Ecological determinants of species composition in the forest vegetation of Tuscany, Italy

José Ramón Arévalo[1], Fernando Cortés-Selva[2] & Alessandro Chiarucci[2,*]

[1]Departamento de Ecología, Facultad de Biología, Universidad de La Laguna, La Laguna, Tenerife, Spain
[2]Dipartimento di Scienze Ambientali "G. Sarfatti", Universita Di Siena, Via P.A. Mattioli 4, Siena IT-53100, Italy
*Author for correspondence: chiarucci@unisi.it

Background and aims – Monitoring plots are important tools for forest management and can help to predict the directions of changes in species composition in a changing climate. Understanding ecological processes in forest communities is one of the most important goals for a proper management of these ecosystems and for biodiversity conservation.

Methods – The compositional data recorded within an inventory were used here to describe plant community composition and investigate how it is affected by climatic or other ecological factors. Six large forests along an altitudinal gradient owned and managed by the regional administration of Tuscany were chosen as study sites. 109 plots of 400 m² were randomly located according to a stratified sampling design, with the number of plots in each forest related to forest size. The number of stems and DBH of all plants with DBH > 3 cm were recorded for each woody species within each plot. In addition, the frequency of understory species was recorded by twelve subplots of 0.25 m², randomly located within each quadrant of each plot.

Key results – Elevation, soil water capacity, minimum precipitation, annual precipitation/temperature ratio and maximum temperature were found to be the explanatory variables for the gradient of woody species composition. After removing plantation plots from analyses, only elevation, soil water capacity and sum of temperature of the months over 5°C were retained as explanatory variables of this gradient. Elevation, soil organic matter and the sum of winter precipitation were the only environmental variables that were related to the compositional gradient of understory species.

Conclusions – Present species composition of these forests is unlikely to remain in a next future according to the IPCC climate predictions, whose moderate scenarios predict in the Mediterranean area a severe decrease in precipitations and a raise of 3–4 degrees on average temperature.

Key words – climate, DCA, forest ecology, forest ecosystems, gradient analysis, vegetation analysis.

INTRODUCTION

Comparative studies on community composition within similar ecosystems of different regions of the world have been carried out from various points of view as species composition, plant community structure and phylogenetic relationships (e.g. Ovington 1983, van der Maarel 1996, Ohsawa 1999). At the local scale, topographic as well as edaphic habitat conditions are decisive factors in determining the local plant community structure and composition, since these factors affect plant species colonization and persistence (Hugget 1995). Structural and spatial characteristics can control many aspects of the plant community, including regeneration patterns or disturbances intensity (Moeur 1993, Arévalo & Fernández-Palacios 2000). Moreover, temperature is prob-

ably one of the most important factors in determining species distribution (Barbour et al. 1977), and temperature is inversely related with altitude, creating a lapse rate (Lowry 1969) reflected by species distribution. It is unclear to what extent global warming will affect species distribution, but it is generally accepted an increase of thermophile and lowland species to expand their altitudinal range margins (Lenoir et al. 2010).

Species composition of forest stands is dependent on many factors (environmental characteristics, species competitive abilities, disturbances…). However, stand history is often one of the most important factors in populated areas or near population centres, because of the long-lasting use of forest resources by man (Oliver & Larson 1990). Understanding the ecological processes in forest plant communities

is one of the most important concerns for forests managers in Italy and other developed countries, since near-natural forest management and restoration are increasingly supported by the local society. Lack of acknowledgment of the ecological processes controlling plant community structure and composition increases the possibility of unsuccessful management or restoration programs.

In Tuscany, located in the centre of Italy, forests exceed one million hectares (more than 47% in surface). About 120,000 ha of forests belong to the Regional Administration of Tuscany and other 100,000 ha to other public institutions, and thus the public forests represent an important territorial resource for Tuscany. The traditional management of the forests of the region has been basically for timber production, but keeping the objective of soil protection. However, consideration of forest ecosystems for environment and landscape issues has increased in recent years, and monitoring programs have been established along the whole Italy, with the Tuscan project being one of the first started (Bartolozzi et al. 2002). Originally, the monitoring network aimed to obtain information exclusively on tree health, but carbon stock and biodiversity issues were included in recent years (Bartolozzi et al. 2002). Presently, these forests are undergoing a continuous monitoring, where species composition, forest health and spatial relationships are the main points of the monitoring. At the beginning the plant diversity monitoring was based on a few large plots (Chiarucci et al. 2001), but then moved to the use of a high number of smaller plots with

a better spatial dispersion and a wider coverage of the underlying ecological gradients due to scale effects (Chiarucci & Bonini 2005).

The aim of this work is to analyse the gradient in species composition at the regional scale in six large forest estates in Tuscany. The main objective is to relate plant species composition to climatic and other ecological parameters, in order to establish a baseline distributional model to be used for descriptive purposes and for predicting future changes in species composition under the predicted climate change (Grabherr et al. 1994, Miller-Rushing & Primack 2008). We will test the hypothesis that climatic conditions are the main determinants of species composition, making forests susceptible to intense changes in the futurein response to the predicted global warming. Understanding compositional gradient and its link with environmental factors could become a useful tool for the management of these forests.

