 | -0.06 | -0.15 |
| MV-H | 0.30* | -0.10 | 0.18 | 0.26 | 0.08 | 0.26 | 0.26 | 0.20 | 0.09 | 0.12 | 0.06 | 0.24 |
| MV-J | 0.34* | -0.16 | 0.17 | 0.30* | 0.14 | 0.27 | 0.28 | 0.22 | 0.12 | 0.17 | 0.08 | 0.27 |
| MV-R | 0.25 | 0.02 | 0.19 | 0.20 | 0.09 | 0.15 | 0.15 | 0.14 | 0.11 | 0.08 | 0.05 | 0.10 |
| SV-D | -0.20 | 0.10 | -0.13 | -0.16 | -0.12 | -0.06 | -0.08 | -0.08 | 0.00 | -0.18 | -0.10 | -0.23 |
| SV-E | 0.08 | 0.03 | 0.12 | 0.13 | 0.06 | $-0.52^{* *}$ | *-0.53** | 0.26 | 0.21 | 0.13 | 0.31* | -0.46** |
| SV-H | -0.21 | 0.06 | -0.14 | -0.19 | -0.16 | 0.05 | 0.02 | -0.16 | -0.08 | -0.23 | -0.19 | -0.16 |
| SV-J | -0.09 | 0.10 | -0.01 | 0.05 | -0.01 | -0.44** | *-0.46** | 0.18 | 0.13 | -0.03 | 0.16 | -0.45** |
| SV-R | -0.24 | 0.07 | -0.16 | -0.21 | -0.13 | 0.20 | 0.18 | -0.25 | -0.14 | -0.26 | -0.29 | -0.02 |
| WV-D | 0.19 | -0.08 | 0.14 | 0.09 | -0.04 | -0.24 | -0.27 | 0.19 | 0.05 | 0.01 | 0.11 | -0.12 |
| WV-E | 0.10 | 0.08 | 0.16 | 0.22 | 0.06 | -0.09 | -0.12 | 0.32* | 0.15 | 0.05 | 0.12 | 0.01 |
| WV-H | 0.21 | -0.22 | 0.06 | -0.07 | -0.11 | -0.31* | -0.31* | -0.03 | -0.08 | -0.02 | 0.08 | -0.22 |
| WV-J | 0.22 | -0.20 | 0.09 | -0.04 | -0.09 | -0.31* | -0.31* | 0.00 | -0.05 | 0.00 | 0.10 | -0.22 |
| WV-R | 0.19 | -0.09 | 0.13 | 0.08 | -0.05 | -0.24 | -0.27 | 0.17 | 0.04 | -0.01 | 0.10 | -0.12 |

## DISCUSSION

## Vegetation differentiation and diversity

Although the riparian forest studied occupies a small area (46 ha), it has relatively high community diversity. This is evident from the length of the DCA axes and the three vegetation types (community types) distinguished. Riparian forests are characterized by complex environmental gradients varying in space and time and resulting in a high diversity of plant communities and species (Nilsson et al., 1994; Ward, 1998; Ward et al., 2002; Renöfält et al., 2005; Lyon \& Gross, 2005). The diversity of riparian ecosystems is considered higher than that of adjacent non-riparian ones, but there are contradictory opinions and results concerning the effects of ecological processes and characteristics of riparian ecosystems (e.g. inundation, natural disturbances, silting, high productivity) on species diversity (see Pollock et al., 1998; Bendix \& Hupp, 2000; Rosales et al., 2001; Decocq, 2002; Suzuki et al., 2002). Scale, climate type, and frequency as well as intensity of disturbances play a determinant role on how diversity is affected by the ecological processes of riparian ecosystems (Bendix \& Hupp, 2000; Suzuki et al., 2002).

The first DCA axis represents one of the main gradients of vegetation differentiation in riparian forests, responsible for vegetation zonation in riparian ecosystems (see Ellenberg, 1988). Specifically, it expresses the differentiation of soil texture and nutrient content. All the other soil variables $\left(\mathrm{pH}, \mathrm{CaCO}_{3}\right.$ content and soil humidity), being correlated with the first DCA axis, are highly dependent on soil texture. Especially soil humidity is much favoured in fine textured soils because of the rise that such soils cause to ground water level. The latter becomes a crucial factor in riparian forests where flooding does not longer exist. Vasilopoulos et al. (2007) found similar ecological factors related with the first DCA axis for the remnants of a natural riparian forest in Nestos Delta (NE Greece), and also for the plantations of fast growing trees, replacing the natural forest in some areas. Decocq (2002) found that for the riparian forest of the River Oise (France) a-diversity at both synusia and plant community levels (local scale) is controlled by abiotic factors, mainly soil properties (soil nutrient, reaction, moisture and depth), light and flooding-induced disturbances. Furthermore, Lyon \& Gross (2005) found that tree assemblages of riparian forests were correlated with soil factors and topography.

