# Tree ring ecological signal is consistent with floristic composition and plant indicator values in Mediterranean *Fagus sylvatica* forests

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## Summary

**1.** We compared the multivariate patterns of tree ring chronologies with those of floristic composition (and of its associated Ellenberg indicator values – EIVs) across the whole elevation gradient of *Fagus sylvatica* forests in Central Italy (from 300 to 1900 m a.s.l.). Both data sets were also compared with bioclimatic parameters obtained from reconstructed, site-representative meteorological data.

**2.** Procrustes analysis showed that the patterns of tree ring chronologies and floristic assemblages were significantly correlated. The two main bio-climatic belts obtained from tree ring analysis showed significantly different floristic composition and significantly different distribution of EIVs.

**3.** Constrained ordination with meteorological data as covariates showed that in both data sets, most of the variation was explained by mean summer temperature, while precipitation parameters had only minor explanatory power.

**4.** Ellenberg indicator values for temperature showed a strong correlation with mean summer temperature obtained from the meteorological data. EIVs for continentality were weakly correlated with annual temperature range. No correlation emerged between the EIVs for moisture and the precipitation parameters. Constrained ordination of the tree ring data set with the floras' mean EIVs as covariates found that the most explanatory variables were the EIVs for temperature followed by the EIVs for light. This latter finding is probably a consequence of temperature control (via summer drought) on canopy Leaf Area Index.

**5.** *Synthesis.* Ecological classification of beech forest stands through either tree ring chronologies or floristic composition yields very similar results. Both bio-indication methods point to the predominant role of growing-season temperatures in controlling patterns and processes of forest ecosystems across wide elevation gradients. Thus, similarities in tree ring chronologies of the past between sites could be used to infer analogies in past floristic assemblages. Moreover, temperature indicator values obtained from floras show excellent accordance with meteorological data, allowing reliable usage of diachronic floristic data for climate change monitoring at detailed spatial scale.

**Key-words:** beech, bioclimate, community classification, dendrochronology, elevation belts, Ellenberg indicator values, mean summer temperature, plant–climate interactions, procrustes analysis, understorey flora

## Introduction

Tree rings are a valuable bioindicator, able to integrate the multiple environmental factors controlling forest growth (Schweingruber 1996). Dendroclimatic studies based on tree ring networks have contributed, in the last decades, to understanding tree growth response to environmental gradients from regional (Meko *et al.* 1993) to continental/hemispherical (Briffa *et al.* 2002) scales. Horizontal and vertical gradients in tree–climate relationships provide the basis for defining bioclimatic units in terms of the leading dendroclimatic signals (Piovesan *et al.* 2005a; Di Filippo *et al.* 2007), thus obtaining a quantitative

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bioclimatic classification of tree populations. Moreover, if long instrumental records are available, it is possible to explore the temporal stability of the observed climate/growth relationships (Biondi 1999) and formulate hypotheses about the potential effects of climatic change on plant functioning and community dynamics (Cook *et al.* 2001; Jump & Peñuelas 2005; Whittaker *et al.* 2005). Dendroecological studies offer a valuable tool for science-based management of forest ecosystems, linking bioclimate and climate fluctuations to forest productivity (Biondi 1999; Piovesan & Schirone 2000).

On the other hand, the herbaceous layer, where most plant biodiversity in temperate forest ecosystems is contained, interacts with the tree stratum in many ways (Gilliam 2007), and its floristic assemblages represent integrated expressions of the values of environmental variables (Diekmann 2003). Plant species presence has thus long been used for ecological indication (Zonneveld 1983), often through the so-called indicator values, reflecting the realized optima of species expressed as ordinal numbers (Ellenberg *et al.* 1991; Landolt 2010). Plant indicator values can be aggregated for whole communities and therefore are likely to be more robust than the attributes of single species (Scherrer & Körner 2011).

However, to our knowledge, no published studies have explored the relationships between the ecological signal obtained from tree ring parameters and the information provided by the vascular flora of forest communities. In this study, we test whether the patterns of tree ring parameters and floristic composition (and its associated 'indicator values') are congruent with each other along an elevation gradient, and provide a similar ecological signal. In addition, we compare these patterns with reconstructed, site-specific meteorological data. Although a number of studies have compared or calibrated average indicator values of plant communities with measured environmental variables (see references in Szymura, Szymura & Maciol 2014), the vast majority of these works dealt with edaphic indicator values only (e.g. Carpenter & Goodenough 2014). Only a very few studies compared indicator values for temperature with measured (Scherrer & Körner 2011) or interpolated (Renetzeder *et al.* 2010; Lenoir *et al.* 2013) temperature variables. However, testing the reliability of floristic indicator values for temperature is of great relevance, as they can be used in diachronic studies to assess the impact of climate change at plant community scale (Renetzeder *et al.* 2010; Delgado & Ederra 2013; Świerkosz, Reczyńska & Pech 2014). The high spatial resolution potentially offered by indicator values of plant communities (e.g. along an elevation gradient) can provide insights in issues such as the amplified rate of climate warming with elevation (Mountain Research Initiative EDW Working Group 2015).

Our study is based on a sample of forest communities dominated by European beech (*Fagus sylvatica* L.; hereafter: *Fagus*) in Central Italy. Several works underlined that, despite the homogenous conditions imposed by the beech canopy, the composition of *Fagus* forest understorey is highly diverse across beech's extensive geographical range, showing complex ecological and geographical patterns: these are largely dependent on differences in altitude, topography and soil conditions

(e.g. Feoli & Lagonegro 1982; Ellenberg 1988; Tsiripidis, Bergmeier & Dimopoulos 2007; Di Pietro 2009; Rosati *et al.* 2010; Marinšek, Šilc & Čarni 2013), but also on post-glacial recolonization patterns from different refugia (Nimis & Bolognini 1993; Willner, Di Pietro & Bergmeier 2009). Moreover, dendroecologists have used *Fagus* extensively during the last two decades (e.g. Rozas 2001; Dittmar, Zech & Elling 2003; Lebourgeois *et al.* 2005), taking advantage of the widespread distribution, sensitivity to climate and longevity of beech (Piovesan *et al.* 2005b). *Fagus* reaches the southern edge of its total geographical range in Italy, where its altitudinal range spans over more than 1600 m, as the species is recorded from c. 200–400 to 2000–2100 m a.s.l. in the C- and S-Apennines (Piovesan *et al.* 2011). Thus, beech forests in the Apennines provide a unique opportunity to explore climate/tree-growth relationships, because of the steep climatic gradient from the Mediterranean lowlands to the subalpine belt. A number of dendrochronological investigations were carried out on Italian *Fagus* forests both at local (e.g. Biondi 1993; Bernabei *et al.* 1996; Piovesan *et al.* 2003) and regional (Biondi 1992; Piovesan *et al.* 2005a; Di Filippo *et al.* 2007, 2012) scales. In particular, studies focused on interannual and decadal growth variations, showed that beech populations can be classified into markedly different bioclimatic belts through tree ring parameters (Piovesan *et al.* 2005a, 2008).

The research questions of this study are:

1. Are the multivariate patterns of tree ring chronologies and floristic composition of *Fagus* forest stands correlated with one another across an elevation gradient from the Mediterranean lowlands to the tree line?
2. Will a classification of forest stands based on dendrochronological parameters yield similar results to a classification based on vascular plant community composition?
3. Do the bio-climatic belts obtained from tree ring chronologies show a significantly different floristic composition, and/or a specific fingerprint of plant 'indicator values'?
4. If the two data sets are found to be correlated, what climatic factors can explain the similarity between them?
5. To what degree are plant 'indicator values' a reliable proxy of climate (as expressed by site-specific, reconstructed meteorological data) across an elevation gradient?

