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ORIGINAL PAPER

Effects of the overstory on the diversity of the herb and shrub layers of Anatolian black pine forests

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Abstract

Understory plants are important components of forests because they are responsible for the majority of the vascular plant diversity of forest ecosystems. The richness and composition of understory communities are closely related to the tree layer diversity, structure and composition. The aim of this study was to examine the understory diversity of Anatolian black pine (*Pinus nigra* Arnold subsp. *pallasiana* (Lamb.) Holmboe)-dominated forests on the Kazdağı Mountains of West Turkey. To describe the overstory structure and composition in a numerically and quantitatively well-defined manner, cumulative abundance profiles (CAPs) of the tree species were used. The resemblance of the sampling plots was classified into five stand types assessing the CAP through the Fuzzy C-Means clustering method. A permutational multivariate analysis of variance (PERMANOVA) was performed to test the variance of the community ecological distance between the five stand types, and the results showed significant differences in these clusters. Many shade-tolerant plants were associated with the mixed stands of Anatolian black pine–Kazdağı fir. The composition of the herb and shrub layer could not be explained by the environmental variables but by differences in the overstory structure of the stands. Pure or nearly pure Anatolian Black pine stands were more diverse than mixed oak–Anatolian black pine and Kazdağı fir–Anatolian black pine stands. However, although dense and young pure Anatolian black pine stands had the most diverse plant species in the shrub layer, they were ranked third in terms of the herb layer diversity. The Anatolian black pine–Kazdağı fir mixed stands had the lowest herb and shrub layer diversity. These results allow us to comprehend the relationship between the overstory structure and composition, and the understory diversity. Understanding this relationship is important for the conservation of understory plant diversity in the management of forest ecosystems.

Keywords *Pinus nigra* subsp. *pallasiana* · Cumulative abundance profile · Fuzzy cluster · Understory diversity · Indicator species

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Introduction

The overstory structure and composition of forests is reflective of the severity, type and patchiness of ecological factors, natural disturbances, and past and current management systems (Montes et al. 2005). As such, the overstory is essential to productivity and forest ecosystem sustainability, and is a convenient indicator of biodiversity (Carvalho 2011). The understory is also a good indicator of the ecosystem health and is directly affected by the overstory structure and composition. Both depend on many factors, such as nutrient cycling and levels, light transmittance, and soil water supply (Légaré et al. 2002; Augusto et al. 2003; Gracia et al. 2007; Barbier et al. 2008; Mölder et al. 2008). The understory vegetation composes a significant portion of the overall plant diversity, provides a habitat and food to many organisms, contributes to nutrient cycling, offers protection against erosion, and affects seed germination, seedling survival and growth in the forest ecosystem (Muller 2003; Augusto et al. 2003; Gilliam 2007). The relationship between the overstory and the understory vegetation is, therefore, complicated. Although some studies have indicated that the herb and shrub layer composition and diversity are not significantly affected by the species of overstory trees (Ewald 2000; Muller 2003; Thomsen et al. 2005), others have stated that the diversity and composition of the understory plant species depend on the density and composition of the overstory tree species (Beatty 1984; Crozier and Boerner 1984; Klinka et al. 1996; Légaré et al. 2001, 2002; Brosofske et al. 2001; Bergstedt and Milberg 2001; Rodríguez-Calcerrada et al. 2011; Huo et al. 2014).

It is important to note any differences between the communities to evaluate the ecological status of these communities for various purposes. Community resemblance indices are calculated based on presence/absence and/or abundance data, but none of these metrics alone is sufficient to express similarity. For instance, in two forest stands, the plant compositions may be the same in terms of the tree species and abundance, but there may be size differences in the tree species depending on their developmental stages. In such a case, resemblance measurements may not be sufficient to describe the characteristics of forest stands using only tree species composition and conventional stand structure variables. Because tree dimensions (e.g., the diameter, height, crown width and basal area) can be measured, forest stands should be classified based on these attributes. Therefore, in determining the similarities of the different forest communities, the overall size structure in addition to the tree species composition should be considered. Although the relative importance value and dominance index are used for expressing similarity, the cumulative abundance profile (hereafter, referred to as the CAP), which is a more realistic alternative, should be considered (De Cáceres et al. 2013). The CAP method provides more information to describe forest stands than can be obtained using the abundance values of the overstory (De Cáceres et al. 2013) and allows for community similarity-based classification analyses to be completed easily. To the best of our knowledge, this study represents the first application of this method to classify stand types with respect to their similarity taking into account both the structure and composition of the tree layer.

Coniferous forests generally have lower vascular plant diversity than broadleaf forests (Barbier et al. 2008). However, few studies have conducted internal comparisons on the scale of individual tree species (Barbier et al. 2008). The effects of the overstory structure and composition on the understory herb and shrub layer diversity in Anatolian black pine-dominated forests have not been previously studied in Turkey.

Although the tree layer structure and composition in a forest change over time, the present study dealt with the current status of the tree layer structure and composition, and its effects on the herb and shrub layers in an Anatolian black pine-dominated forest. To investigate this relationship, we addressed the following questions: (1) how are the species and size structure of the current tree layer communities classified? (2) Can the tree layer influence the diversity and composition of the herb and shrub layer vegetation? (3) What are the indicator species of these stand types? (4) Could environmental factors explain the variability in the composition of the shrub and herb layers?