MATERIAL AND METHODS

Study site

Six large forest estates (hereafter 'forests') owned and managed by the regional administration of Tuscany were chosen as study sites. The six forests were Foreste Pistoiesi (hereafter FP), Foreste Casentinesi (FC), Madonna delle Querce (MQ), Farma-Merse and Belagaio (FM), Livornesi Hills (CL), Bandite di Scarlino and Montioni (BF; fig. 1). Each forest is formed by contiguous or non-contiguous woodlands managed as a single unit. These forests cover a total of 37,240 ha and range in size from 2,098 to 10,311 ha. They are located from the lowlands of the coastline to the Apennine mountains and their vegetation is formed by different plant communities, varying from the evergreen Mediterranean forests dominated by *Quercus ilex*, along the coastlines, to the *Fagus sylvatica* and *Abies alba* forests of mountain sites. Conifer plantations are present in all the forests; planted species are native, such as *Pinus pinea*, *P. pinaster*, *P. halepensis* and *Abies alba*, or non-native, such as *Pinus nigra*.

Sampling design

Forest structure and composition were surveyed by a design-based probabilistic sample of sites. The sites selected for this study (109 sites) were a sub-sample of those used for the second-stage sampling of the Forest Inventory of Tuscany (IFT). The number of sites in each forest was proportional to the true forest surface, i.e. excluding open patches therein. In each site, once located with a high precision GPS, a 20 m × 20 m plot was delimited.

Each plot was divided into four contiguous 10 m × 10 m quadrants. The following data were collected: (i) total list of species within the quadrant/plot, (ii) DBH, density and species identity of each individual plant with DBH > 3 cm and (iii) spatial frequency of each species present within twelve 0.25 m × 1 m subplots, located by a restricted random procedure within the four quadrants (three in each quadrant); each subplot was divided into ten 10 cm × 25 cm cells. Two groups of vascular plants were used in the present paper: woody species (WSP) (defined as species found with individuals

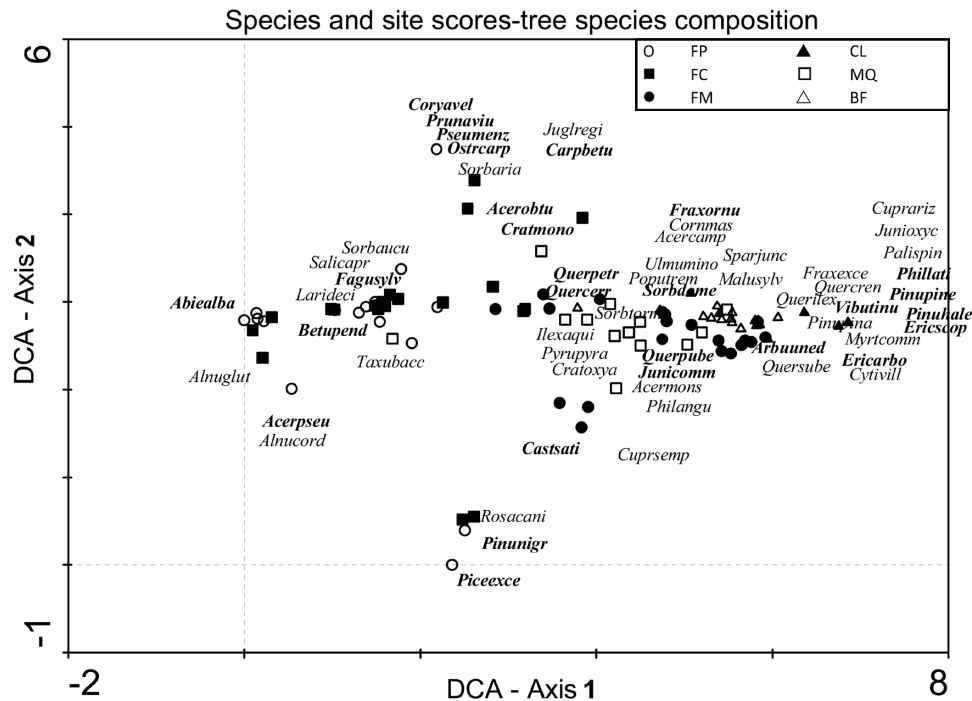**Figure 1** – Distribution of the 6 investigated forests across Tuscany Region.

Figure 2 – Species and site scores in the space defined by axes 1 and 2 of DCA based on the importance value of woody species. Species with more than 1% presence in all plots are indicated in bold. The legend indicated the different forests: Pistoiesi forest (FP), Casentinesi forest (FC), Madonna delleQuerce (MQ), Farma-Merse, Belagaio (FM), Livornesi Hill (CL) and Bandite di Scarline-Montioni (BF). Eigenvalues of axes 1 and 2 were 0.929 and 0.669, respectively, and the cumulative percentage of variance expressed by both axes was 22.4%. The names of the species use the first four letters of the genus and the first four letters of the specific epithet (see electronic appendix 1 for species full names).

with DBH > 3 cm) and understory species (USP) as found in the twelve 0.25 m× 1 m subplots (herbaceous species or woody species which did not reach a 3-cm DBH). Sampling was carried out in 2001. Species nomenclature follows Pignatti (1982).

