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Diversity and ecology of forest communities in Küre Mountains National Park of Turkey

Diversidad y ecología de las comunidades forestales en el Parque Nacional de las Montañas de Küre de Turquía

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SUMMARY

This study aimed at analyzing the diversity and ecological characteristics of forest associations (121 relevés classified under eight associations) in Küre Mountains National Park. Ordination analyses (DCA and CCA) and response curves were used to reveal ecological characteristics of vegetation using soil parameters (pH, electrical conductivity, sand, clay and dust content, soil moisture) and topographical variables (altitude, slope, potential direct incident radiation and heat load). Ecological conditions of communities were also tested using average Ellenberg indicator values (EIVs). Among forest associations, the highest species diversity was found in *Phillyreo latifoliae-Pinetum brutiae* and the lowest diversity in *Hedero-Castanetum sativae*, which had a dense *Rhododendron ponticum* shrub layer. However, *Salicio-Platanetum orientale* and *Buxo sempervirens-Carpinetum betuli* had the highest beta diversity since they harbored unique species composition. Conditional effects of altitude, slope, pH and electrical conductivity, soil dust and sand content, sandy-loam and loam soil types presented significant contributions in species composition. While *Carpino-Quercetum petraeae* was found on soil with high dust content having high pH and electrical conductivity values, *Quercetum roburi-Aceretum campestri* and *Salicio-Platanetum orientale* were related to soil with loam. Species responses to soil and topographical variables varied for most tree species. Light EIVs, which has a high positive correlation with potential direct incident radiation and heat load, related to *Phillyreo latifoliae-Pinetum brutiae* and *Salicio-Platanetum orientale*. Riverside forest communities differed from other communities in nutrient and humidity EIVs. However, EIVs did not show a good correlation with associated soil parameters such as soil moisture-humidity EIVs and soil pH-acidity EIVs.

Key words: ecological differentiation, forest vegetation, Küre Mountains National Park, Turkey.

RESUMEN

Este estudio tuvo como objetivo analizar la diversidad y características ecológicas de asociaciones forestales (121 registros clasificados en ocho asociaciones) en el Parque Nacional Montañas de Küre. Se utilizaron análisis de ordenación (DCA y CCA) y curvas de respuesta para revelar las características ecológicas de la vegetación, utilizando parámetros del suelo (pH, CE, arena, contenido de arcilla y limo, humedad del suelo) y variables topográficas (altitud, pendiente, radiación incidente directa potencial y carga de calor). Las condiciones ecológicas de las comunidades también se probaron utilizando indicadores de Ellenberg (EIV). Entre las asociaciones forestales, la mayor diversidad de especies se encontró en *Phillyreo latifoliae-Pinetum brutiae* y la menor en *Hedero-Castanetum sativae*, que presentó densa capa de arbustos de *Rhododendron ponticum*. *Salicio-Platanetum orientale* y *Buxo sempervirens-Carpinetum betuli* tuvieron la mayor diversidad beta ya que albergaron una composición de especies única. Los efectos de la altitud, pendiente, pH y CE, contenido de limo y arena del suelo y los tipos de suelo franco-arenoso y franco tuvieron contribuciones significativas en la composición de especies. *Carpino-Quercetum petraeae* se encontró en suelos con alto contenido de limo y valores altos de pH y CE; *Quercetum roburi-Aceretum campestri* y *Salicio-Platanetum orientale* se relacionaron con suelos francos. Las respuestas de las especies al suelo y las variables topográficas variaron para la mayoría de las especies de árboles. EIV pequeños, con alta correlación positiva con PDIR y carga térmica, se relacionaron con *Phillyreo latifoliae-Pinetum brutiae* y *Salicio-Platanetum orientale*. Las comunidades de bosques ribereños se diferenciaron de otras comunidades con EIV de nutrientes y humedad. Los EIV no mostraron buena correlación con parámetros del suelo, como EIV de humedad y humedad del suelo y EIV de pH y acidez del suelo.

Palabras clave: diferenciación ecológica, vegetación forestal, Parque Nacional Montañas de Küre, Turquía.

INTRODUCTION

Since plant communities develop as a combination of all factors in environment, their classification will gather this ecological information (Mueller and Ellenberg 1974, Kent and Coker 1992). Therefore, plant communities are characterized by distinctive features such as species composition, species richness, the types of different growth forms, and plant biomass structure as a response to strong environmental gradients (Dwire *et al.* 2004). Such features of plant communities enable ecologists to make statements about prevailing environmental conditions since the overlap of ecological tolerances of many species is smaller than the ecological amplitude of a single species (Çoban 2016). This theory provides the basis for the use of bioindication, where species composition of a given community allows conclusions to be made about environment as surrogates for measured environmental variables (Jean-Claude and Eva 2003, Wamelink *et al.* 2005). One of the most widely used bioindication systems of primary environmental parameters in Central Europe is proposed by Ellenberg *et al.* (1992) who assigned 2726 Central European vascular plant species, with respect to moisture, soil nitrogen status, soil reaction, light regime, temperature and continentality (Schaffers and Sýkora 2000).

Sustainable management of specific forest types requires comprehensive knowledge about mixture combinations, growth relations among species, site conditions, climate factors, biological characteristics and competitive ability of species (Çoban and Özalp 2012). Measured environmental variables can explain only main ecological conditions along with altitudinal zones. However, detailed information about local climate and soil condition within each altitudinal zones would explain most part of compositional variation (Aksoy and Çoban 2017). Especially, forest regions that harbor many forest types with various tree species mixtures require specific forest management plans. Ecological differentiations of forest communities and dominant tree species of the regions with diverse forest structure can provide valuable information for further studies in nature conservation and management. At this point, Küre Mountains, which are among the richest mountains in the western Black Sea Region of Turkey in terms of flora and vegetation diversity, can provide data for revealing ecological characteristics and competition abilities of tree species. The main reasons for this richness are as follows: a variety of climates, topographical diversity with marked changes in ecological and geomorphological characteristics. Küre Mountains is the meeting place of Euro-Siberian, Mediterranean and Irano-Turanian phytogeographical regions. In the field, these can usually be easily recognized by their different vegetational aspects which reflect differences in climate. However, fundamental differences are based on floristic differences, including endemism. There are a number of major vegetation types in these phytogeographical regions as forest, maquis and steppe vegetation.

The main objective of this study is to analyze the ecological characteristics of forest communities and main tree species of Küre Mountains by using measured environmental variables and Ellenberg indicator values (EIVs). Thus, it was hypothesized that 1) diverse ecological characteristics will be reflected in high alpha and beta diversity, 2) topographical (altitude and slope) and derived variables (heat load and direct incident radiation) will significantly affect the variation in species composition, 3) soil characteristics and associated species indicator values (EIVs) will show correlation.

METHODS

Study area. The study area covered the Bartın section (19,000 ha) of Küre Mountains (37,753 ha). Küre Mountains are situated between Bartın River on the west and Kızılırmak River in the east. The altitude of the region varies between 50 m - 1200 m. Euro-Siberian, Mediterranean and Irano-Turanian influences are seen in the region (figure 1). Küre National Park was identified as one of the 100 Forest Hot Spots of Europe which should be protected (Blumer 2010). Küre Mountains had a diverse forest vegetation, which consisted of pure and/or mixed stands of *Quercus robur* L.*, Carpinus betulus* L.*, Quercus petraea* (Matt.) Liebl.*, Pinus nigra* J.F. Arnold*, Fagus orientalis* Lipsky*, Pinus sylvestris* L. and *Abies nordmanniana* (Steven) Spach subsp. *bornmuelleriana* (Matff.) Coode *et* Cullen.

Soil types of the region are grey-brown podzolic soil and red-yellow podzolic soil. Bedrock is mostly limestone. The annual precipitation is about 1040.2 mm and mean annual temperature is 12.9 °C. The climate type of the region is classified as B2B1'rb4 by the Thornthwaite climate classification system, which translates as characterized by humid, mesothermal, no or a little water deficiency in summer, and under the effect of oceanic climate (Uz *et al*. 2001, Şengönül *et al.* 2009, Ekici 2012, Göncüoğlu *et al.* 2015).