## Materials and methods

### STUDY AREA AND SITE SELECTION CRITERIA

The central section of the Italian Peninsula features a steep elevation gradient: altitude ranges from sea level to c. 2900 m, with only 126 km between the Tyrrhenian Sea to the west and the Adriatic to the east. While coastal locations show a true Mediterranean regime, with annual rainfall of c. 600–900 mm, 2–3 months of summer drought, and no significant winter frost, the main mountain ranges feature between 1300 and 1600 mm year$^{-1}$ of rainfall, only a very weak dry period in summer and winter minima markedly below freezing point (Fig. 1) (Blasi *et al.* 2014).
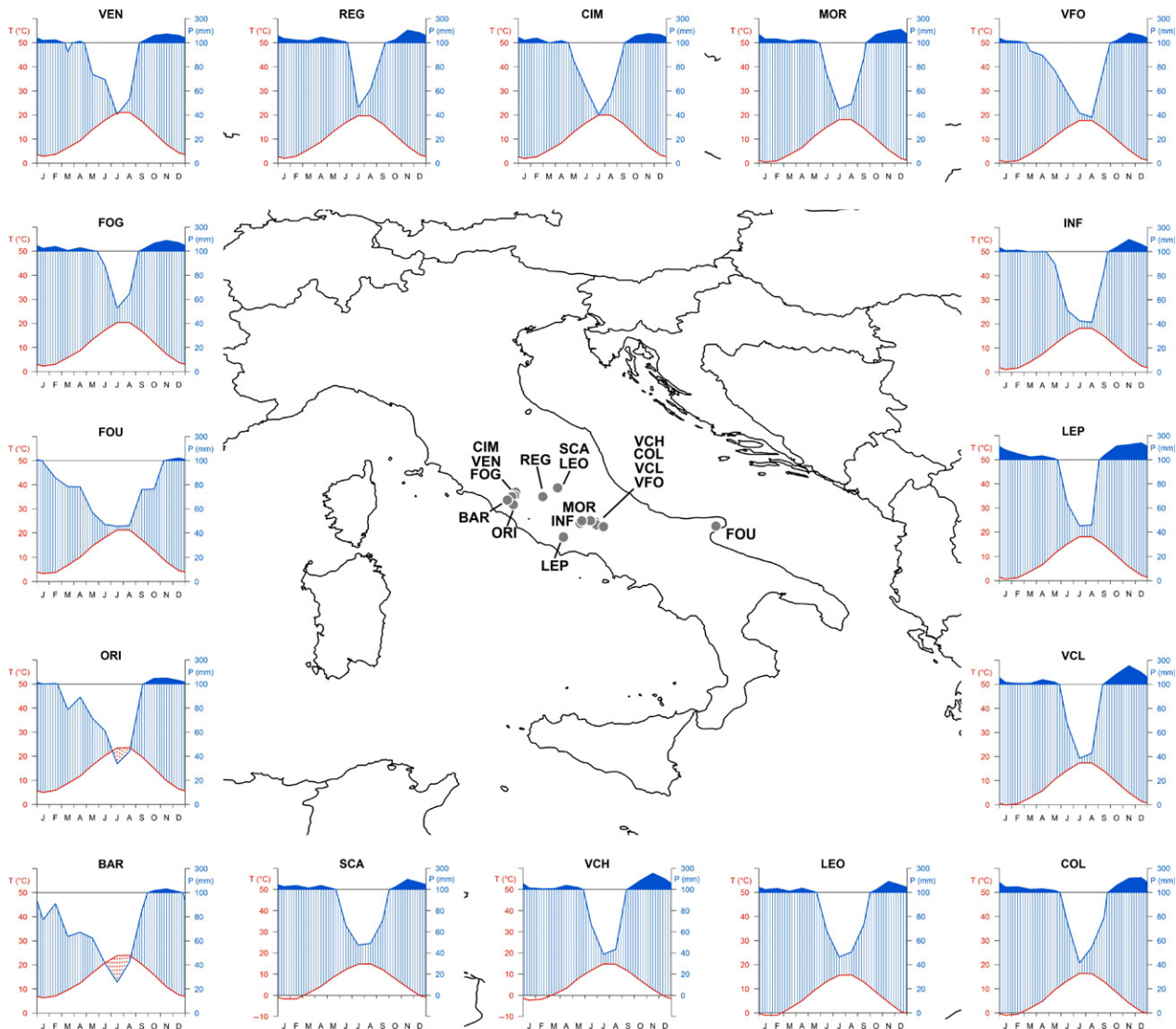
**Fig. 1.** Map of Italy with the study sites (abbreviations as in Table 1). For each site, Bagnouls–Gaussen climatic diagrams are shown (arranged clockwise in order of increasing elevation, starting from the bottom-left corner).

We sampled 16 forest sites (Fig. 1 and Table 1): all were dominated by *Fagus sylvatica*, managed as high-forest and located between c. 41°30′ and 42°30′N. The study sites were selected in order to completely cover the wide altitudinal range of *F. sylvatica* in the studied territory (we included forests growing from 270 to 1850 m a.s.l.), as well as the two main groups of parent material on which beech forests are developed within the region: Pleistocene volcanic rocks (lava flows or ignimbrites) and Mesozoic limestones. Soils developed on volcanic bedrock are generally deep (> 1 m), and often showing marked andic properties, thus belonging to the Udands suborder of Andisols (Lorenzoni *et al.* 1995). On calcareous bedrock, soils have variable depth (0.4–1 m) and are classified as Rendolls and Udolls (Chiucchiarelli *et al.* 2006).

Sampled sites were always chosen among those with few signs of human disturbance in the last decades (Di Filippo *et al.* 2012). Restricting the sample to mature forests was necessary not only in order to obtain longer tree ring cores, but also to exclude the effects of secondary succession or post-harvesting stand development on floristic composition (Gilliam 2007; Amici *et al.* 2013; Mölder, Streit & Schmidt 2014). Moreover, in all sampled forests, the upper canopy was made up almost exclusively of *Fagus* trees, with only a very sparse

occurrence of isolated individuals of *Acer* sp.pl., and – in the lowest elevation sites – of *Quercus cerris*: this physiognomic homogeneity was essential in order to exclude the effect of canopy differences on floristic composition (Mölder, Bernhardt-Römermann & Schmidt 2008).

Finally, since an important part of the variation in beech forest composition has been shown to reflect the history of post-glacial recolonization from different refugia (Willner, Di Pietro & Bergmeier 2009), all sampled sites were chosen from central Italy, a biogeographically homogeneous area (Filibeck *et al.* 2005; Rosati *et al.* 2010), which can be assumed as having been recolonized from the same refugia (Di Pietro 2009; Willner, Di Pietro & Bergmeier 2009).

## METEOROLOGICAL RECORDS

Synthetic records of monthly minimum, mean and maximum temperatures and of total monthly precipitation were reconstructed for each year of the 1963–2000 period (as this is the common period to all the tree ring chronologies, see section here on 'tree ring sampling') for each sampled site by means of the anomaly method (New, Hulme & Jones 2000; Mitchell & Jones 2005) as described in Brunetti *et al.* (2012). This method is based on the assumption that the spatio-tem-