Statistical analysis

In this paper, Detrended Correspondence Analysis (DCA; Hill & Gauch 1980) was performed, using CANOCO (ter Braak & Šmilauer 1998), to analyse how species composition changesalong the main gradient. For WSP, the analysis was based on the dominance index: "(relative percentage of basal area of the species i + relative percentage of density of species i)/2" (modified from Müller-Dombois & Ellenberg 1974). The analysis was repeated after removing the plots that were classified as plantations (eighteen plots) and using them as passive samples for display purposes. For USP, the DCA was based on the spatial frequency value of each species within each plot (out of the twelve subplots).

We used stepwise multiple regression to determine which environmental variables are related to the distribution of site scores along DCA axis 1 (these values will be the dependent variable in the regression). We set the criteria for inclusion of variables as $P < 0.05$ for entering and $P > 0.10$ for removal (based on the t-test of the coefficient of the specific variable), as is standard for stepwise multiple regression (George &

Mallery 2005). Our result was significant with $P < 0.05$ for the overall model.

The independent variables were elevation, slope, % of organic matter, water capacity, soil pH, % of limestone content, folded aspect, potential direct incident radiation (hereafter radiation) using the formula proposed by McCune & Keon (2002), together with the following climatic variables: total annual rainfall, maximum precipitation per month, minimum precipitation per month, total summer precipitation, total winter precipitation, mean annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, sum of summer temperatures (degree days), sum of winter temperatures, sum of temperatures of the months with temperature > 5°C, annual precipitation/annual temperature and summer precipitation/summer temperature (electronic appendix 2). Soil chemistry data were extracted from the regional soil map of Tuscany (http://www.regione.toscana.it), while climatic data were obtained from a model realized for the whole Tuscany using the data of the past thirty years ("DESERNET" INTERREG IIIB – MEDOCC – Regione Toscana – IBIMET – CNR).

In order to check for co-variation in the compositional gradients of woody and understory vegetation the site scores along the first axis of the three DCA ordination diagrams (WSP, WSP without plantations and USP) were correlated by using the Pearson correlation coefficient.

The regression analyses were implemented using the SPSS statistical package (George & Mallery 2005).

Table 1 – Multiple regression analysis for axis 1 of DCA.
Model I, using the importance value of the WSP in the plots; Model II, the same data set without plantation plots and using these plots as passive in the analysis; Model III, the frequency of the USP in the twelve subplots within each plot. In the table are indicated the values of the t-test for the variables as well as the associated probability (P) of each one (likelihood of the t-test values could occur by chance).

Model I. Multiple regression for DCA axis 1 of the plots using WSP					
Model F	**P**	**Variables**	***β***	***t-test***	***P***
		Elevation	-0.619	-5.416	0.000
		Soil water capacity	-0.098	-2.191	0.031
94.250	<0.001	Minimum P	-0.307	-2.537	0.013
		Annual P/T	0.310	3.357	0.001
		Max T	0.249	2.432	0.017
Model II. Multiple regression for DCA axis 1 of the plots using WSP without plantations					
Model F	***P***	**Variables**	***β***	***t-test***	***P***
		Elevation	-0.703	-9.544	0.000
166.71	<0.001	Soil Water Capacity	-0.122	-2.956	0.004
		$\sum$ T monthsT > 5ºC	0.204	2.771	0.007
Model III. Multiple regression for DCA axis 1 of the plots using USP					
Model F	***P***	**Variables**	***β***	***t-test***	***P***
		Elevation	-0.383	-3.017	0.003
67.6	<0.001	% Org. matter	-0.221	-2.878	0.005
		$\sum$ P winter	-0.292	-2.587	0.011

RESULTS

Recorded species

The sampling resulted in a total of 277 species recorded, 62 of which were WSP and 215 USP. Sixteen WSP were observed in the woody species sample but not in the understory one (Appendix I). Other 144 species were present in the plots but were absent in the woody and in the understory data samples (see Chiarucci & Bonini 2005 for a total sample).

Woody species

The first ordination axis of the DCA, based on the abundance of WSP (fig. 2), suggested a rather clear compositional gradient in relation to elevation from the negative to the positive side, from the mountain forests FC and FP to the coastline forests BF and CL, through the hilly forests MQ and FM. The first DCA axis had a length of almost 7 SD (biodiversity standard deviation), indicating that plots in the FP forest have no species in common with the plots in BF. The WSP showed a parallel gradient from mountain species, such as *Abies alba*, *Betula pendula* and *Fagus sylvatica*, to coastline species as *Pinus pinea*, *Quercus ilex*, *Q. suber*, *P. halepensis*, *Erica arborea* and *E. scoparia*. The WSP typical of hilly sites and/or intermediate forest types were located in the middle of the gradient (*Juniperus communis*, *Quercus pubescens*, *Ulmus minor* and *Acer campestre*).

Only elevation, water capacity, minimum precipitation, annual precipitation/temperature, and maximum temperature were selected in the regression model to predict, as independent variables, the scores of the sites along axis 1 of the DCA (table 1, model I).

Woody species without plantation plots

The DCA done making passive the plantation plots (as they could be interfering with the WSP distribution) showed results very similar to those obtained with the whole data set (fig. 3). The only apparent difference was a lower discrimination among FM and MQ, even though no plots were removed for the analysis from these forests. The most important species through the gradient were *A. alba* and *F. sylvatica* in the mountain forests (FC and FP) and *P. pinaster*, *Erica arborea*, *Viburnum tinus* and *P. pinea* in the coastline forests (BF and CL).