The second DCA axis expresses the degree of dis-
turbance. Indeed, the distinction of species groups according to the vegetation communities they prefer, revealed that a significant proportion (35.2\%) of the recorded species in the study area are of synanthropic origin, belonging mainly to the Stellarietea mediae (Mucina, 1997). Ruderal species are common in riparian forests (Naiman et al., 1993; Nilsson et al., 1994; Tabacchi et al., 1996; Bendix \& Hupp 2000; Glaeser \& Wulf, 2009). However, these species may be common where natural disturbances of riparian ecosystems occur, not because they can tolerate them, but because they are rapid colonizers of bare ground, free from competition (Bendix \& Hupp, 2000). However, in landscapes under human influences, riparian communities are influenced both by natural (hydrological, geomorphological) and human-induced disturbance regimes. Furthermore, riparian systems may be easily invaded by "external" species following changes in landscape structure (Tabacchi et al., 1996; Lyon \& Gross, 2005). In the present study, based on the correlation of diversity and evenness indices, as well as of stand structure characteristics with the DCA axes (see the discussion below), we may infer that the second DCA axis represents mainly anthropogenic disturbances. Such types of disturbances were documented during sampling and concern grazing and recreational activities. The fact that the studied riparian forest is surrounded by agricultural land is also expected to increase the hemeroby of its floristic composition (Tabacchi et al., 1996; Lyon \& Gross, 2005).

Most of the diversity and evenness indices are correlated mainly with the first DCA axis. This indicates that total species as well as species group diversity and evenness are differentiated along the main ecological gradient. The first vegetation unit has the highest soil moisture, nutrient content and finest soil texture, but presents the lowest total species and forest vegetation species diversity. On the other hand, the highest diversity and evenness of fresh-water vegetation species is presented in this unit. Although synanthropic species diversity and richness is low in this vegetation unit, their evenness is maximized. The first vegetation unit is more strongly affected by factors such as waterlogging and silting than the other two units as it is found growing along the streams crossing the study area. Although fresh-water specialist species richness is high in this vegetation unit, total plant species richness is very low. This is corresponding to many other authors findings (e.g. Mountford \& Chapman, 1993; Deiller et al., 2001; Van Looy et al., 2004; Glaeser \&

Wulf, 2009). According to them, riparian areas suffering frequent and very strong natural disturbances from inundations, silting and waterlogging, present the very low floristic diversity. In these riparian areas many species are excluded by habitat filtering and only riparian specialists, or species that can tolerate the above-mentioned natural disturbances can grow and reproduce. On the other hand, the increase in diversity and evenness of forest vegetation species from the first to the second and then to the third vegetation unit (Table 4) reveals a gradient of decreasing disturbance and stress from waterlogging. This gradient corresponds to the terrestrialization gradient described by other authors for older terraces in riparian landscapes, no longer affected by floods (cf. Worbes, 1997; Deiller et al., 2001; Richardson et al., 2007; Glaeser \& Wulf, 2009). As the natural disturbance constraints disappear, the opportunity arises for new species to colonize, and long term species composition may change due to the immigration of non-alluvial species. In the present study, these species are diagnostic of temperate forests and scrub (e.g. Melissa officinalis, Brachypodium sylvaticum subsp. sylvaticum, Hedera helix, Tamus communis, Vicia grandiflora, Crataegus monogyna). Furthermore, along this gradient of disturbance, Mediterranean, grassland and synanthropic vegetation species also increase, although their diversity and evenness do not significantly differentiate between the three vegetation units.

Floristic diversity is also affected by the human disturbance gradient represented by the second DCA axis. As human disturbance (its intensity assessed intuitively by indicators such as grazing, proximity to cultivations and drainage pipes) increases, the total species diversity and evenness, as well as the diversity of grassland and synanthropic species also increase.

Stand structure characteristics are correlated with both DCA axes. The height, DBH and basal area of Ulmus trees are negatively correlated, whereas the basal area of Fraxinus trees is positively correlated with the first DCA axis. These correlations are due to the differences in tree composition and structure between the three vegetation units, which are discriminated along the first DCA axis. This difference in tree composition and structure is obvious from the different height and diameter (DBH) frequency distribution between the vegetation units (Figs 3 and 4 and Table 6).