**Table 1.** Elevation, bedrock type (Lim = limestones; Vol = volcanic), sample size and climatic variables for the study sites

| Code | Name | Elevation (m a.s.l) | Bedr. | No. of cored trees | $T_m$ | $T_s$ | $T_{spr}$ | $M_j$ | $m_j$ | $I_c$ | $P$ | $P_s$ | $I_{os}$ |
|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| BAR | Barbarano Romano | 275–300 | Vol | 12 | 14.6 | 22.7 | 12.8 | 10.2 | 2.9 | 17.3 | 929 | 127 | 1.9 |
| CIM | Monte Cimino | 950–1050 | Vol | 117 | 10.8 | 19 | 9.2 | 6.1 | −1.1 | 17.6 | 1318 | 172 | 3 |
| COL | Collelongo | 1500–1750 | Lim | 30 | 7.5 | 15.4 | 5.7 | 2.9 | −3.9 | 16.9 | 1543 | 185 | 4 |
| FOG | Monte Fogliano | 675–875 | Vol | 39 | 11.2 | 19.4 | 9.5 | 6.4 | −0.7 | 17.7 | 1449 | 221 | 3.8 |
| FOU | Foresta Umbra | 700–775 | Lim | 27 | 11.8 | 19.9 | 10.4 | 5.9 | 1.2 | 17.3 | 882 | 155 | 2.6 |
| INF | Valle dell'Inferno | 1175–1250 | Lim | 42 | 9.3 | 17.1 | 7.7 | 4.9 | −2.4 | 16.9 | 1278 | 159 | 3.1 |
| LEO | Vallonina | 1550–1750 | Lim | 20 | 7 | 14.6 | 5.4 | 3.1 | −4.9 | 16.6 | 1391 | 196 | 4.5 |
| LEP | Lepini | 1200–1300 | Lim | 21 | 9.3 | 17.3 | 7.5 | 4.5 | −2.2 | 17.2 | 1694 | 170 | 3.3 |
| MOR | Morino | 1150–1175 | Lim | 23 | 9.2 | 17.1 | 7.7 | 5.1 | −2.9 | 17 | 1238 | 159 | 3.1 |
| ORI | Oriolo Romano | 400–500 | Vol | 54 | 14.1 | 22.6 | 12.5 | 9 | 2 | 18.3 | 1100 | 151 | 2.2 |
| REG | Fonte Regna | 875–1000 | Lim | 37 | 10.6 | 18.6 | 9.2 | 6.4 | −2 | 17.3 | 1509 | 244 | 4.4 |
| SCA | Scangive | 1775–1825 | Lim | 63 | 6.3 | 13.8 | 4.6 | 2.5 | −5.8 | 16.4 | 1411 | 193 | 4.7 |
| VCH | Valle Cervara high | 1600–1850 | Lim | 67 | 6 | 13.8 | 4.2 | 1.6 | −5.1 | 16.6 | 1517 | 159 | 3.8 |
| VCL | Valle Cervara low | 1200–1500 | Lim | 21 | 8.4 | 16.4 | 6.7 | 3.7 | −3 | 17.1 | 1503 | 159 | 3.2 |
| VEN | Monte Venere | 750–850 | Vol | 76 | 11.8 | 20.1 | 10.2 | 7 | −0.1 | 17.8 | 1291 | 176 | 2.9 |
| VFO | Val Fondillo | 1200–1250 | Lim | 23 | 8.7 | 16.6 | 7.3 | 4.8 | −3.6 | 17 | 1170 | 154 | 3.1 |

$T_m$, mean annual temperature (°C); $T_s$, mean summer temperature; $T_{spr}$, mean spring temperature; $M_j$, mean maximum temperature for the coldest month (January); $m_j$, mean minimum temperature for the coldest month (January); $I_c$, Continentality index (°C); P, annual precipitation (mm); $P_s$, summer precipitation (mm); $I_{os}$, Summer ombrothermic index (mm/°C).

poral structure of the signal of a meteorological variable over a given area can be described by the superimposition of two fields: the climatological normals over a given reference period (i.e. the climatologies), characterized by remarkable spatial gradients, and the departures from them (i.e. the anomalies), generally characterized by higher spatial coherence and linked to climate variability. Climatologies and anomalies can be reconstructed in a completely independent way from each other and based on different data sets. Climatologies were reconstructed following the procedure described in Brunetti *et al.* (2014). Anomalies were reconstructed using weighted averages, as described in Brunetti *et al.* (2006). Finally, the two fields were superimposed to get temporal series in absolute values for each site.

From the monthly meteorological records thus reconstructed, a number of parameters of bioclimatic significance (Cress *et al.* 2009; Rivas-Martinez, Rivas-Saenz & Penas 2011; Canu *et al.* 2015) were calculated as means on the 1963–2000 time series and used as explanatory variables for tree ring and floristic multivariate patterns and to test the plant 'indicator values' (Table 1): $T_m$ = mean annual temperature; $T_s$ = mean summer temperature; $T_{spr}$ = mean spring temperature; $M_j$ = mean maximum temperature for the coldest month (January); $m_j$ = mean minimum temperature for the coldest month (January); $I_c$ = Continentality index (Rivas-Martinez, Rivas-Saenz & Penas 2011), that is annual temperature range (the difference between mean temperature of the hottest and coldest months of the year); $P$ = annual precipitation; $P_s$ = summer precipitation; $I_{os}$ = Summer ombrothermic index (Rivas-Martinez, Rivas-Saenz & Penas 2011); this latter is calculated as $I_{os} = (P_{June} + P_{July} + P_{August})/(T_{June} + T_{July} + T_{August})$, where $P$ and $T$ are mean monthly precipitation and mean monthly temperature, respectively.

### TREE RING SAMPLING

Within each studied forest, we cored at 1.3 m from the ground at least 20 dominant–co-dominant trees using an increment borer. Trees were selected as the best combination of old age and trunk integrity. Each core was air-dried in the laboratory, processed to make the tree-rings more visible, and then, ring-widths were measured with a 0.01 mm resolution using the CCTRMD system and the CATRAS software (Aniol 1983). Each floating series was checked for measurement errors and cross-dated (Holmes 1983). In order to amplify the climatic

signal in tree rings, the cross-dated series of each sampled site were combined into a site chronology according to the methods reported in Di Filippo *et al.* (2007). In general, the process of amplification of the climatic signal in tree rings variability is based on a series of statistical steps that makes the so-called process of standardization: removal of the effect on growth of the biological age/size trend and of forest disturbance events and removal of the physiological preconditioning from previous growth using autoregressive modelling. Single standardized tree ring series are then averaged into a site chronology to retain the common (climatic) information at each sampled location. For each chronology, the valid period for dendroclimatic analysis was evaluated according to its expressed population signal to compare site chronologies with strong environmental signals (EPS > 0.85; Wigley, Briffa & Jones 1984). All computations were made with the package 'dplR' of the R software environment (R Development Core Team 2012). The time series common to all site chronologies corresponded to the period 1963–2000, and only the data from these years were thus retained for subsequent analyses.

### FLORISTIC SAMPLING

At each site, we considered the complete vascular plant composition, that is including all species belonging to ground layer, shrub layer and canopy. For 11 sites, the vascular plant list was compiled through field sampling in early summer in 2012 and 2013. Sampling areas were arranged in order to include all the stands sampled for tree rings and the areas in between: sampled area at each site was between c. 0.5 and 1 hectares. For the remaining five sites, published or unpublished vegetation plots (see Appendix S1, Supporting information) were already available for the forest stands where the trees were cored: in these cases, the pooled species list from the plots was used to compile the site's flora (cumulative area at each site was then between c. 0.2 and 0.5 hectares). Nomenclature was standardized following Conti *et al.* (2005).

### DATA ANALYSIS

Both data sets (i.e. the 1963–2000 site chronologies and the species-by-site presence/absence matrix) were analysed through ordination and hierarchical cluster analysis (HCA). To allow meaningful comparison

between the multivariate analysis outputs from the two data sets, non-metric multidimensional scaling (NMDS) was chosen as ordination method because of its suitability to different data types (Clarke 1993). Bray–Curtis dissimilarity was used as dissimilarity measure for both NMDS and HCA: this metric is rank-order similar and thus appropriate for both continuous variables (the tree ring data set) and presence/absence data (the floristic matrix) (Clarke, Somerfield & Chapman 2006).

Distance-based redundancy analysis (dbRDA), again with Bray–Curtis dissimilarity, was used to quantify in each of the two data sets the proportion of variance that can be explained by the (standardized) climatic parameters obtained from the meteorological records. Distance-based RDA is a constrained ordination technique not requiring multivariate normality or, unlike classical RDA, that distance between observation be Euclidean (Mc Ardle & Anderson 2001; Roberts 2009).