Methods. The vegetation was collected between 2014-2017 and classified according to Braun-Blanquet method (Braun-Blanquet 1932). Sizes of the relevés varied between 100-400 m^2. Eight associations belonging to forest vegetation (a total of 121 relevés and 245 plant taxa) were determined (Tunçkol 2017). A total of six soil samples were taken from the sites representing each association. Two sets of soil samples were taken from the depths of 0-10 and 10-20 cm using 114 cm^3 core sampler (AMS Soil Core Sampler). Soil samples (weighing about 2 kg) were air dried and sieved (< 2 mm) for analyses. Soil particle-size distribution was analyzed with a Bouyoucos hydrometer method, thus enabling soil texture determination (Gee and Bauder 1986). Soil pH and electrical conductivity (EC) were measured using a digital pH meter (Thomas 1996) and an electrical conductivity meter (Rhoades 1996) in a soil and water suspension (Hanna instruments HI 255 pH/EC Meter).

Ellenberg Indicator Values (EIVs) (Ellenberg *et al.* 1992, Pignatti *et al.* 2001) were assigned to species data and an average EIVs weighted by species cover was calculated for each relevé under JUICE (Tichy and Holt 2006). Shannon alpha diversity index and average Whittaker beta diversity (βw=S/α-1, S: total number of species, α: average number of species in each unit) were calculated for each relevé under JUICE. Soil parameters (pH, soil electrical conductivity, sand, clay and dust content, soil moisture) and topographical variables (altitude, slope, potential direct incident radiation and heat load) were used in the analysis as measured variables. The potential direct incident radiation and heat load were calculated with the equations of McCune and Keon (2002).

For performing the multivariate analysis, Braun-Blanquet cover values were transformed into percentage values (r: 1 %, +: 2 %, 1: 3 %, 2: 13 %, 3: 38 %, 4: 68 %, 5: 88 %).

The Detrended correspondence analysis (DCA) was used to summarize the variation in species composition using the species data and interpret this summary with the help of measured and derived environmental variables (EIVs) under CANOCO 5.04 (Šmilauer and Lepš 2014). Canonical Correspondence Analyses (CCA) were run to determine the relationships between species and environmental variables.

Environmental variables significantly affecting the variation in species composition were determined using interactive forward selection with unrestricted permutations as simple (marginal) and conditional effects (*P* values adjusted using False discovery rate). The response curves of tree species on the best subset of environmental variables were calculated based on the Generalized Linear Model (GLM). The selection of the best model was performed with the stepwise selection using F-statistic (the lowest deviance value).

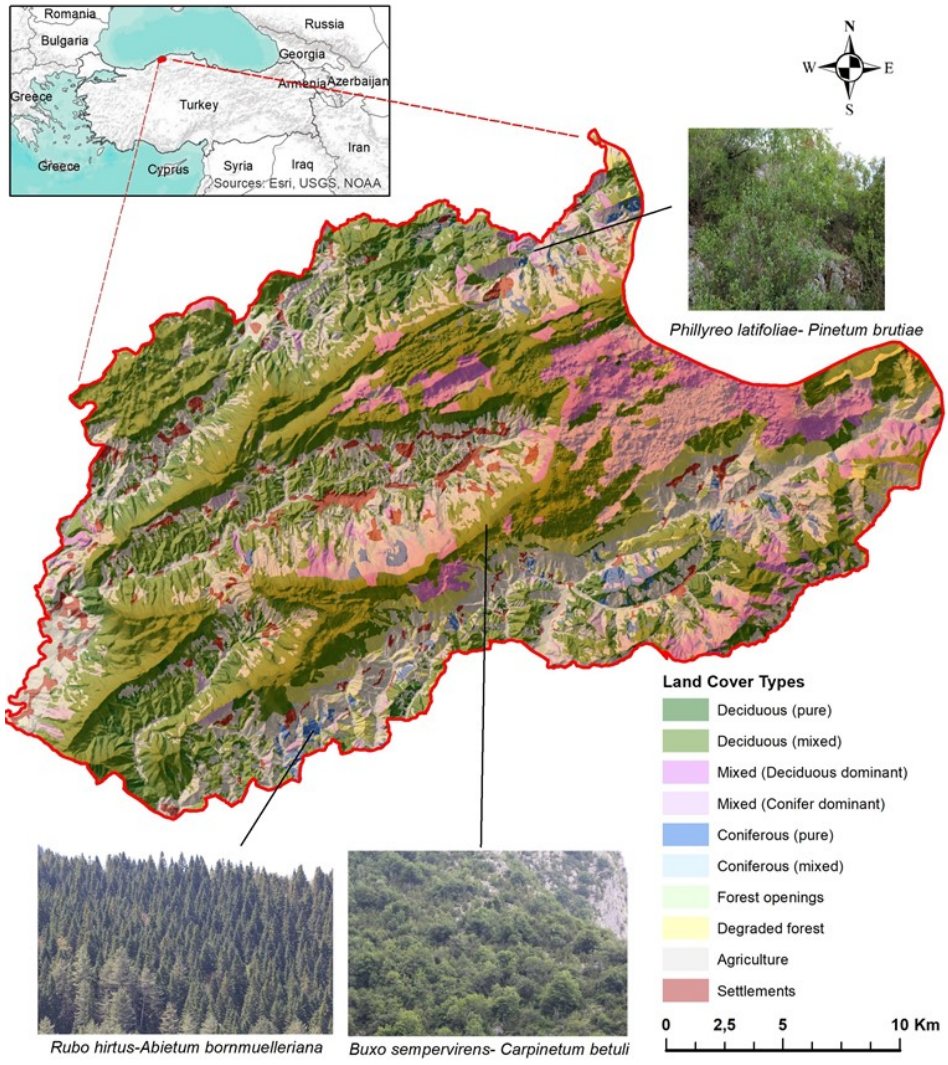

Figure 1. Location of Küre Mountains National Parks (Bartın Section).

Ubicación del Parque Nacional Montañas de Küre (sección Bartin).

RESULTS

Forest communities were described under eight associations as *Quercetum roburi-Aceretum campestri* (Tunçkol 2017), *Salicio-Platanetum orientale* (Tunçkol 2017), *Phillyreo latifoliae-Pinetum brutiae* (Schwarz 1936), *Buxo sempervirens- Carpinetum betuli* (Aksoy 2006), *Carpino-Quercetum petraeae* (Yurdakulol *et al.* 2002), *Ilici colchicae-Fagetum orientalis* (Quezel *et al.* 1992), *Rubo hirtus-Abietum bornmuelleriana* (Aksoy 2006), *Hedero-Castanetum sativae* (Yurdakulol *et al.* 2002) (table 1).

Buxo sempervirens-Carpinetum betuli and *Rubo hirtus-Abietum bornmuelleriana* occurred at a higher altitudinal zone (over 600 m) and others at a lower zone (below 600 m). Only *Buxo sempervirens- Carpinetum betuli* occurred on steep slopes (figure 2).

Among forest associations, the highest species diversity was found in *Phillyreo latifoliae-Pinetum brutiae* (average 17 species, 2.70 H′), followed by *Carpino-Quercetum petraeae* (average 18 species, 2.33 H′) and *Salicio-Platanetum orientale* (average 16 species, 2.33 H′). The lowest diversity was found in *Hedero-Castanetum sativae* (average eight species, 1.33 H′), which had a dense *Rhododendron ponticum* L. shrub layer and *Quercetum roburi-Aceretum campestri* (average 8 species, 1.72 H′) (figure 3) located on riverbanks. However, *Salicio-Platanetum orientale* and *Buxo sempervirens-Carpinetum betuli* had the highest beta diversity among other associations since they harbored unique species composition compared to other forest associations.