Materials and methods

Study area

The study was conducted in the Gönen Dam Watershed area in Western Turkey, which covers an area of 113,700 ha and ranges from 90 to 1400 m a.s.l. (Fig. 1). According to long-term data from the nearest meteorological station (with an elevation of 252 m) located in Yenice Province, the mean annual precipitation is 847.3 mm, and the mean annual temperature is 12.8 °C. The altitude of the sampling plots selected for use in this study ranged from 231 to 1192 m. The Gönen Dam watershed is located in the northeast part of the Kazdağı Mountains (formerly known as Ida Mountain) in Western Anatolia (26.960–27.540°E, 39.640–40.100°N). The natural flora of the Kazdağı region is composed of approximately 800 taxa, 78 of which are endemic to Turkey; 28 of these endemic species are endemic to only Kazdağı (Satıl et al. 2006). In particular, the mountain peak section contains sensitive plant communities that have a high number of endemic and rare plant species. Therefore, the Kazdağı Mountains have been classified as an IPA (Important Plant Area) for Europe (Özhatay and Özhatay 2005).

The vegetation types in the Kazdağı Mountains consist of forest formation, scrub formation and high mountain-vegetation formation (Özel 1999). Forests in the Kazdağı Mountains are composed of pure or mixed conifer and broadleaf trees, such as *Pinus nigra* subsp. *pallasiana*, Calabrian pine (*Pinus brutia*), Kazdağı fir (*Abies nordmanniana* (Steven) Spach subsp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode & Cullen), Turkey oak (*Quercus cerris* L.), Hungarian oak (*Q. frainetto* Ten), sessile oak (*Q. petraea* (Mattuschka) Liebl.), oriental beech (*Fagus orientalis* Lipsky.), sweet chestnut (*Castanea sativa* Mill.), hornbeam (*Carpinus betulus* L.). Some parts of the Kazdağı Mountains are protected as national parks, nature conservation areas and genetic conservation areas, but the study area is located in the unprotected area.