The NMDS ordinations obtained from the two data sets were compared through Procrustes analysis, a method aimed at minimizing the sum-of-squared distances ($m^2$) between corresponding objects in an Euclidean space (Gower 1975). Within community ecology, Procrustes analysis can be used to compare two sets of site scores from two separate ordinations (e.g. Bajocco, Rosati & Ricotta 2010; Ritt *et al.* 2011), by scaling, rotating and dilating one ordination solution to match the other ordination (Lisboa *et al.* 2014). The significance of the Procrustean fit was tested by means of a Monte Carlo statistic using PROTEST (Jackson 1995; Peres-Neto & Jackson 2001).

The significance of the difference in floristic composition among dendrochronological groups was tested through PERMANOVA (nonparametric multivariate analysis of variance) (Anderson 2005), using Bray–Curtis distance measures. A test of the homogeneity of multivariate dispersions within groups (PERMDISP) was performed, as PERMANOVA makes the implicit assumption that dispersions are roughly constant across groups (Anderson 2004). Indicator species analysis (Dufrene & Legendre 1997) was used to detect the species most significantly associated with each dendrochronological group.

To compare the bio-indicator information from tree ring patterns with that obtained from the floristic assemblages, the Ellenberg indicator values (EIVs) specific for the Italian flora (Pignatti, Menegoni & Pietrosanti 2005) were assigned to the recorded plant species. The EIVs characterize the adaptation of a plant to edaphic and climatic conditions in comparison with other species: each species is given values denoting the position at which it reaches peak abundance along environmental gradients (Diekmann 2003). A 9- or 12-point ordinal scale for each of the following parameters is used: moisture, soil nitrogen status, soil pH, light, temperature and continentality (Ellenberg *et al.* 1991; Pignatti, Menegoni & Pietrosanti 2005).

The degree of correlation between tree rings patterns and EIVs was then assessed using (after standardization) the average EIVs of the flora of each site as 'environmental variables' in a dbRDA of the tree rings data set. Finally, PERMANOVA was used to test the significance in EIVs distribution differences (for each indicator, we calculated site-by-site dissimilarities using Bray–Curtis distance) among the clusters of sites obtained from tree ring HCA.

Statistical analysis was computed with the softwares PRIMER v.6.1.11, PERMANOVA + v.1.0.1 (Primer-E Ltd., Luton, UK) and the Vegan package for R (Oksanen *et al.* 2012).

## Results

### DENDROCHRONOLOGY PATTERNS

In the NMDS of tree ring chronologies (Fig. 2), the axis of maximum variation (axis 1) corresponded to a temperature gradient: low-elevation sites (altitude < 1000 m a.s.l., mean annual temperature > 10.6 °C) are clustered in a distinct group to the left, while the remainder of the forests (1000–1800 m a.s.l., mean annual temperature between c. 9 and 6 °C) are placed to the right.

When the whole set of parameters obtained from the climate records was used as environmental variables in the dbRDA of the dendrochronological data set, all the temperature-related parameters ($T_m$, $T_s$, $T_{spr}$, $M_j$, $m_j$ and $I_c$) were found to be strongly correlated with axis 1 and to be highly redundant with each other (not shown). The temperature-related parameter showing the highest correlation value with axis 1 was $T_s$ (mean summer temperature); this variable was then chosen to rerun the dbRDA, together with the precipitation-related parameters (i.e. $I_{os}$ and $P$; $P_s$ was not included in the new analysis because of its collinearity with the former) (Table 2). With this reduced set of explanatory variables, axis 1 explained 69% of fitted model variation and had a very strong negative correlation with $T_s$ ($r = -0.98$; permutation test was highly significant). $I_{os}$ showed a strong correlation with axis 2 ($r = 0.72$), which was also negatively correlated with $P$; however, axis 2 explained only 21% of the model, and the correlation with $P$ was not statistically significant (Table 2).

Hierarchical cluster analysis of the tree ring data set (Fig. 3) yielded two main groups, clearly corresponding to different elevation (and thus temperature) belts. This pattern was very strong, as it did not change if different dissimilarity metrics were tested; only when using Pearson's correlation as dissimilarity measure (not shown), a subgroup composed by three sites from relatively low altitude (c. 1100–1200 m a.s.l.: LEP, MOR and INF − see Table 1 for site abbreviations) could be detected inside the mid- to high-elevation group.

### FLORISTIC PATTERNS

A total of 224 vascular plant species was found; median species number per site was 58 (min 26, max 97) (see Appendix S2 for complete species matrix). NMDS of the species matrix yielded an arrangement of sites largely corresponding to an elevation (and thus temperature) gradient (Fig. 2). A minor component of variation appears to be related to precipitation gradient. The dbRDA of the floristic data set with the reconstructed meteorological data showed, similar to the dbRDA of the dendrochronological data set, that all the temperature-related parameters were strongly correlated with axis 1 and redundant with each other (not shown). The temperature-related parameter showing the highest correlation value with axis 1 was, again, $T_s$ (mean summer temperature). As with the tree ring data set, a dbRDA with only $T_s$, $I_{os}$ and $P$ as environmental variables was subsequently performed (Table 2): axis 1 explained 74% of fitted model variation and had a very strong negative correlation with $T_s$ ($r = -0.96$; permutation $P = 0.001$). Axis 2 explained only 19% of fitted model: annual precipitation showed a negative correlation with this axis, while $I_{os}$ had a weaker (positive) correlation. However, only this latter variable was found statistically significant, while (as in the tree ring data set) annual precipitation was non-significant (Table 2).
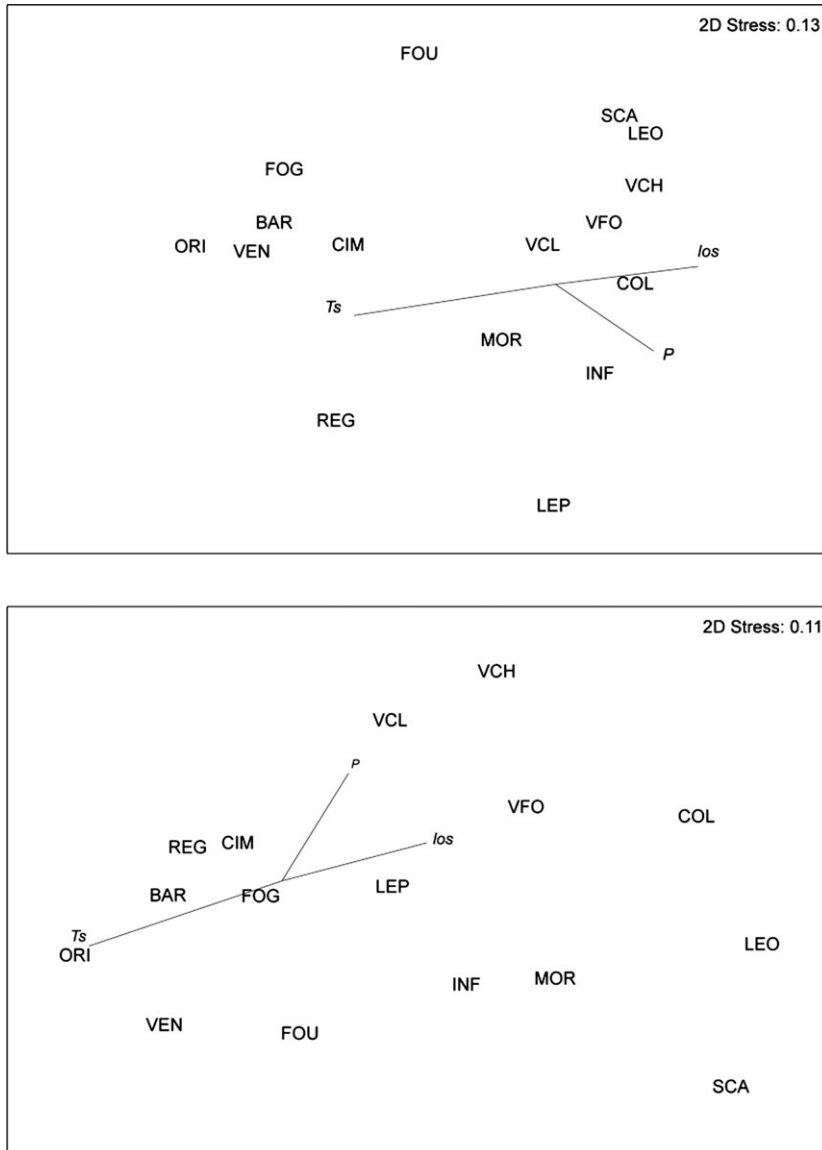
**Fig. 2.** NMDS scatter diagrams of the tree-ring data set (top) and of the floras (bottom). Site name abbreviations as in Table 1. Vectors of mean summer temperature ($T_s$), annual precipitation ($P$) and summer ombrothermic index ($I_{os}$) are superimposed as an aid for scatter diagram interpretation.