The Detrended Correspondence Analysis (DCA) revealed a strong floristic differentiation among relevés except *Quercetum roburi-Aceretum campestri* and *Salicio-Platanetum orientale* which had overlapping ordination. Vegetation data had heterogeneous composition with the length of the first axis being 4.83 SD and that of the second axis 4.64 SD. The first two axes explained 8.85 % of the variation in species composition. Environmental variables accounted for 21.3 % of the total variation in DCA. While the first axis was associated with altitudinal gradient, the second axis was associated with a moisture gradient. Humidity and nutrient EIVs were associated with *Quercetum roburi-Aceretum campestri* and *Salicio-Platanetum orientale. Phillyreo latifoliae-Pinetum brutiae* and *Buxo sempervirens-Carpinetum betuli* associations were associated with temperature and light EIVs, which also showed correlation with the potential direct incident radiation and heat load. However, soil moisture content did not show correlation with humidity EIVs, although it related to soil pH and electrical conductivity towards *Carpino-Quercetum petraeae* (figure 4).

Since the response data were compositional and had a gradient of 5.68 SD units long, the linear method was not appropriate. For this reason, CCA, which is a unimodal constrained method, was used. All variables explained 21.9 % of the total variation and most of the factors significantly affected variation in species composition except sand content, heat load and clay content at P (adj) < 0.05 level (P values adjusted using False discovery rate). Where conditional effects of the factors considered: soil electri-

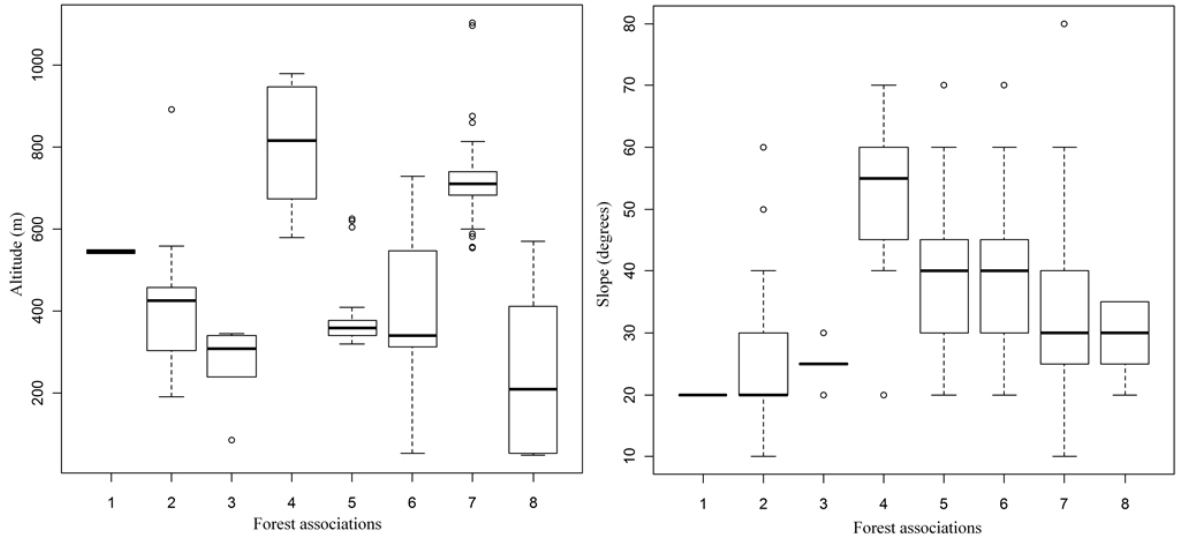

Figure 2. Altitude and slope of forest associations (1: *Quercetum roburi-Aceretum campestri*, 2: *Salicio-Platanetum orientale*, 3: *Phillyreo latifoliae-Pinetum brutiae*, 4: *Buxo sempervirens- Carpinetum betuli*, 5: *Carpino-Quercetum petraeae,* 6: *Ilici colchicae-Fagetum orientalis*, 7: *Rubo hirtus-Abietum bornmuelleriana,* 8: *Hedero-Castanetum sativae*).

Altitud y pendiente de asociaciones forestales (1: *Quercetum roburi-Aceretum campestri*, 2: *Salicio-Platanetum orientale*, 3: *Phillyreo latifoliae-Pinetum brutiae*, 4: *Buxo sempervirens- Carpinetum betuli*, 5: *Carpino-Quercetum petraeae,* 6: *Ilici colchicae-Fagetum orientalis*, 7: *Rubo hirtus-Abietum bornmuelleriana,* 8: *Hedero-Castanetum sativae*).

Table 1. Percentage synoptic table of forest associations (only species on tree layer were given; 1: *Quercetum roburi-Aceretum campestri*, 2: *Salicio-Platanetum orientale*, 3: *Phillyreo latifoliae-Pinetum brutiae*, 4: *Buxo sempervirens- Carpinetum betuli*, 5: *Carpino-Quercetum petraeae,* 6: *Ilici colchicae-Fagetum orientalis*, 7: *Rubo hirtus-Abietum bornmuelleriana,* 8: *Hedero-Castanetum sativae*).

Cuadro sinóptico porcentual de asociaciones forestales (solo se proporcionaron especies en el estrato arbóreo; 1: *Quercetum roburi-Aceretum campestri*, 2: *Salicio-Platanetum orientale*, 3: *Phillyreo latifoliae-Pinetum brutiae*, 4: *Buxo sempervirens- Carpinetum betuli*, 5: *Carpino-Quercetum petraeae,* 6: *Ilici colchicae-Fagetum orientalis*, 7: *Rubo hirtus-Abietum bornmuelleriana,* 8: *Hedero-Castanetum sativae*).

Variable / Species	Abbreviation	Association Nº							
		1	2	3	4	5	6	7	8
Number of relevés		2	17	5	8	21	31	30	7
Total number of species		12	89	39	74	101	90	94	30
Species in tree layer									
Ulmus glabra Huds.	*UlmuGlab*	100					3	3	
Quercus robur L.	*QuerRobu*	100	12						
Acer campestre L.	*AcerCamp*	100			13			13	
Alnus glutinosa (L.) Gaertn.	*AlnuGlut*	50	18				3		
Salix caprea L.	*SaliCapr*	50	12						
Populus tremula L.	*PopuTrem*		47			5	13		
Salix alba L.	*SaliAlba*		29						
Pinus brutia Ten.	*PinuBrut*			100			3		14
Ostrya carpinifolia Scop.	*OstrCarp*				50				14
Fraxinus angustifolia Vahl	*FraxAngu*				38		3	3	14
Pinus nigra J.F.Arnold	*PinuNigr*					71	3	3	14
Abies bornmuelleriana Mattf.	*AbieBorn*						3	63	
Acer platanoides L.	*AcerPlat*					5	10	20	
Carpinus orientalis Mill.	*CarpOrie*		29		25				
Castanea sativa Mill.	*CastSati*						52		100
Fagus orientalis Lipsky	*FaguOrie*					10	84	90	43
Quercus petraea (Matt.) Liebl.	*QuerPetr*			40	25	95	23	13	14
Carpinus betulus L.	*CarpBetu*		29		38	19	81	57	43
Tilia platyphyllos Scop.	*TiliPlat*						3	3	14
Platanus orientalis L.	*PlatOrie*		12						
Acer trautvetteri Medw.	*AcerTrau*				13				
Malus sylvestris (L.) Mill.	*MaluSylv*		12						
Populus alba L.	*PopuAlba*		6				6		
Ulmus minör Mill.	*UlmuMino*		6						
Tilia tomentosa Moench	*TiliTomn*						13		
Pinus pinaster Aiton	*PinuPina*						3		
Fraxinus excelsior L.	*FraxExce*						6	10	
Cerasus avium L.	*CeraAviu*		6				6	10	
Buxus sempervirens L.	*BuxuSemp*							10	
Sorbus aucuparia L.	*SorbAucu*		6					7	
Pinus sylvestris L.	*PinuSylv*		6					3	
Sorbus torminalis (L.) Crantz	*SorbTorm*					5	3	10	
Corylus avellana L.	*CoryAvel*							3	