After removing the plantation plots from the analysis, only elevation, soil water capacity and the sum of temperatures of the months over 5 ºC remained as explanatory variables of the site scores along axis 1 (table 1, model II).

Understory species

A similar gradient of the plots and the six forests, from mountain to coast vegetation, was obtained by the DCA based on the USP (fig. 4). However, the length of axis 1 was higher than the previous analyses with WSP or WSP without plantations plots, indicating more abrupt compositional changes in understory species than in woody species. The compositional gradient was evidenced by the shift in the dominance of *Gymnocarpium dryopteris*, *Laburnum alpinum*, *Oxalis acetosella* and *Prenanthes purpurea*, in mountain forests (FP and FC forests), to the dominance of *Asparagus tenuifolius*, *Smilax aspera*, *Urospermum picroides*, *Quercus ilex*, *Viburnum tinus*, *Phillyrea latifolia* and *Cyclamen repandum*, in the coastline forests (BF and CL). The forests located in the middle of the gradient (MQ and FM) were characterised by a higher number of species and the main dominant species

Table 2 – Pearson correlation coefficients between the DCA scores along axis 1 of the three analyses.
WSP, using the importance value of the WSP in the plots; WSP NP, using the importance value of the WSP in the plots but excluding the plantation plots; USP, using the frequency of the USP in the plots. All correlations were highly significant (P < 0.001, n = 109).

	WSP	WSP NP	USP
WSP	1	-	-
WSP NP	0.979	1	-
USP	0.719	0.721	1

were *Pinus pinaster*, *Cytisus scoparius*, *Brachypodium rupestre*, *Galium mollugo* and *Rosa sempervirens* (fig. 5).

Only elevation, soil organic matter and the sum of winter precipitation were retained as independent variables in the model predicting site scores along DCA axis 1 based on the frequency of the species in the subplots (table 1, model III).
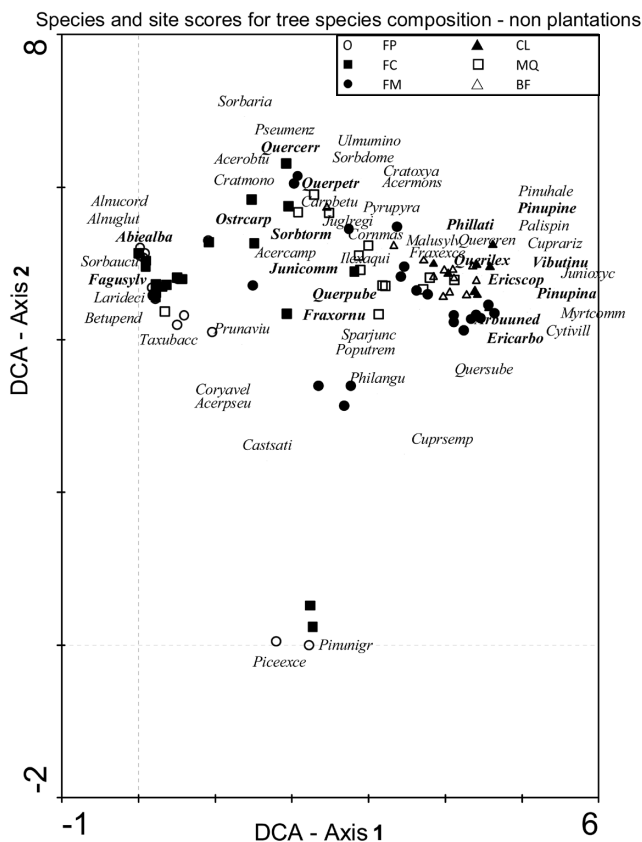
Figure 3 – Species and site scores in the space defined by axes 1 and 2 of DCA based on the importance value of woody species, but with the plantations plots considered as passive in the analysis (eighteen plots removed: nine from FP, eight from FC and one from CL). Species with more than 1% presence in all plots are indicated in bold. Eigenvalues of axes 1 and 2 were 0.891 and 0.632, respectively, and the cumulative percentage of variance expressed by both axes was 16.0%.

Covariation in the compositional gradients of woody and understory vegetation

The correlation of the plot scores along the first DCA axis of the three ordination analyses revealed significant relationships among the different samples (WSP, WSP without plantations and USP, table 2). The correlation coefficient was particularly high between the site scores for both the ordination of the WSP, suggesting that the species introduced for forestry plantations did not interfere much with the distributional pattern of WSP (table 2).