**Table 2.** Results of dbRDA of the tree ring data set and the floristic data set (left and right columns, respectively, within each axis heading), with selected climatic parameters as environmental covariates. First two rows show the percentage of variation explained by each axis; the remainder of the rows refer to multiple partial correlation values between environmental covariates and dbRDA coordinate axis ($P$ values refer to permutation test for significance of environmental covariates). See Table 1 for climatic variables abbreviations

|  | Axis 1 | | Axis 2 | | Axis 3 | | $P$ | |
|---|---|---|---|---|---|---|---|---|
|  | Tree ring | Flora | Tree ring | Flora | Tree ring | Flora | Tree ring | Flora |
| % explained variation (out of fitted model) | 69.37 | 74.23 | 20.99 | 19.15 | 9.64 | 6.63 | | |
| % explained variation (out of total variation) | 32.97 | 31.98 | 9.98 | 8.25 | 4.58 | 2.86 | | |
| $T_s$ | −0.979 | −0.956 | 0.043 | 0.160 | 0.200 | 0.247 | 0.001 | 0.001 |
| $I_{os}$ | 0.170 | 0.293 | 0.715 | 0.572 | 0.678 | 0.766 | < 0.05 | < 0.05 |
| $P$ | 0.113 | 0.019 | −0.698 | −0.805 | 0.707 | 0.593 | n.s. | n.s. |

dbRDA, Distance-based redundancy analysis.

Hierarchical cluster analysis of the floristic data set (Fig. 3) yielded a first branching separating three high-elevation sites from the remainder of the locations; the next node divided the lowest sites (< 1000 m a.s.l., $T_m$ > 10.6 °C) from the mid-elevation (and some high-elevation) stands. Other dissimilarity measures, more specifically suited for presence/absence data (e.g. Ochiai) (not shown), yielded only two main clusters, composed by sites below and above 1000 m a.s.l., respectively. The low-elevation group, however, was always retained unchanged whatever the dissimilarity metric. This cluster was clearly
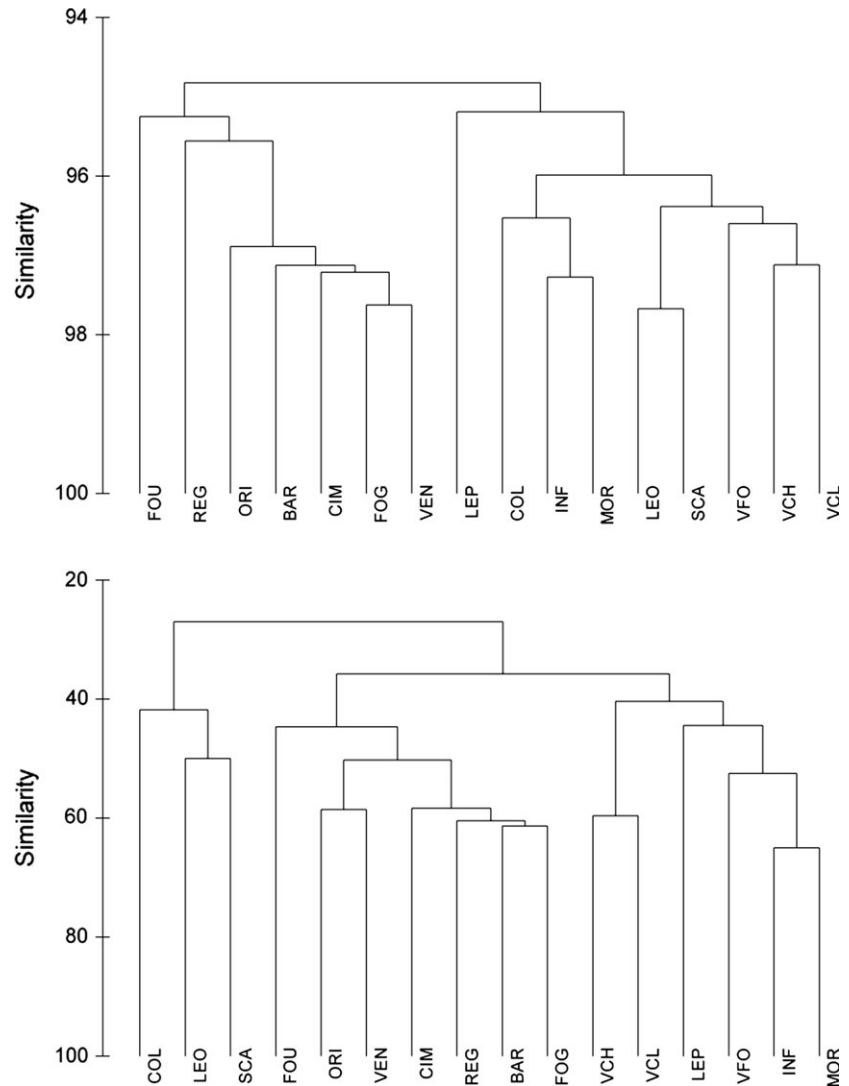
**Fig. 3.** Cluster analysis (UPGMA, Bray–Curtis dissimilarity) of the tree ring (top) and floristic (bottom) data sets.

characterized by a higher total species richness (and, in particular, a higher diversity of woody species) and a large set of Mediterranean and/or termophilous species.

Finally, when comparing the mean EIVs for temperature, moisture and continentality obtained from the floras with the relevant climatic parameters obtained from the meteorological records (Table 3), we found a very strong positive correlation between the EIV for temperature and all temperature parameters, the highest correlation coefficient being with mean summer temperature ($r = 0.92$, $P < 0.001$). The EIV for continentality showed a (weak) positive correlation with the meteorological continentality index. No significant correlation emerged between the EIV for moisture and any of the precipitation parameters, although the EIV for moisture had a weak negative correlation with the temperature parameters and with continentality index (Table 3).

COMPARISON BETWEEN DENDROCHRONOLOGICAL AND FLORISTIC PATTERNS

Procrustes analysis and subsequent randomization test yielded a significant result ($r = 0.711$, $m^2 = 0.4945$, $P = 0.002$; based on 999 permutations), showing that the NMDS ordinations of the two data sets (floristic composition and tree ring chronologies) exhibited greater concordance than expected at random. The sites showing the best congruency were all the sites belonging to the lower altitudinal belt (< 1000 m a.s.l., $T_m > 10.6$ °C), with the addition of VFO which belongs to the mid-elevation belt; the highest residuals were found for a high-mountain site (VCH) and for three mid-elevation forests (LEP, INF and MOR) (Fig. 4).