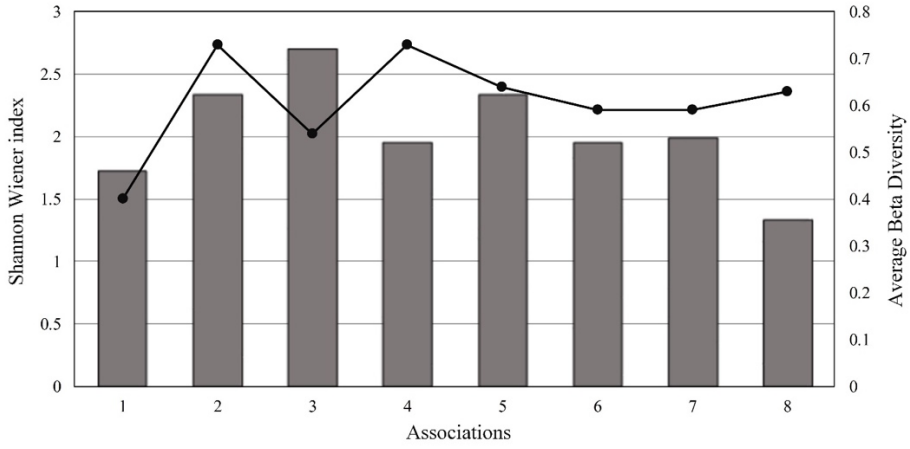

Figure 3. Shannon-Wiener species diversity (column chart) and average beta diversity (black line) of forest communities (1: *Quercetum roburi-Aceretum campestri*, 2: *Salicio-Platanetum orientale*, 3: *Phillyreo latifoliae-Pinetum brutiae*, 4: *Buxo sempervirens-Carpinetum betuli*, 5: *Carpino-Quercetum petraeae,* 6: *Ilici colchicae-Fagetum orientalis*, 7: *Rubo hirtus-Abietum bornmuelleriana,* 8: *Hedero-Castanetum sativae*).

Diversidad de especies de Shannon-Wiener (gráfico de columnas) y diversidad beta promedio (línea negra) de las comunidades forestales (1: *Quercetum roburi-Aceretum campestri*, 2: *Salicio-Platanetum orientale*, 3: *Phillyreo latifoliae-Pinetum brutiae*, 4: *Buxo sempervirens- Carpinetum betuli*, 5: *Carpino-Quercetum petraeae,* 6: *Ilici colchicae-Fagetum orientalis*, 7: *Rubo hirtus-Abietum bornmuelleriana,* 8: *Hedero-Castanetum sativae*).

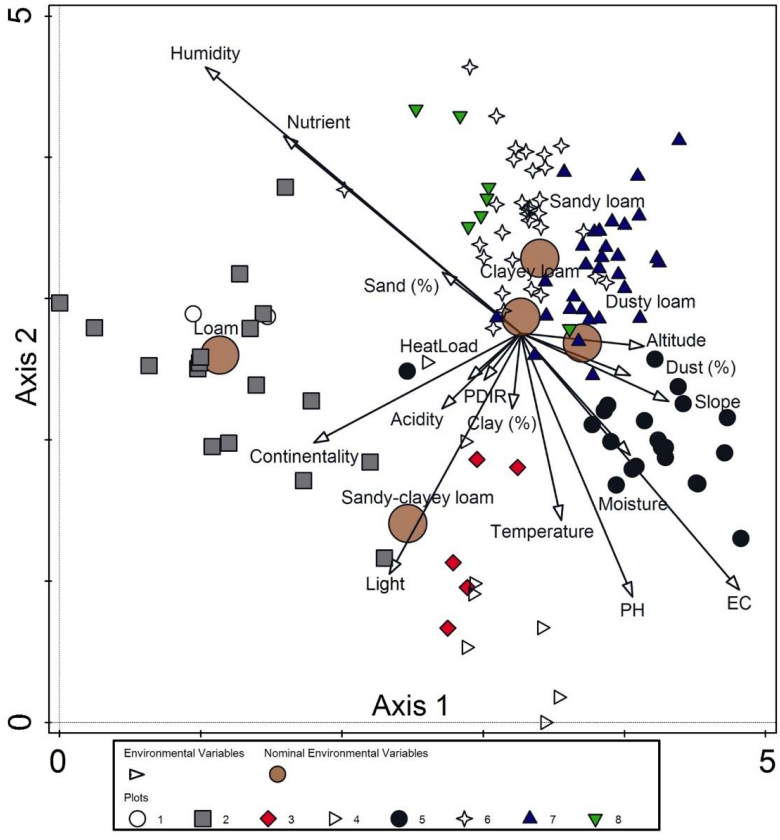

Figure 4. Detrended Correspondence Analysis (DCA) of forest vegetation (1: *Quercetum roburi-Aceretum campestri*, 2: *Salicio-Platanetum orientale*, 3: *Phillyreo latifoliae-Pinetum brutiae*, 4: *Buxo sempervirens-Carpinetum betuli*, 5: *Carpino-Quercetum petraeae,* 6: *Ilici colchicae-Fagetum orientalis*, 7: *Rubo hirtus-Abietum bornmuelleriana,* 8: *Hedero-Castanetum sativae*).

Análisis de correspondencia sin tendencia (DCA) de la vegetación forestal (1: *Quercetum roburi-Aceretum campestri*, 2: *Salicio-Platanetum orientale*, 3: *Phillyreo latifoliae-Pinetum brutiae*, 4: *Buxo sempervirens-Carpinetum betuli*, 5: *Carpino-Quercetum petraeae,* 6: *Ilici colchicae-Fagetum orientalis*, 7: *Rubo hirtus-Abietum bornmuelleriana,* 8: *Hedero-Castanetum sativae*).

cal conductivity, altitude, sandy-loam soil type, loam soil type, slope, dust content, sand content and pH had a significant contribution in species composition at P (adj) < 0.05 (table 2).

Mesic *Ilici colchicae-Fagetum orientalis* and *Rubo hirtus-Abietum bornmuelleriana* with their associated species were correlated with altitude, nevertheless soil type did not make a significant contribution. On the other hand, soil characteristics made a significant effect on the variation of species composition at lower altitudes. *Carpino-Quercetum petraeae* was found on soil with high dust content with a high pH and also electrical conductivity values. On the other hand, *Quercetum roburi-Aceretum campestri* and *Salicio-Platanetum orientale* were related to soil with loam (figure 5).

Table 2. Effects of environmental variable on species composition.

Efectos de la variable ambiental sobre la composición de especies.

Name	Simple term effects			
	Explains %	pseudo-F	*P*	*P*(adj)
Electrical conductivity	3.5	4.3	0.002	0.03
Altitude (m)	3.1	3.8	0.002	0.03
Sandy-clay loam	2.9	3.5	0.002	0.03
pH	2.8	3.5	0.002	0.03
Dusty loam	2.8	3.4	0.002	0.03
Loam	2.4	2.9	0.002	0.03
Moisture%	2.3	2.8	0.002	0.03
Slope (degrees)	2.1	2.5	0.002	0.03
Dust%	1.6	1.9	0.002	0.03
Sandy loam	1.5	1.9	0.002	0.03
Clay loam	1.4	1.7	0.002	0.03
Potential direct incident radiation	1.2	1.5	0.010	0.04
Sand%	1.2	1.4	0.020	0.06
Heat load	1.1	1.3	0.096	0.19
Clay%	0.8	1.0	0.510	0.51
Conditional term effects				
Electrical conductivity	3.5	4.3	0.002	0.005
Altitude (m)	3.3	4.2	0.002	0.005
Sandy-clay loam	2.6	3.4	0.002	0.005
Loam	2.3	3.0	0.002	0.005
Dusty loam	1.6	2.1	0.002	0.005
Slope (degrees)	1.3	1.7	0.026	0.043
Dust%	1.5	2.0	0.002	0.005
pH	1.2	1.7	0.022	0.041
Sand%	1.3	1.8	0.004	0.008
Clay loam	1.0	1.3	0.056	0.084
Sandy loam	1.0	1.3	-	-
Potential direct incident radiation	0.9	1.2	0.102	0.139
Moisture%	0.7	0.9	0.532	0.665
Heat load	0.7	0.9	0.630	0.726
Clay%	0.2	0.3	0.888	0.951