DISCUSSION

The ordination of the data revealed that the 109 investigated plots were variable in terms of species composition, mostly in accordance to the six forests they belonged to and to the altitudinal and precipitation gradients. Climatic variables as well as some soil variables were very important in explaining the plot and species distribution, but the most explanatory variable was elevation, a very common situation in ecosystems with marked altitudinal gradients (Pauchard & Alaback 2004, Ullmann et al. 1995, Godfree et al. 2004). For each of the three separate analyses, elevation was the most important environmental variable to explain the species compositional gradient at the plot scale, for both woody and understory species. The altitudinal distribution of plants from mountain to coastal areas is partly related to gradients of environmental stress (see e.g. Fernández-Palacios 1992, Alpert et al. 2000, Godfree et al. 2004), as temperature, precipitation or solar radiation. Elevation is the most important environmental determinant because it acts as a combination of other ecological factors with a more direct action on the distribution of plant species and, consequently, on species composition.
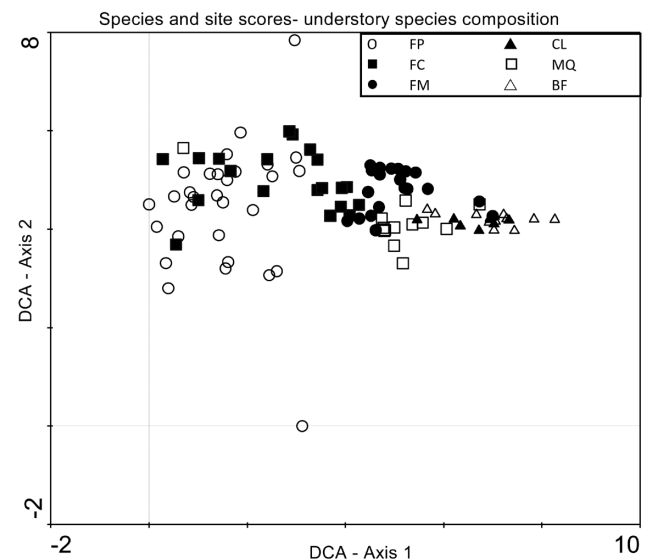

Figure 4 – Site scores in the space defined by axes 1 and 2 of DCA based on the frequency value of the understory species. Eigenvalues of axes 1 and 2 were 0.844 and 0.706, respectively, and the cumulative percentage of variance expressed by both axes was 8.8%.
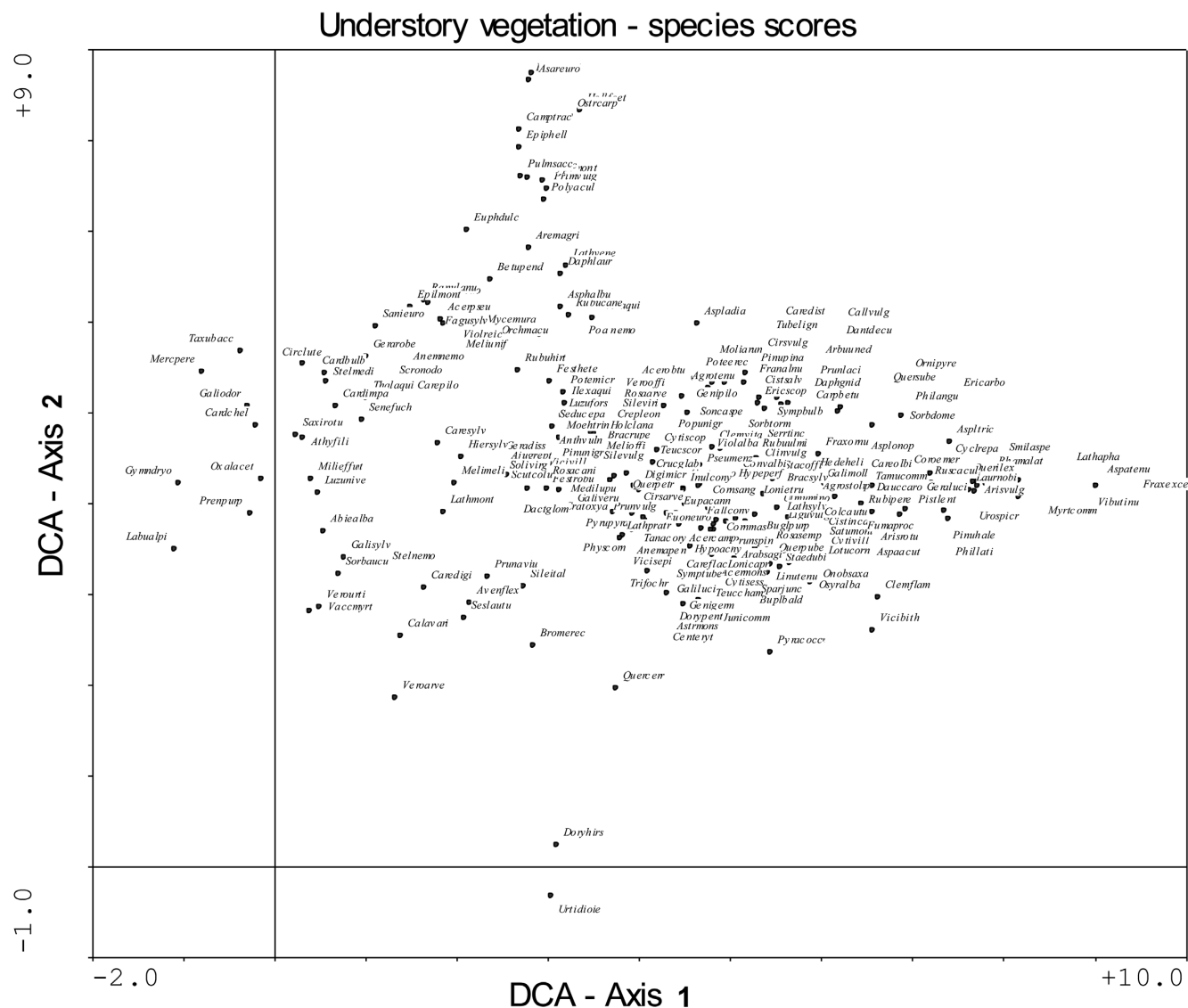
Understory vegetation - species scores

Figure 5 – Species scores in the space defined by axes 1 and 2 of DCA based on the frequency value of the understory species.