In the HCA dendrograms, both data sets showed a well-distinct cluster made up by the same low-elevation sites (Fig. 3); thus, the difference in floristic composition, between the two main bioclimatic groups obtained from the dendrochronological classification, was found to be highly significant (PERMANOVA: $F = 5.969$, $P < 0.001$). Indicator species analysis showed that the low-elevation group of sites was differentiated by thermophilous and/or Mediterranean species, while the other cluster (i.e. the sites above 1000 m, with $T_m$ between 9 and 6 °C) was characterized by drought-sensitive and frost-resistant taxa (Table 4). If a three-cluster subdivision of the tree rings data set was considered, the difference in floristic composition among the pooled groups of the den-

**Table 3.** Correlation matrix (Pearson's *r*) between mean EIVs (for temperature, continentality and moisture) and climatic parameters of sites

| | $T_m$ | $T_{spr}$ | $T_s$ | $M_j$ | $m_j$ | $P$ | $P_s$ | $I_{os}$ | $I_c$ |
|---|---|---|---|---|---|---|---|---|---|
| EIV-Temp. | 0.915*** | 0.917*** | 0.920*** | 0.888*** | 0.891*** | −0.468 | −0.02 | −0.581* | 0.853*** |
| EIV-Contin. | 0.354 | 0.34 | 0.384 | 0.327 | 0.347 | 0.154 | −0.031 | −0.319 | 0.560* |
| EIV-Moist. | −0.552* | −0.557* | −0.561* | −0.501* | −0.556* | 0.21 | 0.016 | 0.364 | −0.543* |

EIV, Ellenberg indicator values.
Significant correlation values are marked as ***$P < 0.001$ or *$P < 0.05$. See Table 1 for climatic variables abbreviations.
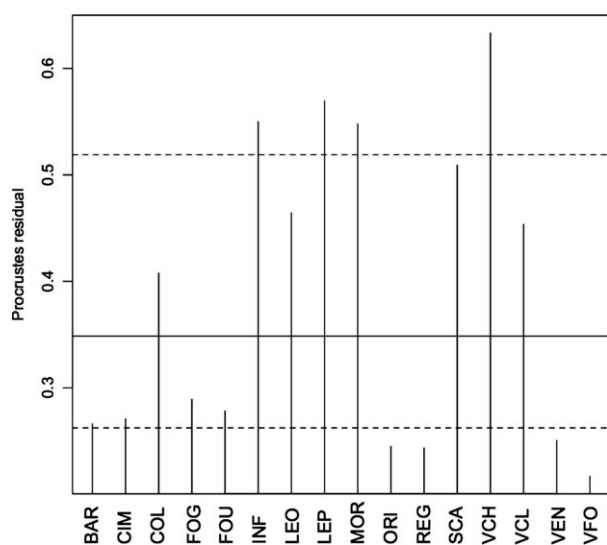


**Fig. 4.** Residuals of the Procrustes analysis, comparing the NMDS ordinations obtained from the two data sets (floristic composition and tree ring chronologies). The residuals are an inverse measure of congruency (a small residual indicates a close agreement) between the site scores from the two data sets, after having scaled, rotated and dilated one ordination configuration to match the other ordination. Site names abbreviations as in Table 1.

**Table 4.** Indicator species for the two main bioclimatic groups of the tree ring data set. IV= indicator values, ranging from zero (no indication) to 100 (perfect indication); only the species with both IV > 65 and $P < 0.05$ are shown

| Group | Species name | IV |
|---|---|---|
| Low | *Evonymus europaeus* | 100** |
| Low | *Ruscus aculeatus* | 85.7** |
| Low | *Symphytum tuberosum* | 85.7** |
| Low | *Tamus communis* | 85.7** |
| Low | *Galium aparine* | 81.8** |
| Low | *Allium pendulinum* | 75.9* |
| Low | *Cyclamen hederifolium* | 75.9** |
| Low | *Hedera helix* | 75.9* |
| Low | *Anemone apennina* | 75.0** |
| Low | *Melica uniflora* | 75.0* |
| Low | *Mercurialis perennis* | 75.0* |
| Low | *Chaerophyllum temulentum* | 71.4** |
| Low | *Corylus avellana* | 71.4** |
| Low | *Lathyrus venetus* | 69.2* |
| Low | *Lamium maculatum* | 68.1* |
| High | *Acer platanoides* | 66.7** |
| High | *Adenostyles australis* | 66.7* |
| High | *Prenanthes purpurea* | 66.7* |
| High | *Stellaria nemorum* subsp. *montana* | 65.7* |

Statistical significance (Monte Carlo) of IVs is coded as *$P < 0.05$ and **$P < 0.01$.

drochronological classification was still highly significant ($F = 3.91$, $P < 0.001$); however, when comparing groups pair-wise, the flora was significantly different only between the low- and high-elevation clusters (PERMANOVA post hoc test, Bonferroni-corrected: $P < 0.001$) and, much less markedly, between the low- and mid-elevation clusters ($P = 0.02$) – but not between the mid- and high-elevation ones.

The difference in EIVs distribution among the two main groups of the dendrochronological classification was found to be significant (PERMANOVA: $P < 0.01$ for all six EIVs). The test for homogeneity in multivariate dispersion showed that the two main groups did not significantly differ for their dispersion around centroids ($P = 0.01$). The pair-wise tests considering also the subgroup (obtained from the dendrochronological classification) of mid-altitude sites showed a significant difference ($P < 0.01$) for every EIV for the low-elevation/high-elevation pair, and less markedly for the low-elevation/mid-elevation pair ($P = 0.01$–0.02); the mid-elevation/high-elevation comparison was always found not significant.

When mean EIVs of each site's flora were used as environmental covariates for a dbRDA of the dendrochronological

data set (Fig. 5 and Table 5), axis 1 (explaining 64% of the model, and 35% of total variation) showed a very strong negative correlation ($r = −0.88$) with the EIVs for temperature, and a weaker negative correlation with the EIVs for light ($r = −0.40$); both were highly significant. Axis 2 (explaining only 15% of fitted model) was negatively correlated with the EIVs for nutrients, and positively correlated with the pH and continentality indicator values; however, only pH was found to be statistically significant.

## Discussion

### DENDROCHRONOLOGY PATTERNS

The pattern of similarities in tree ring chronologies among sites was clearly controlled by the elevation-driven climatic gradient; namely, dbRDA and NMDS showed that temperature explained most of the variation in the data; summer drought index, although statistically significant, explained a smaller fraction of variation, while annual precipitation was not significant. As suggested in previous studies (Piovesan

**Fig. 5.** Distance-based RDA of the tree ring data set. Average Ellenberg indicator values (EIVs) of the floras at each site were standardized and used as environmental covariates in the constrained ordination. EIVs' vectors abbreviations: T = temperature; C = continentality; R = soil pH; U = moisture; N = nutrients; L = light intensity.
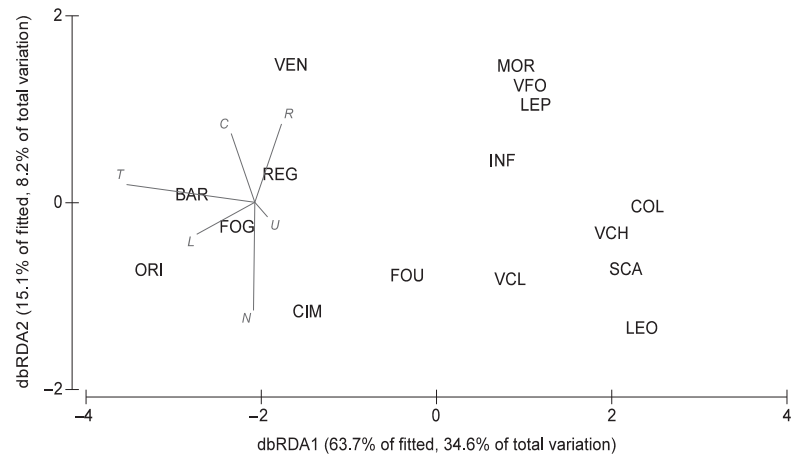
**Table 5.** Results of dbRDA of the tree ring data set with mean EIVs of each site's flora as environmental covariates (only the first three axis are shown)

|  | Axis 1 | Axis 2 | Axis 3 | *P* |
|---|---|---|---|---|
| % explained variation (out of fitted model) | 63.68 | 15.11 | 9.53 | |
| % explained variation (out of total variation) | 34.59 | 8.21 | 5.18 | |
| L | −0.398 | −0.205 | −0.390 | < 0.01 |
| T | −0.880 | 0.114 | 0.362 | < 0.01 |
| C | −0.162 | 0.444 | −0.688 | n.s. |
| U | 0.088 | −0.094 | −0.262 | n.s. |
| R | 0.183 | 0.505 | 0.412 | < 0.05 |
| N | −0.009 | −0.696 | 0.071 | n.s. |

dbRDA, Distance-based redundancy analysis; EIV, Ellenberg indicator values.
T – EIVs for temperature; C – EIVs for continentality; R – EIVs for soil pH; U – EIVs for moisture; N – EIVs for nutrients; L – EIVs for light intensity. Outputs are arranged as in Table 2.