Response models of trees over altitudinal gradient showed increasing linear response for *Acer platanoides, Fraxinus excelsior, Fraxinus angustifolia* and *Ostrya carpinifolia.* Other trees showed a quadratic distribution over altitude (table S1 in Supplementary material). While the optimum distribution of *Abies nordmanniana* subsp. *bornmuelleriana* and *Fagus orientalis* was found between 800-900 m, it was found under 600 m for *Pinus brutia*, *Pinus nigra*, *Quercus petraea*, *Tilia tomentosa*, *Castanea sativa* and *Salix alba* in the study area (figure 6). While *Buxus sempervirens* and *Ostrya carpinifolia* showed an increasing linear distribution, *Carpinus betulus* had a decreasing response on the slope. Other trees had quadratic distribution on the slope (table S1 in Supplementary material). *Castanea sativa*, *Fagus orientalis*, *Fraxinus excelsior*, *Pinus nigra*, *Quercus petraea* and *Ostrya carpinifolia* had their optimum on steep slopes (over 30 degrees) and *Abies nordmanniana* subsp. *bornmuelleriana*, *Pinus brutia*, *Alnus glutinosa*, *Salix caprea*, *Quercus robur* and *Platanus orientalis* had optimum on moderately steep slopes (under 30 degrees) (figure 6).

Species responses to soil content varied for most species. Most species showed quadratic distribution on soil parameters. However, *Carpinus betulus* had a clear decreasing linear response on dust content and *Quercus robur* an increasing linear response on sand content (table S2 in Supplementary material). While *Pinus nigra* and *Castanea sativa* showed a good development on the soil with a higher dust content (over 50 %), *Fagus orientalis, Abies nordmanniana* subsp. *bornmuelleriana*, *Carpinus betulus* and *Acer campestre* did it on soil with higher sand content (over 70 %). On the other hand, species such as *Carpinus orientalis, Salix alba* and *Populus tremula* had optimum soil dust content around 30-45 %. In terms of soil pH and electrical conductivity, some species such as *Castanea sativa*, *Abies nordmanniana* subsp. *bornmuelleriana*, *Fagus orientalis*, *Populus tremula*, *Quercus robur* showed similar responses. *Pinus nigra* and *Quercus petraea*, which were found on alkaline soils presenting high electrical conductivity. *Pinus brutia, Pinus nigra* and *Quercus petraea* had an increasing response on moderately alkaline soils (pH 7-8). *Castanea sativa, Tilia tomentosa, Pinus pinaster* and *Fagus orientalis* had their optimum on moderately acidic soils (pH 5.6-6) and *Populus tremula, Ulmus minor* and *Alnus glutinosa* on slightly acidic soils (pH 6.1-6.5). On the other hand, *Salix caprea*, *Quercus robur*, *Abies nordmanniana* subsp. *bornmuelleriana* and *Carpinus orientalis* were found on neutral soils (figure 7).

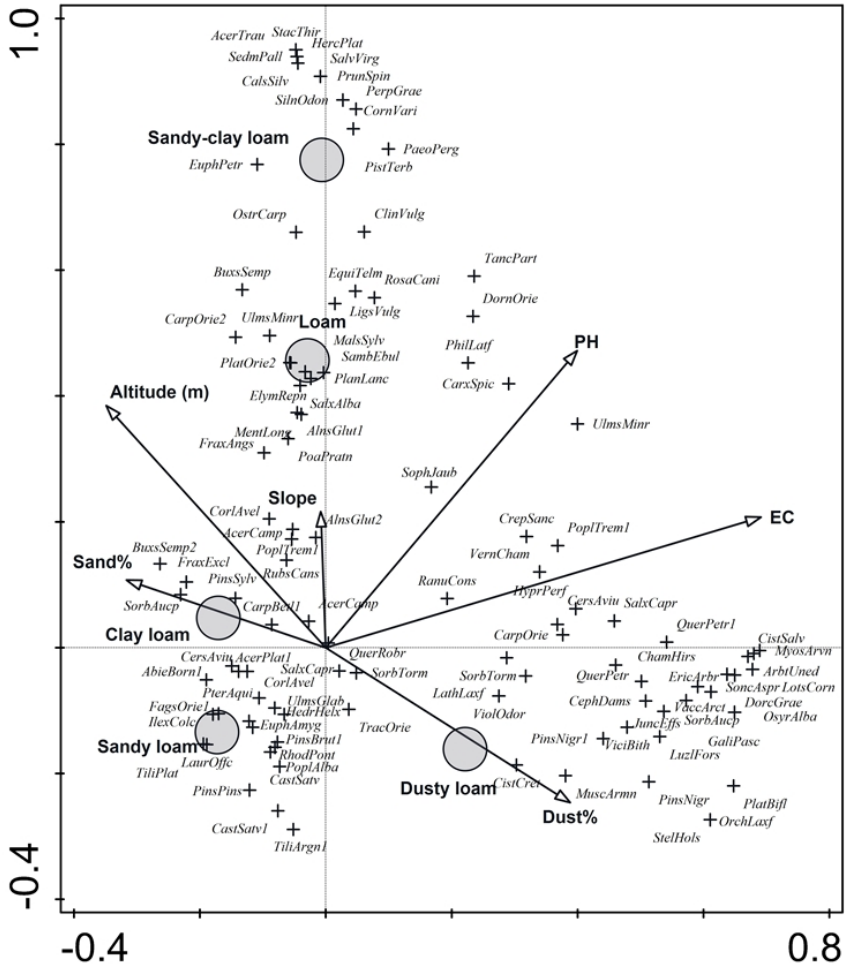

Figure 5. Canonical Correspondence Analysis (CCA) graph of forest vegetation (see table 1 for abbreviations of the species, number at the end of the abbreviations 1: tree layer, 2: second tree layer, others are in shrub or herb layers).

Análisis de Correspondencia Canónica (CCA) de la vegetación forestal (ver cuadro 1 para las abreviaturas de las especies, número al final de las abreviaturas = 1: capa de árboles, 2: segunda capa de árboles, otras están en capas de arbustos o hierbas).

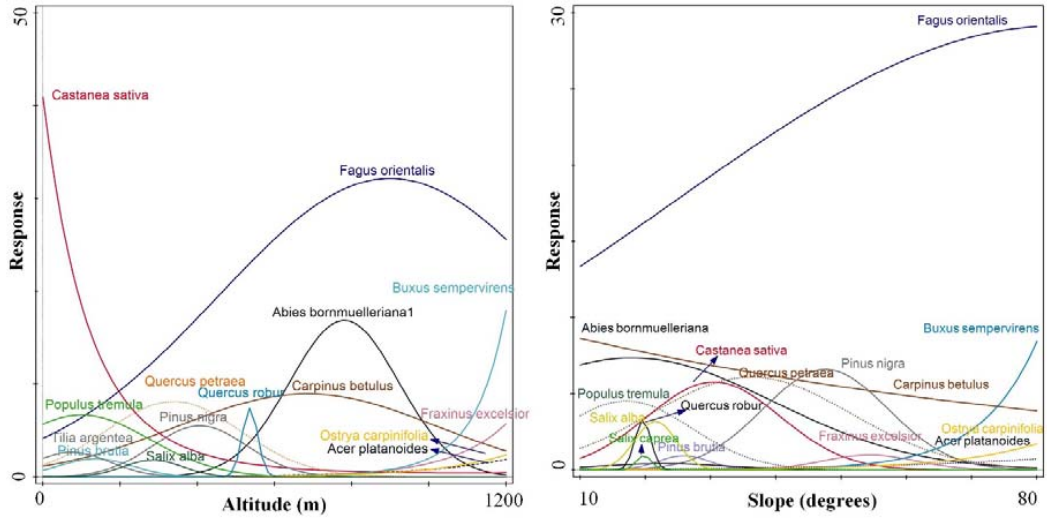

Figure 6. Species response curves against topographical variables.