The distributional pattern of the dominant species here observed perfectly reflects the well known dominance of tree species, with *Quercus ilex* dominating along the coastline and in sites with higher temperature, *Q. cerris* and *Q. pubescens* dominating intermediate sites, in hilly habitats, and *Fagus sylvatica* dominating the mountain forests (Pignatti 1982, Chiarucci & Bonini 2005). In addition, forests of this region are known to have an almost linearly decreasing pattern of woody species richness from lower to higher elevations (Chiarucci & Bonini 2005, Bacaro et al. 2008) and this was reflected by a more complex species composition of the lower elevation forests.

In the case of the woody species, another important variable related with their distribution was the soil water capacity. This edaphic factor indicates the degree of humidity that can be maintained by the soil, and is an important variable affecting the performance of woody species in some stages of their life cycle, such as the germination of many tree spe-

cies (Madsen & Larsen 1997, Arévalo & Fernández-Palacios 2008).

Mediterranean climate typically shows the rainfall distribution centred during the winter period, when there is a lower need of water for plant growth, and the consequent summer drought is more pronounced at lower altitudes and the coastline than at higher altitudes (Mazzoleni et al. 1992, Blasi et al. 1998). Other important variables explaining the compositional gradients for the woody species were the minimum temperature of the coldest month, the ratio between the mean annual rainfall and the mean annual temperature, and the maximum temperature of the warmest month. On the other hand, only the sum of the temperatures for the months with T > 5°C was a significant variable in the analysis performed excluding the plantation plots. These results indicated the complex combination of climatic variables in controlling the woody species composition of the Tuscan forests. By using a GLM approach, Bacaro et al. (2008) found that elevation, slope and sun radiation were the only factors included in a

model explaining more than 83% of the total deviance of woody species richness in the same set of plots. In this paper, different sets of variables were used to explain the main gradient of woody species composition, but the most important variable was still elevation. Moreover, precipitation was also an important explanatory variable of the species distribution, even thoughtit does not increase linearly from the coast to the mountains.

The climatic control on species composition is a well known process at both the landscape (e.g. Kadmon & Danin 1999) and the community scale (e.g. Sternberg & Shoshany 2001, Bergmeier 2002) in the Mediterranean area, and the results here observed were well in agreement to this pattern. These results were also supported when the plantations plots were removed, confirming that this pattern is mostly a natural one. While elevation, as a variable combining the effects of many other factors, is a very informative variable for explaining distribution of species when strong gradients are present, in the Mediterranean region precipitation and other direct climatic parameters are more important because they have a direct biological effect on species performance and then on species distribution. As an example, in Mediterranean forests water availability is a limiting factor for seedling recruitment (Borchert et al. 1989, Herrera et al. 1994, Lloret et al. 2004).

In the case of the understory species, other factors related to altitude were important in conditioning the distribution of the species, but all of these were obscured by the importance of elevation. The composition patterns of understory species were found to be well related to that of woody species, but the gradient of the former group of species was longer than that of the latter ones, suggesting a stronger effect of environmental factors on understory species. The more complex pattern of species composition is also in agreement with the model performed by Bacaro et al. (2008), in which five variables (elevation, forest physiognomy, tree density, soil pH and % cover of the tree layer) were needed to explain 58% of the variance of total species richness at the plot-scale. In addition, the understory species composition is also related to the forest canopy that has some control over the understory habitat, providing favourable environmental conditions for some species and unfavourable conditions for others. This effect has been revealed several times, when exotic woody plants have been used in forestation, favouring the regeneration of a native understory (Arévalo & Fernández-Palacios 2005).

Moderate environmental conditions, namely low water and thermal stress, and high productivity (Whittaker & Heegaard 2003) at mid-elevations may be the most important factors for peak species richness in this zone, the well known unimodal or humped-back curve, as it is revealed in figures 2 and 3 (more species scores locate in the middle of the scatterplot around the middle altitude areas) and in previous studies using the same set of data (Chiarucci & Bonini 2005, Bacaro et al. 2008). Drought stress increases towards lower altitudes while the winter thermal stress is more important at the higher altitudes. Both act as filters against the establishment of non-adapted species. These results support the concept of the diversity-productivity relationship (Rosenzweig

& Abramsky 1993), since the combination of hydrologic and thermal stresses limits the availability of resources.