*et al.* 2005a, 2008), temperature of current summer has a major role in explaining tree ring width patterns along altitudinal gradients in the Apennines. However, summer temperature is a proxy of vegetative period length, and thus of leafing time, a parameter showing considerable variation along elevation gradients (Alessandrini *et al.* 2010). In low-elevation beech populations (altitude < 1000 m and mean annual temperature > 10.6 °C), the leafing starts in early spring so trees may be affected by drought already in late spring/early summer (May–June); while in higher elevation sites, as a consequence of delayed budburst, the main climatic limiting factor for radial growth is water deficit during summer, especially June and July. Moreover, in high-mountain beech forests (altitude > 1500 m), the prevailing climate signal is related to spring temperature: beech is favoured by low April temperatures that cause a delayed leaf unfolding (allowing late-frost escape) and/or a delayed snow melt providing an extra water supply during the growing season. It is also favoured by warm May temperatures for sustaining metabolism reactivation and reducing late-frost risk (Piovesan *et al.* 2003). Due to such contrasting needs in May climate (warm in high

mountain, cold/wet at low altitude), low-elevation beech forests have a distinct late-spring climate signal, which is opposite to that of high-elevation sites at the point that the tree-ring chronologies at the extremes of the altitudinal gradient (400–600 m vs. 1700–1800 m) are anticorrelated (see Fig. 4b in Piovesan *et al.* 2005a). Phenological observations have shown that beech growing season decreases with increasing elevation (Lausi & Pignatti 1973), so that the role of spring months changes with elevation. At lower elevation sites, because of higher temperatures, trees have their crown completely developed already in May, and a dry spell can cause water stress; while at higher elevation, mild temperatures protect the bud burst and foliage from late-spring frost and reactivate metabolism (Piovesan *et al.* 2005a, 2008).

## FLORISTIC PATTERNS AND INDICATOR VALUES

Temperature regime (and in particular mean summer temperature) emerged in dbRDA as the most predictive variable for floristic composition. Consistently, NMDS and HCA of the floristic data set were clearly arranged along an elevation gradient. Annual precipitation did not perform as a statistically significant variable in explaining the variation of floristic composition between sites, while $I_{os}$ [i.e. the summer precipitation/temperature ratio − an index widely used in vegetation science to express the degree of summer drought stress in Mediterranean countries and to define the border between the Mediterranean and Temperate biomes (e.g. Cress *et al.* 2009; Blasi *et al.* 2014; Canu *et al.* 2015)] had only weak explanatory power. However, within the Mediterranean macroclimate, *Fagus* can be found only in areas where − either because of orographic rain or due to biotope compensation − summer drought is locally reduced and moisture is homogenously available (Scoppola & Caporali 1998), and thus, the extent of the moisture gradient to which beech understorey flora is exposed is very small.

Non-metric multidimensional scaling and HCA showed that low-elevation sites on limestone substrates were more similar to the low-elevation volcanic sites than to the mid-elevation limestone sites, confirming the overriding role of temperature regime in controlling floristic composition. This may seem

quite unexpected compared to what observed in C-Europe, where acidophilous beechwoods have a markedly different floristic composition and are typically species poor (e.g. Ellenberg 1988; Willner, Moser & Grabherr 2004). However, in spite of the parent material, soil pH of the beech forests on volcanic substrates included in our study is relatively high, with values often ranging between 5.5 and 6.0 (Lorenzoni *et al.* 1995). Moreover, it has been repeatedly observed in the descriptive literature that in Italy, the role of bedrock type in influencing beech understorey decreases along a latitudinal gradient from the Alps to the Southern Apennines (Di Pietro 2009): the reasons are not well known, but are probably connected to historical–biogeographical differences in the regional species pool. Within our study (limited to the Central Apennines), volcanic sites do have a small number of exclusive, acidophilous species (e.g. *Mespilus germanica, Festuca heterophylla*), but at the same time, all low-elevation sites share a very rich contingent of Mediterranean, frost-sensitive species that blurs the substrate-driven differences (unfortunately, within central Italy there are only very few examples of high-altitude beechwoods on acid bedrock, and they could not so far be included in the tree ring network because of the scarcity of mature stands).

In this work, we also tested the climate-related EIVs obtained as mean values of each floristic assemblage against site-specific meteorological series. Most papers aimed at comparing EIVs with physical field measurements did not include the EIVs for temperature and continentality. Odland (2009) and Ewald (2003) compared the mean EIV for temperature from plotless floristic data and from phytosociological relevés, respectively, with the general lapse rate of temperature along altitudinal gradients. Renetzeder *et al.* (2010) found that mean EIVs for temperature of plant communities showed a good linear relationship with interpolated growing-season temperature (with a $10 \times 10$ km resolution). Scherrer & Körner (2011) correlated mean Landolt indicator values for temperature from small-scale vegetation plot (in the alpine belt) with measured, microclimate temperature data obtained from miniature data-loggers, finding a strong linear relationship with night-time soil temperatures. Lenoir *et al.* (2013) found a significant linear relationship between the average EIVs for temperature of vegetation plots in northern Europe and the local soil temperature of summer months obtained from miniature data-logger, and a very strong relationship with the interpolated growing-season mean air temperature obtained from the WorldClim data base ($1 \times 1$ km resolution): this is in accordance with the excellent correlation found in our study between EIVs for temperature and mean summer temperature obtained from the reconstructed climatic records. The relationship between EIVs and physical temperature was surprisingly strong, even though the EIVs in our study were obtained as unweighted averages rather than, as is common practice in vegetation ecology, from cover-weighted averages (Diekmann 2003). This is, however, consistent with the above-mentioned results by Lenoir *et al.* (2013), who used unweighted averages, and with the study by Carpenter & Goodenough (2014), who found that (for soil moisture, pH

and nitrate) unweighted EIVs correlated with environmental measures better than abundance-weighted ones did. Carpenter & Goodenough (2014) explained their findings suggesting that presence of rare plants can be important in quantification of environmental parameters. For the purposes of climate monitoring, unweighted values will not record changes in species abundances, originated by climate change-induced variations in competitiveness; on the other hand, weighted averages are often based on visual estimates of species cover, introducing an observer bias (e.g. Kercher *et al.* 2003), and relative abundances may fluctuate because of factors such as forestry practices, grazing or canopy development (Diekmann 2003).

We found only a weak (although significant) relationship between the continentality index (annual temperature range) and the EIVs for continentality, probably because beechwoods in Italy are confined to the most oceanic sites: as suggested by Diekmann (2003), the smaller the length of a gradient, the weaker the performance of corresponding indicator values.

We found no correlation between precipitation parameters and the EIVs for moisture (EIVM). Renetzeder *et al.* (2010) reported a similar finding. However, precipitation regime is only one of the many factors controlling available soil moisture (Schaffers & Sýcora 2000; Wamelink *et al.* 2002): micro-habitat properties such as soil water-holding capacity, slope aspect and air moisture connected with topographic features can be of greater relevance than annual precipitation. This holds particularly true for our low-altitude sites, where the precipitation regime would be inadequate (because of the long summer drought) for the very existence of the beech forests. In this elevation belt, they grow only as extrazonal communities in sites characterized by special geo-morphological features (e.g. a deep gorge at BAR and a lake caldera at VEN) (Scoppola & Caporali 1998), maintaining high levels of atmospheric and soil moisture at the biotope scale during the dry season (in a gorge near BAR, air relative humidity was found to be constantly $> 85\%$ during the dry season, while outside values were $< 65\%$: Ciccioli *et al.* 2010). Moreover, although many studies found that EIVM was among the best-performing EIVs (references in Loreto *et al.* 2014), two recent papers have recorded poor performances of EIVM even when compared with measurement of ground water level (Carpenter & Goodenough 2014; Szymura, Szymura & Macioł 2014).