Curvas de respuesta de las especies frente a variables topográficas.

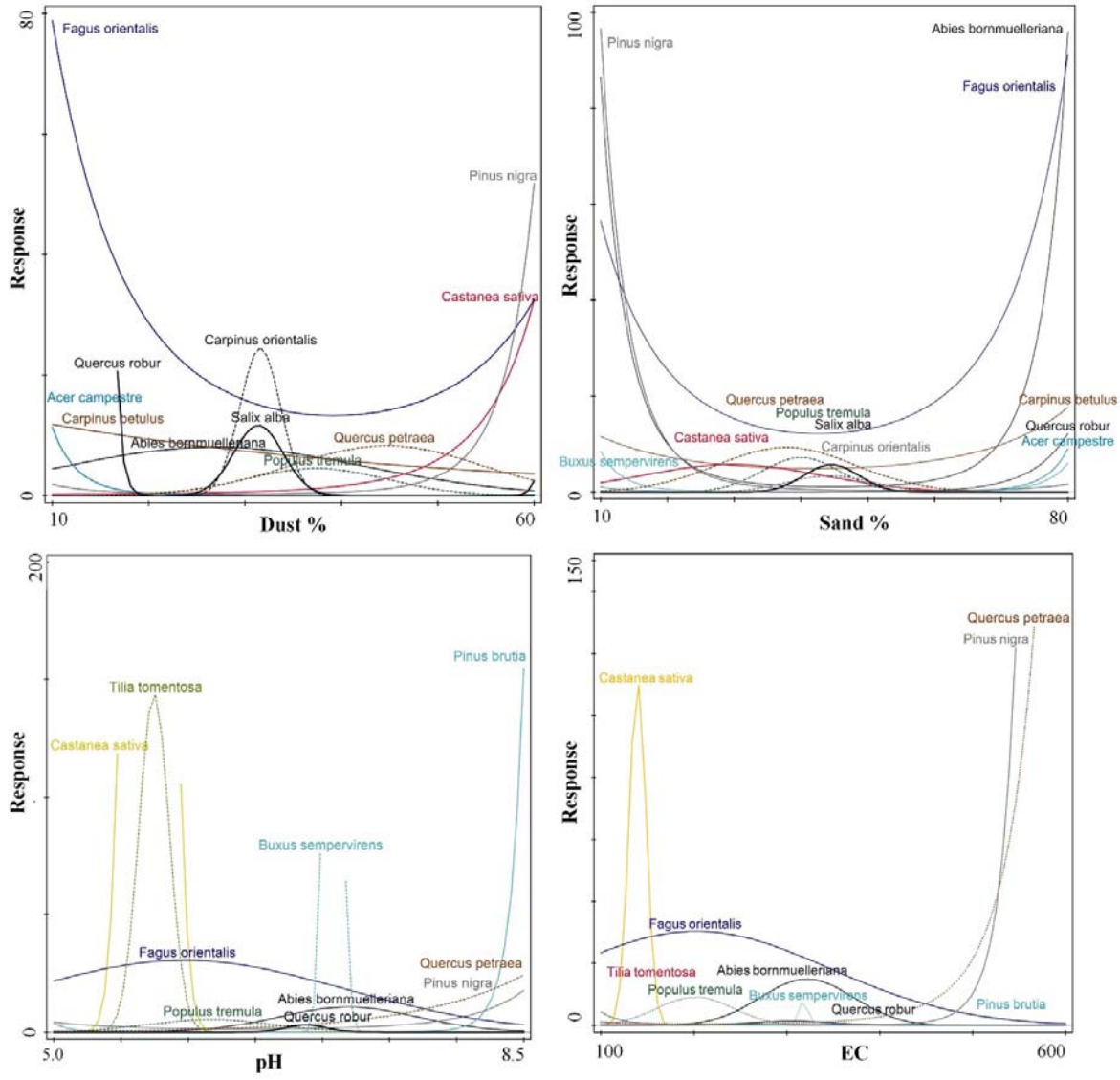

Figure 7. Species response curves against soil parameters (EC: electrical conductivity).

Curvas de respuesta de especies frente a parámetros del suelo.

DISCUSSION

According to Bartels and Chen (2010), understory plants are limited by light availability under closed and stratified canopies in young/mature stages of stand development. However, resource quantity and heterogeneity may be key factors in structuring understory species diversity in stands that experience intermediate disturbances. In the study area, the highest species diversity is found in *Phillyreo latifoliae-Pinetum brutiae*, which has a low canopy cover and single-layered stand structure. In addition, *Carpino-Quercetum petraeae* and *Salicio-Platanetum orientale* had also higher species diversity compared to other deciduous forest communities owing to leaf structure enabling transmission of more light in the understory and low canopy cover. The species diversity of the abovementioned communities is also confirmed by the study of Messier *et al.* (1998) who reported shade-intolerant species (deciduous or coniferous) transmit more light than do shade tolerant tree species. This situation is also revealed with the higher light EIVs of these units (figure 4). Light EIVs, which has a high positive correlation with the potential direct incident radiation and heat load, related to *Phillyreo latifoliae-Pinetum brutiae* and *Salicio-Platanetum orientale*. Even though intermediate scale disturbance may increase light conditions in the understory, severe disturbances contribute to the spread of *Rhododendron* spp. in the temperate forest systems, which decrease species diversity (Royo and Carson 2006) as shown with *Hedero-Castanetum sativae* association, which has a dense *Rhodo-*

dendron ponticum layer. However, forests with azonal character and extreme site conditions (steep slopes) have higher beta diversity such as *Salicio-Platanetum orientale* and *Buxo sempervirens- Carpinetum betuli*. Thus, the first hypothesis was approved since different forest types (coniferous, deciduous-mixed and riparian forests) occurring on heterogeneous ecological conditions exhibit high alpha and/or beta diversity in the region. This was shown both with the alpha and beta diversity of the communities and the gradient length in the DCA ordination indicating a large beta diversity.

Assessment of many species occurring together allows a more reliable estimation of site conditions than does assessment of a single species, as the overlap of ecological tolerances of many species is smaller than the ecological amplitude of a single species. For this reason, mean indicator values of species in a sample plot or community may provide more reliable information (Çoban 2016). For instance, *Quercetum roburi-Aceretum campestri* and *Salicio-Platanetum orientale*, which occur on riversides, differed from other communities with nutrient and humidity EIVs. The high nutrient cycling capacity of riparian forests compared to upland ecosystems is probably the consequence of their open structure to fluvial sources via flood deposits and to lateral fluxes of nutrients from the drainage basin (Pinay *et al.* 1995).

Changes in plant community composition are usually well correlated with changes in soil conditions such as pH, organic matter, weathering processes and nutrient availability (Wardle *et al.* 2004). On the other hand, climate is primarily effective on the variation of forest community composition over altitudinal gradient. Soil characteristics also change depending on the climate. The effects of elevation on growth are due to multiple interacting factors, including temperature, soil depth, precipitation and exposure. In addition to altitude, topographical variables such as slope and aspect influence the forest composition. While aspect can affect species composition and soil properties --including soil moisture, pH, organic matter content and nutrient cycling-- slope gradient can affect soil thickness, water and nutrient retention, among other factors (Gilliam *et al*. 2014, Robin-Abbott and Pardo 2017). At this point, the effects of site condition parameters may vary in combination with other variables. For instance, *Rubo hirtus-Abietum bornmuelleriana*, which prefer higher altitudes, cannot compete with *Buxo sempervirens- Carpinetum betuli* on steep slopes (figures 2 and 4). However, the effect of the potential direct incident radiation and heat load calculated from slope gradient and aspect is not significant in combination of variables. These indexes may give better results for wide areas (*e.g.* at continental scale). Nonetheless, the slope gradient made alone a significant contribution, especially for *Buxus sempervirens, Pinus nigra, Ostrya carpinifolia* since it affected soil thickness. Therefore, the second hypothesis is true only for measured topographical variables though not for potential direct incident radiation and heat load which may give better results for larger areas.