CONCLUSIONS

Inventories are important for increasing baseline knowledge on ecosystems and to inform decision makers, but more research is needed on community function and dynamics. The present analyses allowed to determine how several ecological parameters influence the species composition of forest vegetation in Mediterranean ecosystems and how a few important variables are determinant to explain present-day species composition. In the future, the climate change supposed to happen under different predictive models is expected to strongly influence species composition for different groups of organisms (e.g. Parmesan 1996, Grace et al. 2002) and some records have already been found, especially in Alpine ecosystems (e.g. Walther et al. 2005). The compositional analysis of Tuscan forests done in this study revealed the direct and indirect (by means of elevation) influence of climate in controlling plant species composition at the local scale. Despite the problem associated with defining equilibrium stages and trends to potential vegetation (Chiarucci et al. 2010), the climatic changes predicted by IPCC in the Mediterranean area are likely to determine significant changes in the species composition of these forests. In fact, the moderate scenarios of the IPCC predict a severe decrease in precipitations and a raise of 3–4°C on average temperature (de Castro et al. 2004). These changes are in the range here observed across different forests, which differed in terms of species composition. To determine the magnitude of the compositional changes and the capacity of species to migrate according to the climatic shift will be a major task of next research.

SUPPLEMENTARY DATA

Supplementary data are available in pdf format at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of: (1) pooled list of species from the two samplings (WSP and USP); and (2) geomorphologic features and climatic variables used in the analysis (mean and standard deviation).

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REFERENCES

Alpert P., Bone E., Holzapfel C. (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology and Evolution 3: 52–66. http://dx.doi.org/10.1078/1433-8319-00004

Arévalo J.R., Fernández-Palacios J.M. (2000) Seed bank analysis of tree species in two stands of the Tenerife laurel forest (Canary Islands). Forest Ecology and Management 130: 177–185. http://dx.doi.org/10.1016/S0378-1127(99)00182-6

Arévalo J.R., Fernández-Palacios J.M. (2005) Gradient analysis of exotic Pinus radiata plantations and potential restoration of natural vegetation in Tenerife, Canary Islands (Spain). Acta Oecologica 27: 1–8. http://dx.doi.org/10.1016/j.actao.2004.08.003

Arévalo J.R., Fernández-Palacios J.M. (2008) Natural regeneration of Pinus canariensis Chr. Sm. ex DC. in Buch in forest plantations after thinning. The Open Forest Science Journal 1:54–60. http://dx.doi.org/10.2174/1874398600801010054

Bacaro G., Rocchini D., Bonini I., Marignani M., Maccherini S., Chiarucci A. (2008) The role of regional and local scale predictors for plant species richness in Mediterranean forests. Plant Biosystems 142: 630–642. http://dx.doi.org/10.1080/11263500802411064

Barbour M.G., Burk J.H., Pitts W.D. (1977) Terrestrial plant ecology. Menlo Park, The Benjamin/Cummings Publishing Company Inc.

Bartolozzi L., Bonini I., Boretti R., Bussotti F., Cenni E., Chiarucci A., Cozzi A., De Dominicis V., Ferretti M., Grossoni P., Landi G., Leonzio C., Vignozzi G. (2002) Forest ecosystem monitoring in Tuscany (Italy): past activities, present status and future perspectives. Journal of Limnology 61: 129–136. http://dx.doi.org/10.4081/jlimnol.2002.s1.129

Bergmeier E. (2002) Plant communities and habitat differentiation in the Mediterranean coniferous woodlands of Mt. Parnon (Greece). Folia Geobotanica et Phytotaxonomica 37: 309–331. http://dx.doi.org/10.1007/BF02805214

Blasi C., Carranza M.L., Filesi L., Tilia A., Acosta A. (1998) Relation between climate and vegetation along a Mediterranean-temperate boundary in central Italy. Global Ecology and Biogeography 8: 17–27. http://dx.doi.org/10.1046/j.1365-2699.1999.00121.x

Borchert M.I., Davis F.W., Michaelsen J., Oyler L.D. (1989) Interactions of factors affecting seedling recruitment of blue oak (Quercus douglasii) in California. Ecology 70: 389–404. http://dx.doi.org/10.2307/1937544

Chiarucci A., Araújo M.B., Decocq G., Beierkuhnlein C., Fernández-Palacios J.M. (2010) The concept of potential natural vegetation: an epitaph? Journal of Vegetation Science 21: 1172–1178. http://dx.doi.org/10.1111/j.1654-1103.2010.01218.x

Chiarucci A., Bonini I. (2005) Quantitative floristics as a tool for the assessment of plant diversity in Tuscan forests. Forest Ecology and Management 212: 160–170. http://dx.doi.org/10.1016/j.foreco.2005.03.041

Chiarucci A., De Dominicis V., Wilson J.B. (2001) Structure and floristic diversity in permanent monitoring plots in forest eco-

systems of Tuscany. Forest Ecology and Management 141: 201–210. http://dx.doi.org/10.1016/S0378-1127(00)00329-7

De Castro M., Gallardo C., Calabria S. (2004) Regional IPCC Projections until 2100 in the Mediterranean Area. In: Marquina A. (ed.) Environmental Challenges in the Mediterranean 2000–2050: 75–90. NATO Science Series: IV Earth and Environmental Sciences. Netherlands.

Fernández-Palacios J.M. (1992) Climatic responses of plant species on Tenerife (Canary Islands). Journal of Vegetation Science 3: 595–602. http://dx.doi.org/10.2307/3235826

George D., Mallery P. (2005) SPSS for windows step by step. A simple guide and reference 12.0 update (5th Ed.). Boston, Allyn & Bacon.