## CONSISTENCY BETWEEN THE TWO DATA SETS

The multivariate patterns in the ordination space of the two data sets were found to be highly similar through Procrustean analysis, meaning that sites sharing similar tree ring chronologies (in turn, due to similar inter-annual climatic variations) also had more similar floristic assemblages than expected by chance. In both data sets, dbRDA showed that the climatic variable explaining most of the variation was summer temperature, with summer drought index playing a minor role and precipitation values being non-significant. Moreover, soil type did not seem to play an important role: within each of the

two data sets, low-elevation sites with limestone bedrock were found to be more similar to the low-elevation volcanic sites than to the mid-elevation limestone sites, while in the tree-ring dbRDA, the amount of variation explained by the EIVs for pH was very small.

Almost all the sites featuring the smallest residuals after Procrustes transformation (Fig. 4) are placed below 1000 m a.s.l. (the only exception is VFO, perhaps because of its transitional position, in both data sets, between mid- and high-mountain forests, in turn due to its location in a wet and cool narrow valley), and in the reconstructed meteorological data have $T_m > 10.6$ °C and $M_j > 6$ °C (Table 1). Previous studies on beech tree ring patterns in central Italy showed as limiting factor for tree growth within this elevation belt, the occurrence of warm and dry spells in late spring (Piovesan *et al.* 2005a). Accordingly, we found that the floristic assemblages of these low-elevation forests are differentiated from the remainder of the sites by herbaceous species which are tolerant of summer drought and indicators of mild winters (Rameau *et al.* 2008), for example *Cyclamen hederifolium, C. repandum, Ruscus aculeatus, Tamus communis* (Table 4 and Appendix S2). Also some geophytes that develop their aerial parts very quickly in early spring, and disappear as soon as *Fagus* comes into leaf, are found only in this group of sites (e.g. *Allium pendulinum, Ranunculus ficaria*), as they are favoured where the snow cover is very short, thus allowing for a longer time for development before the ground is shaded by the beech canopy.

In the elevation belt where the remainder of the sites are found (spanning from c. 1200 m to the tree line) previous tree ring studies have shown the crucial role of the recurrent events of late frost in May and even June (Piovesan *et al.* 2003). From the site-specific meteorological records reconstructed in the present work, it emerged that at these sites $T_m$ is between *c.* 9 and 6 °C and $M_j$ is ≤ 5 °C (Table 1) [interestingly, 5 °C is known to be the eco-physiological threshold at which meristem growth activity is zero (Körner 2008)]. The floras of these sites are on one hand characterized by a low richness of ephemeral geophytes (which are excluded from this habitat due to the prolonged snow cover) and termophilous species; on the other hand, these higher elevation sites feature a set of frost-resistant, drought-sensitive *taxa*, often with a Boreal or even Arctic–Alpine geographical range (Table 4 and Appendix S2): for example *Adenostyles australis* [a late-flowering hemicryptophyte, thus well adapted to a long duration of snow cover; due to its large, hygromorphic leaves, it requires constant water availability through the vegetative season, which can be provided by the melting of late snow (Ellenberg 1988)], *Orthilia secunda* [a cold-tolerant hemicryptophyte, mainly distributed in boreal habitats (especially taiga) in Eurasia and North America (Beatty & Provan 2010)], *Paris quadrifolia* [a late-flowering geophyte (aerial parts emerge in April and flowers appear in June), known not to be frost sensitive and reported as an indicator species of constantly moist habitats, being very sensitive to spring drought and habitat desiccation (Jacquemyn, Brys & Hutchings 2008)].

On the basis of species composition, a further subdivision was detected in HCA on the uppermost part of *F. sylvatica*'s total elevation range, separating only the sites higher than c. 1600–1700 m: these sites have very shallow soils and a high rock cover in the understorey, thus featuring a particularly low species richness, and almost completely lacking geophytes. Instead, in the tree ring data set, a lower rank subdivision (shown by some dissimilarity metrics only) is placed at c. 1300–1400 m. As a result, when a three-cluster arrangement of the tree ring samples was tested for differences in floristic composition, no statistically significant values were obtained in the post hoc test between the mid- and high-elevation clusters. Thus, the high-elevation sites of VCH, SCA and LEO featured large Procrustes residuals. The largest error of the whole sample was found for VCH, probably because – while its dendrochronological pattern is the one typically expected for its altitude (Piovesan *et al.* 2003, 2005a) – its floristic composition is instead characterized by a number of species indicating structural heterogeneity and canopy gaps (e.g. *Anthriscus nitida, Arabis alpina, Galium aparine, Senecio rupestris, Urtica dioica*), since this site is the only primary old-growth forest in the sample (Piovesan *et al.* 2005b). Moreover, it lacks some boreal species typically found at other high-elevation sites, perhaps because of a dryer microclimate in the understorey, since this forest is located on a system of small rocky spurs.

Mean values of EIVs were found to be significantly different between the two main clusters of sites defined by the tree-ring patterns. In the dbRDA of the tree ring data set, when the EIVs from the floristic data set were used as environmental covariates, the EIV for temperature was strongly and highly significantly correlated with the ordination axis explaining most of the variation (Fig. 5). Also the EIV for light had a significant, although less marked, correlation with the main gradient in the data. This seems consistent with the finding by Iio *et al.* (2014) that in dry-climate biomes Leaf Area Index (LAI) can be controlled by drought stress: low-elevation beechwoods will have a lower LAI due to a more Mediterranean climate and thus a higher light intensity reaching the herb layer. However, the lowest sites, although chosen among almost-pure beech forests, have a higher cover of other tree species (mostly *Q. cerris* and *Acer obtusatum*), which have an inherently lower shading power and a different phenological rhythm, allowing more light-demanding species to survive in the understorey (Mölder, Bernhardt-Römermann & Schmidt 2008; Amici *et al.* 2013).

## Conclusions

This is the first study exploring how the multivariate patterns of tree ring chronologies are correlated to floristic composition (and to its associated indicator values). We showed that in Mediterranean beech forests, there is a high degree of congruency between the two types of data across a long elevation gradient. Using synthetic records of temperature and precipitation specifically reconstructed for the sampled sites, we found that summer temperature gradient is the main factor control-

ling the dissimilarity patterns in both data sets. The finding that two very different types of ecological indicators, that is the tree ring parameters and the EIVs obtained from the floras, show highly consistent patterns with each other along a climate gradient, is an important confirmation of the reliability of both bio-indication methods. Moreover, a possible application of our findings for vegetation history and global change research is that similar dendrochronological patterns between sites, from a particular time-window of the past, might also imply a similar floristic composition of the considered forests during that same past period. On the other hand, if a site is found to have changed its bioclimatic position across a long-term tree ring network, over time (Piovesan *et al.* 2008), this could imply a switch in floristic assemblages as well (e.g. a shift from montane to colline bioclimatic belt caused by global warming: Peñuelas & Boada 2003). Finally, our finding of a strong relationship between the EIVs for temperature and meteorological records supports the significance of diachronic floristic data for tracking and monitoring climate changes at the habitat scale and may help with the forecasting of climate change effects on biotic assemblages.

## Acknowledgements

## Data accessibility

Floristic data set: uploaded as online supporting information. Tree ring data set: uploaded as online supporting information.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Sources for floristic data.

**Appendix S2.** Floristic dataset (species-by-site matrix).

**Appendix S3.** Tree ring dataset (pre-whitened tree ring chronologies).