Soil types of the forests are important for water and nutrient availability. In general, soils with sufficient water, nutrients and adequate drainage (*e.g.*, sandy loams to clay loams) can be accepted as favorable site conditions for most trees. Clay soils are often fertile, although heavy and poorly drained. Sandy soils are lighter, though they lack water and nutrients (Robin-Abbott and Pardo 2017). For this reason, sandy loam soil type provided favorable conditions for *Abies nordmanniana* subsp. *bornmuelleriana* and *Fagus orientalis*. On the other hand, more tolerant species such as *Pinus nigra* and *Quercus petraea* are associated with dusty soils (figures 4, 5 and 7). MacDonald (2003) defined this phenomenon as "Competitive Exclusion Principle", which means fully competitive species cannot co-occur. Therefore, small scale variations in site conditions (*i.e.* altitudinal zones, steep slopes, soil type etc.) within an environment enable an array of species with similar site requirements as shown in figures 6 and 7, where species showed varied responses to environmental parameters.

In conclusion, although only 21.9 % of the total variation could be explained with the measured environmental variables, an ecological differentiation among forest communities could be made using topographical (altitude and slope) and some of the soil variables (soil type, EC, pH, dust and sand content) as also shown with different response curves of main tree species. In general, distribution of *Buxo sempervirens-Carpinetum betuli* and *Rubo hirtus-Abietum bornmuelleriana* within higher altitudinal zone (over 600 m) differed with the steepness of the site. On the other hand, soil characteristics affected distribution of other forest communities at lower altitudes where *Phillyreo latifoliae-Pinetum brutiae* occurred on alkaline soils, *Hedero-Castanetum sativae* on soil with high dust content, *Carpino-Quercetum petraeae* on high soil electrical conductivity and *Ilici colchicae-Fagetum orientalis* with low dust content though high sand content providing weathering processes.

The main differences were also reflected using EIVs for humidity, nutrient, light and temperature EIVs using limited numbers of species having indicator values. However, EIVs did not show a good correlation with associated soil parameters such as soil moisture-humidity EIVs and soil pH-acidity EIVs. According to Londo *et al.* (2006), nutrients can become either toxic or unavailable at extremes pH, while soils with a pH of 6.0-7.0 often have the highest concentration of available nutrients (Williston and Lafayette 1978). The extreme pH and electrical conductivity values are found for *Pinus brutia, Pinus nigra* and *Quercus petraea*, which negatively correlated with nutrient and humidity EIVs. Therefore, only nutrient and humidity EIVs seem to be associated with soil pH and electrical conductivity values in the study area. However, calibration and assignment EIVs for the flora of Turkey may give better results.

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SUPPLEMENTARY MATERIAL

Table S1. Results of species response curves of trees for topographical parameters.

Resultados de las curvas de respuesta de especies de árboles para parámetros topográficos.

Predictors	Altitude (m)					
Distribution	Poisson					
Link function	log					
GLM fitted for 31 response variables:						
Response	Type	R^2[%]	F	*P*	Optimum	Tolerance
Abies bornmuelleriana	quadratic	36.3	468.4	<0.00001	NA	NA
Acer campestre	quadratic	15.1	11.7	0.00002	NA	NA
Acer platanoides	linear	19.3	18.8	0.00003	NA	NA
Carpinus betulus	quadratic	3.8	44.7	<0.00001	NA	NA
Castanea sativa	quadratic	26.0	252.9	<0.00001	NA	NA
Fagus orientalis	quadratic	7.5	189.0	<0.00001	NA	NA
Fraxinus angustifolia	linear	14.3	11.2	0.00107	NA	NA
Fraxinus excelsior	linear	37.6	48.7	<0.00001	NA	NA
Pinus brutia	quadratic	38.6	34.1	<0.00001	NA	NA
Pinus nigra	quadratic	16.8	121.1	<0.00001	NA	NA
Pinus pinaster	quadratic	69.1	9.9	0.00072	305.04	4.47
Pinus sylvestris	quadratic	42.1	5.2	0.00676	506.77	38.51
Populus alba	quadratic	25.3	18.3	<0.00001	242.13	66.64
Populus tremula	quadratic	22.5	138.3	<0.00001	NA	NA
Quercus petraea	quadratic	15.6	161.6	<0.00001	NA	NA
Tilia tomentosa	quadratic	48.1	43.4	<0.00001	NA	NA
Tilia platyphyllos	quadratic	34.4	6.4	0.00226	597.78	51.34
Acer trautvetteri	quadratic	96.7	9.3	0.09732	1035.88	7.48
Alnus glutinosa	quadratic	9.7	11.6	0.00003	NA	NA
Buxus sempervirens	quadratic	34.9	38.9	<0.00001	NA	NA
Carpinus orientalis	quadratic	5.8	14.5	<0.00001	NA	NA
Corylus avellana	quadratic	73.8	3.5	0.05191	737.27	5.08
Malus sylvestris	quadratic	88.2	7.2	0.01338	460.75	6.46
Ostrya carpinifolia	linear	25.4	22.7	<0.00001	NA	NA
Platanus orientalis	quadratic	84.2	20.7	0.0038	442.49	4.61
Quercus robur	quadratic	57.4	123.6	<0.00001	536.15	20.03
Salix alba	quadratic	23.1	57.4	<0.00001	NA	NA
Salix caprea	quadratic	17.6	11.8	0.00002	NA	NA
Sorbus aucuparia	quadratic	37.0	5.6	0.00503	814.38	75
Ulmus glabra	quadratic	41.0	11.2	0.00004	573.65	50.19
Ulmus minor	quadratic	97.9	14.1	0.00239	562.61	2.53

Continue

Table S1 Continued

Predictors	Slope (degrees)					
Distribution	Poisson					
Link function	log					
GLM fitted for 27 response variables:						
Response	Type	R2[%]	F	*P*	Optimum	Tolerance
Abies bornmuelleriana	quadratic	4.6	59.9	<0.00001	17.93	21.79
Acer campestre	linear	7.3	11.3	0.00106	NA	NA
Acer platanoides	linear	6.7	6.5	0.01178	NA	NA
Carpinus betulus	linear	0.8	19.2	0.00003	NA	NA
Castanea sativa	quadratic	8.7	85.2	<0.00001	30.49	10.21
Fagus orientalis	quadratic	1.6	40.7	<0.00001	83.31	58.68
Fraxinus excelsior	quadratic	35.0	22.7	<0.00001	54.35	7.06
Pinus brutia	quadratic	27.1	23.9	<0.00001	25.85	3.87
Pinus nigra	quadratic	18.9	136.8	<0.00001	47.61	9.61
Pinus pinaster	quadratic	33.7	4.9	0.0127	30.02	1.11
Populus alba	quadratic	8.2	6.0	0.0034	37.6	8.16
Populus tremula	quadratic	16.7	103.1	<0.00001	16.98	10.09
Quercus petraea	quadratic	4.2	43.1	<0.00001	36.18	15.34
Tilia tomentosa	quadratic	9.7	8.8	0.00028	22.92	9.55
Tilia platyphyllos	quadratic	23.2	4.3	0.01515	35.74	3.23
Acer trautvetteri	quadratic	77.1	7.4	0.0126	70.28	2.25
Alnus glutinosa	quadratic	25.6	30.7	<0.00001	18.97	6.04
Buxus sempervirens	linear	45.5	101.5	<0.00001	NA	NA
Carpinus orientalis	quadratic	8.5	21.3	<0.00001	55.47	15.52
Corylus avellana	linear	62.6	6.0	0.01971	NA	NA
Malus sylvestris	quadratic	47.8	3.9	0.0254	19.79	1.23
Ostrya carpinifolia	linear	23.5	21.0	0.00001	NA	NA
Platanus orientalis	quadratic	47.8	11.8	0.00015	19.81	1.16
Quercus robur	quadratic	48.3	104.0	<0.00001	19.6	1.22
Salix alba	quadratic	37.6	93.4	<0.00001	21.52	3.17
Salix caprea	quadratic	46.8	31.4	<0.00001	19.74	1.14
Ulmus minor	quadratic	33.7	4.9	0.0127	30.02	1.11

Table S2. Results of species response curves of trees for soil parameters.