Godfree R.C., Lepschi B.J., Mallinson D.J. (2004) Ecological filtering of exotic plants in an Australian sub-alpine environment. Journal of Vegetation Science 15: 227–236. http://dx.doi.org/10.1111/j.1654-1103.2004.tb02257.x

Grabherr R.S., Gottfriend M., Pauli H. (1994) Climatic effects on mountain plants. Nature 369: 448. http://dx.doi.org/10.1038/369448a0

Grace J., Berninger F., Nagy L. (2002) Impacts of climate change on the tree line. Annals of Botany 90: 537–544. http://dx.doi.org/10.1093/aob/mcf222

Herrera C.M., Jordano P., López-Soria L., Amat J.A. (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs 64: 315–344. http://dx.doi.org/10.2307/2937165

Hill M.O., Gauch H.G. Jr. (1980) Detrended Correspondence Analysis: an improved ordination technique. Vegetatio 42: 47–58. http://dx.doi.org/10.1007/BF00048870

Hugget R. (1995) Geoecology. An evolutionary approach. London, Routledge.

Kadmon R., Danin A. (1999) Distribution of plant species in Israel in relation to spatial variation in rainfall. Journal of Vegetation Science 10: 421–432. http://dx.doi.org/10.2307/3237071

Lenoir J., Gégout J.C., Dupouey J.L., Bert D., Svenning J.C. (2010) Forest plant community changes during 1989-2007 in response to climate warming in the Jura Mountains (France and Switzerland). Journal of Vegetation Science 21: 949–964. http://dx.doi.org/10.1111/j.1654-1103.2010.01201.x

Lloret F., Peñuelas J., Ogaya R. (2004) Establishment of co-existing Mediterranean tree species under a varying soil moisture regime. Journal of Vegetation Science 15: 237–244. http://dx.doi.org/10.1111/j.1654-1103.2004.tb02258.x

Lowry W.P. (1969) Weather and life. New York, Academic Press.

Madsen P., Larsen J.B. (1997) Natural regeneration of beech (Fagus sylvatica L.) with respect canopy density, soil moisture and soil carbon content. Forest Ecology and Management 97: 95–105. http://dx.doi.org/10.1016/S0378-1127(97)00091-1

Mazzoleni S., Lo Porto A., Blasi C. (1992) Multivariate analysis of climatic patterns of the Mediterranean basin. Vegetatio 98: 1–12. http://dx.doi.org/10.1007/BF00031632

McCune B., Keon D. (2002) Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13: 603–606. http://dx.doi.org/10.1111/j.1654-1103.2002.tb02087.x

Miller-Rushing A.J., Primack R.B. (2008) Global warming and flowering times in Thoreau's concord: a community perspective. Ecology 89: 332–341. http://dx.doi.org/10.1890/07-0068.1

Moeur M. (1993) Characterizing spatial patterns of trees using stem-mapped data. Forest Sciences 39:756–775.

Müller-Dombois D., Ellenberg H. (1974) Aims and methods of vegetation ecology. New York, Wiley & Sons.

Ohsawa M. (1999) Comparative ecology of laurel forest in western and eastern hemispheres. In: Ohsawa M., Wildprett W., del Arco (eds) A comparative study on evergreen broad-leaved forest and trees of the Canary Islands and Japan: 3–7. Chiva, Chiva University.

Oliver C.D., Larson B.C. (1990) Forests stand dynamics. New York, Ed Mcgraw.

Ovington J.D. (1983) Temperate broad-leaved evergreen forests. In: Goodall D.W. (ed.) Ecosystems of the world. New York, Elsevier.

Parmesan C. (1996) Climate and species' range. Nature 382: 765–776. http://dx.doi.org/10.1038/382765a0

Pauchard A., Alaback P. (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. Conservation Biology 18: 238–248. http://dx.doi.org/10.1111/j.1523-1739.2004.00300.x

Pignatti S. (1982) Flora d'Italia. Bologna, Edagricole.

Rosenzweig M.L., Abramsky Z. (1993) How are diversity and productivity related? In: Ricklefs R.E., Schluter D. (eds) Species diversity in ecological communities: 52–65. Chicago, Chicago University Press.

Sternberg M., Shoshany M. (2001) Influence of slope aspect on Mediterranean woody formations: comparison of a semiarid and an arid site in Israel. Ecological Restoration 16: 335–345. http://dx.doi.org/10.1046/j.1440-1703.2001.00393.x

ter Braak C.J.F., Šmilauer P. (1998) Reference manual and user's guide to Canoco for Windows: Software for canonical community ordination (version 4). New York, Microcomputer Power.

Ullmann I., Bannister P., Wilson J.B. (1995) The vegetation of roadside verges with respect to environmental gradients in southern New Zealand. Journal of Vegetation Science 6: 131–142. http://dx.doi.org/10.2307/3236264

Van der Maarel E. (1996) Vegetation dynamics and dynamic vegetation science. Acta Botanica Neerlandica 45: 421–442.

Walther G.R., Beißner S., Burga C.A. (2005) Trends in the upward shift of alpine plants. Journal of Vegetation Science 16: 54–548. http://dx.doi.org/10.1111/j.1654-1103.2005.tb02394.x

Whittaker R.J., Heegaard E. (2003) What is the observed relationship between species richness and productivity? Comment. Ecology 84: 3384–3390. http://dx.doi.org/10.1890/02-3128