Combining findings from analyzing soil properties, the DBH frequency distribution in all vegetation
units and the dendrochronological investigation in the third vegetation unit, suggest that in the first vegetation unit the majority of Fraxinus trees are younger than Fraxinus trees in the third vegetation unit. The second vegetation unit has stands of intermediate age between the other two units. Furthermore, the Cox Index for clumping indicated a clustered horizontal distribution of Fraxinus angustifolia trees for the first two vegetation units and a regular distribution for the third one. Therefore, the three vegetation units may not be differentiated based only on soil properties and proximity to streams, but also because they represent different succession stages. According to Glaeser \& Wulf (2009) differences in the herbaceous layer composition in forests could be attributed to differences in habitat continuity in unflooded riparian forests, a fact which is known to occur in zonal forests as well.

The second DCA axis is correlated with tree and woody species layer cover, the height of Fraxinus trees and the basal area of Fraxinus trees and that of Fraxinus and Ulmus trees together. The decrease of the above characteristics indicates increased intensity of disturbances, possibly human (Table 7).

The Spearman correlation between the stand structure characteristics and the diversity/evenness indices (Table 7) reveals that the highest is the cover of tree layer (measured as percentage cover or basal area), the lowest are the total species diversity and evenness measures. Furthermore, the more mature the Ulmus trees (maturity is indicated by height and DBH), the less the evenness of synanthropic species. As diversity of the latter species does not follow the same pattern, we can say that in the stands with younger Ulmus trees, few ruderal species dominate in the understorey. The effect of total tree layer cover, height and DBH of Ulmus trees on the floristic diversity and evenness may be attributed to: a) light conditions within stands (lower tree layer cover or height and DBH of Ulmus trees permit more light to penetrate the understorey), and b) increased disturbances affecting both stand structure characteristics and understorey floristic composition.

## Implications for conservation

The natural monument of Lesini is an important relict riparian Fraxinus angustifolia subsp. oxycarpa forest and a habitat island surrounded mainly by a matrix of strongly contrasting habitats (mainly agricultural land).

At the beginning of the 20th century, the former swamps of Lesini were still characterized by a widespread lake during winter flooding. The first attempts to transform part of this land for agricultural purposes were undertaken in 1930 (Vött et al., 2003, 2007). The number of trees per hectare at the lower classes of diameter is not significantly greater in regard to the higher ones, except in the first vegetation unit. Szijj (1983) focused on the absence of any regeneration in the studied forest and on the great intensity of goat grazing resulting in a domination of typical pasture weeds on the forest's ground vegetation. Since 1985, the year when the studied forest was characterized as a natural monument, fencing of the forest has kept large goat herds out. Presently, grazing pressure by cattle and pigs is more or less evenly distributed throughout the forest. If this would be the principal cause for the lack of younger trees in these parts of the forest it would also put the same pressure on areas of the other vegetation units. However, irrespective of the grazing pressure, where there is enough water availability as occurs in the first vegetation unit, the forest contains younger (4-20 cm DBH) Ulmus minor and Fraxinus angustifolia individuals.

Annual precipitation in western Greece has declined by ca. $20 \%$ since the 1970 s (Feidas et al., 2007) with the last two decades of the 20th century representing the driest period within the century (Sarris et al., 2010). This, in combination with the reduction of frequency and intensity of flood events, may reduce the regeneration of riparian tree species in a large part of the Lesini forest. This situation could have dire consequences for this forest's future as dry conditions in the eastern Mediterranean are expected to further intensify as a result of global warming (based on different climate model projections for the 21st century; IPCC, 2007). Although, the older stands are important sources of diaspores (Bossuyt et al., 1999; Glaeser \& Wulf, 2009), the lack of young riparian trees constitutes a major problem for the persistence of riparian forest (Deiller et al., 2001).

The regeneration of riparian forest requires the restoration of hydrological and sediment input processes. Naturalness of the flooding regime and hydrological conditions need to be safeguarded or reinstalled, as far as possible (Hughes et al., 2001; Glaeser \& Wulf, 2009). As the functional integrity of the riv-er-floodplain complex is restored, biodiversity should follow (Ward et al., 1999). Furthermore, in riparian forest influenced by floods, forest dynamics appear to be reversible and are subjected to dominant allogenic
processes. On the contrary, forest dynamics on the terraces, which are not influenced by floods, are irreversible and subjected to dominant autogenic processes (Decamps et al., 1988).

Riparian forests, especially in the Mediterranean lowlands, like other protected ecosystems, suffer from lack of safeguarding and implementation of the law concerning their conservation. They should no longer be used for woodcutting or grazing and their surroundings should be used in a non-intensive way. Intensive agriculture and drainage pipes should be abandoned in areas surrounding these forests in order to aid the re-establishment of the ecological conditions and allow the spread of existing stands (Dimopoulos \& Bergmeier, 2008).

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