Resultados de las curvas de respuesta de especies de árboles para parámetros de suelo.

Predictors	Sand%					
Distribution	Poisson					
Link function	log					
GLM fitted for 25 response variables:						
Response	Type	R2[%]	F	*P*	Optimum	Tolerance
Abies bornmuelleriana	quadratic	20.3	262.6	<0.00001	NA	NA
Acer campestre	quadratic	25.9	20.0	<0.00001	NA	NA
Acer platanoides	linear	7.8	7.6	0.00671	NA	NA
Carpinus betulus	quadratic	2.5	29.4	<0.00001	NA	NA
Castanea sativa	quadratic	13.4	130.6	<0.00001	29.72	13.3
Fagus orientalis	quadratic	8.9	226.0	<0.00001	NA	NA
Fraxinus angustifolia	linear	8.9	7.0	0.00948	NA	NA
Fraxinus excelsior	linear	13.6	17.7	0.00005	NA	NA
Pinus brutia	quadratic	21.7	19.2	<0.00001	31.84	4.93
Pinus nigra	quadratic	32.1	231.4	<0.00001	NA	NA
Pinus pinaster	quadratic	76.6	11.0	0.00159	63.89	0.426
Populus tremula	quadratic	25.6	157.7	<0.00001	39.96	5.8
Quercus petraea	quadratic	17.8	184.0	<0.00001	37.75	10.32
Acer trautvetteri	quadratic	66.4	6.4	0.01889	50.46	0.628
Alnus glutinosa	quadratic	6.0	7.1	0.00118	56.95	16.65
Buxus sempervirens	quadratic	15.0	16.7	<0.00001	NA	NA
Carpinus orientalis	quadratic	28.5	71.9	<0.00001	44.36	6.22
Malus sylvestris	quadratic	47.5	3.9	0.02351	44.6	3.13
Ostrya carpinifolia	quadratic	27.3	12.2	0.00001	48.94	7.59
Platanus orientalis	quadratic	47.5	11.7	0.00003	44.6	3.13
Quercus robur	linear	36.7	158.0	<0.00001	NA	NA
Salix alba	quadratic	44.9	111.6	<0.00001	44.55	4.07
Salix caprea	linear	21.1	28.4	<0.00001	NA	NA
Sorbus aucuparia	linear	24.3	7.3	0.0079	NA	NA
Ulmus glabra	quadratic	23.9	6.5	0.00207	NA	NA
Predictors	Dust%					
Distribution	Poisson					
Link function	log					
GLM fitted for 25 response variables:						
Response	Type	R2[%]	F	*P*	Optimum	Tolerance
Abies bornmuelleriana	quadratic	5.0	64.0	<0.00001	26.87	15.53
Acer campestre	quadratic	22.3	17.2	<0.00001	??	??
Acer platanoides	linear	5.1	5.0	0.02784	NA	NA

Continue

Table S2 Continued

Carpinus betulus	linear	3.3	78.8	<0.00001	NA	NA
Castanea sativa	quadratic	27.6	269.1	<0.00001	NA	NA
Fagus orientalis	quadratic	6.0	152.5	<0.00001	NA	NA
Fraxinus angustifolia	linear	8.4	6.6	0.01165	NA	NA
Fraxinus excelsior	quadratic	8.7	5.6	0.00468	41.59	9.46
Pinus brutia	quadratic	19.6	17.3	<0.00001	40.01	6.02
Pinus nigra	quadratic	36.8	265.7	<0.00001	NA	NA
Pinus pinaster	quadratic	63.1	9.1	0.00087	18.31	0.213
Populus alba	linear	5.5	8.0	0.00551	NA	NA
Populus tremula	quadratic	15	92.6	<0.00001	37.36	7.29
Quercus petraea	quadratic	16.5	170.6	<0.00001	44.68	9.91
Tilia tomentosa	quadratic	10.3	9.3	0.00018	NA	NA
Acer trautvetteri	quadratic	66.3	6.4	0.01463	31.2	0.271
Alnus glutinosa	linear	3.2	7.8	0.00611	NA	NA
Carpinus orientalis	quadratic	52.1	131.4	<0.00001	31.59	2.1
Ostrya carpinifolia	quadratic	6.9	3.1	0.04873	30.96	9.76
Platanus orientalis	quadratic	30.7	7.6	0.00082	31.68	4.03
Quercus robur	quadratic	60.9	131.0	<0.00001	NA	NA
Salix alba	quadratic	44.9	111.6	<0.00001	31.39	2.56
Salix caprea	linear	23.3	31.2	<0.00001	NA	NA
Sorbus aucuparia	quadratic	34.6	5.2	0.00861	23.08	1.79
Ulmus glabra	quadratic	28.3	7.7	0.00071	NA	NA
Predictors	pH					
Distribution	Poisson					
Link function	log					
GLM fitted for 23 response variables:						
Response	Type	R2[%]	F	*P*	Optimum	Tolerance
Abies bornmuelleriana	quadratic	17.4	224.6	<0.00001	7.19	0.519
Acer campestre	quadratic	29.3	22.6	<0.00001	6.99	0.255
Castanea sativa	quadratic	63.3	616.4	<0.00001	5.71	0.116
Fagus orientalis	quadratic	7.8	197.4	<0.00001	5.97	1.19
Pinus brutia	quadratic	43.4	38.3	<0.00001	NA	NA
Pinus nigra	quadratic	4.8	34.6	<0.00001	NA	NA
Pinus pinaster	quadratic	42.2	6.1	0.00442	5.92	0.097
Pinus sylvestris	linear	29.3	7.3	0.00788	NA	NA
Populus alba	linear	23.2	33.6	<0.00001	NA	NA
Populus tremula	quadratic	21.5	132.1	<0.00001	6.16	0.462
Quercus petraea	linear	18.9	392.4	<0.00001	NA	NA
Sorbus torminalis	quadratic	0.1	0.02464	0.97567	NA	NA

Continue

Table S2 Continued

Tilia tomentosa	quadratic	31.6	28.4	<0.00001	5.75	0.112
Acer trautvetteri	quadratic	56.6	5.4	0.00855	7.82	0.052
Alnus glutinosa	quadratic	19.8	23.8	<0.00001	6.46	0.416
Buxus sempervirens	quadratic	37.7	42.0	<0.00001	7.08	0.055
Carpinus orientalis	quadratic	9.2	23.1	<0.00001	6.87	0.534
Ostrya carpinifolia	quadratic	13.4	6.0	0.00332	NA	NA
Quercus robur	quadratic	43.4	93.5	<0.00001	6.87	0.152
Salix alba	quadratic	11.7	29.1	<0.00001	6.88	0.451
Salix caprea	quadratic	34.5	23.2	<0.00001	6.85	0.196
Sorbus aucuparia	quadratic	32.5	4.9	0.00921	7	0.206
Ulmus minor	quadratic	56.6	8.1	0.00179	6.35	0.047
Predictors	EC					
Distribution	Poisson					
Link function	log					
GLM fitted for 10 response variables:						
Response	Type	R2[%]	F	*P*	Optimum	Tolerance
Abies bornmuelleriana	quadratic	44.8	578.3	<0.00001	NA	NA
Carpinus betulus	quadratic	5.1	60.2	<0.00001	NA	NA
Castanea sativa	quadratic	63.3	616.4	<0.00001	139.36	9.17
Fagus orientalis	quadratic	11.2	283.8	<0.00001	NA	NA
Pinus brutia	quadratic	8.7	7.7	0.00075	NA	NA
Pinus nigra	quadratic	38.6	278.8	<0.00001	NA	NA
Quercus petraea	quadratic	53.0	549.1	<0.00001	NA	NA
Platanus orientalis	quadratic	57.4	14.1	0.00001	167.06	6.74
Quercus robur	quadratic	23.2	50.1	<0.00001	305.03	45.23
Salix alba	quadratic	56.8	141.0	<0.00001	171.34	11.28