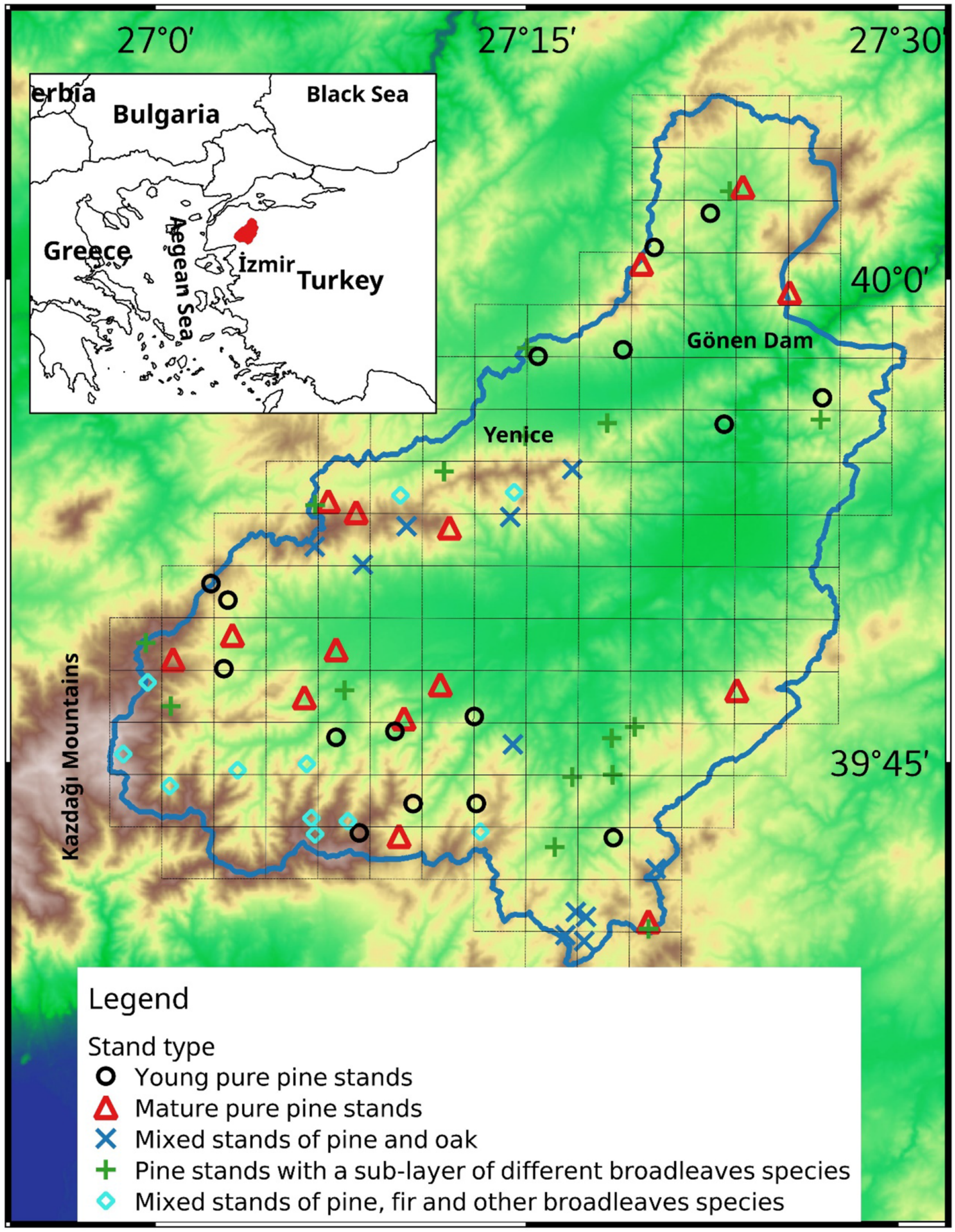

Fig. 1 Location map of the study area in Western Turkey (upper left) and distribution of the 69 sampled stands of the Anatolian black pine-dominated forests within the Gönen Dam Watershed

The Anatolian black pine is the most widespread conifer species in these mountains, and it is one of the target species for conservation in the Gene Management Zone (Çengel et al. 2000). The altitudinal range of the Anatolian Black pine forests in the Kazdağı Mountains usually starts from 400 m in the northern regions to 800 m in the southern regions and reaches altitudes of up to 1500–1550 m (Özel 1999). However, one of our *Pinus nigra* sampling plots was located at 231 m a.s.l. around Kalkım. In the northern areas of these mountains, the Anatolian black pine grows both as pure stands and as mixed forests with the Kazdağı fir and various deciduous tree species, including oak sp., sweet chestnut, hornbeam, and beech. Anatolian black pine-dominated stands compose a part of the naturally regenerated forest in the study area. Pure Anatolian black pine stands have been managed as even-aged high forests with uniform shelterwood system, whereas mixed stands have instead been managed as uneven-aged high forests with single trees and/or group management system. These forests have been managed by the state according to formal forest management plans.

Field data collection

The watershed boundaries were determined with a DEM (digital elevation model) with a resolution of 30 m. The watershed area was then systematically divided into a 3 × 3-km grid and a 20 × 20-m sampling plot was then randomly assigned to each grid cell, excluding any agricultural or residential areas. To avoid the edge effect but to keep the distance walkable, sampling plots were located 50–200 m from a road. GPS was used to locate the sampling plots in the study area. A total of 138 permanent plots were established, 69 of which were Anatolian black pine-dominated stands and were used in this study (Fig. 1).

Within each plot, all of the trees with a diameter at breast height (dbh) greater than or equal to 8 cm were measured. The shrub species found in this area were identified, and the number and abundance of each species were recorded. The herb layer plants were assessed in five 1-m × 1-m subplots, one established in the center and four at the corners of each 20-m × 20-m plot. In these five subplots, all vascular plant species in each plot were identified, and the coverage percentage was recorded. Without considering the life form, all plants that were less than 50 cm in height were included in the herb layer, and all woody plant species, large tree saplings and shrubs higher than 50 cm and smaller than < 8 cm in diameter at breast height were defined as shrub layer plants. We also recorded the presence/absence of herbaceous plant species in the entire plot area to determine the plant species that did not exist within these five subplots. To ensure the consistency of the data, cover values for each of the plant layers (the tree, shrub and herb layer) were determined by the same person for all of the sampling plots. The abundance of each species in the shrub and herb layers of each plot was rated using the Braun Blanquet method (Braun-Blanquet 1964) and then transformed into a 0–9 ordinal scale as described by Van der Maarel (1979). The vegetation in each subplot was sampled in September and October of 2011, May, June, July and September of 2012, and May and June of 2013. In the first 2 years, permanent plots were established, the tree DBH was measured, and the number and coverage of the shrub species in the shrub layer were determined for each plot. Additionally, herbaceous vascular plant specimens were collected from each plot and then identified in the ISTO (Forest Faculty of Istanbul University Herbarium), because herbaceous plant identification at the species level in the field is not always possible. In the third year, we went to the fields with a list of herbaceous plant species for each permanent plot. The cover value of each species in the herb layer was recorded from May to June of 2013. Nomenclature and identification of vascular plants follow Flora of Turkey and the East Aegean Islands (Davis et al. 1965–1985), and The Plant List (2013, version 1.1, published on the Internet; http://www.theplantlist.org/).

Data preparation and analysis

The study was conducted to assess variations in the understory herb and shrub layer diversity as they are related to the overstory tree community composition and structure and not along a certain spatial, temporal or environmental gradient (Anderson et al. 2011). Therefore, tree communities were classified using the Fuzzy C-Means clustering method according to the CAPs of the overstory tree species. We used the CAP method because it is a function that calculates the size based on the abundance of organisms (De Cáceres et al. 2013), and takes into account the size of the organisms in the resemblance indices. Clustering analyses and analyses of the CAPs were performed using the "vegclust" package (De Cáceres et al. 2010a). The CAPs were determined according to the tree layer species and the number of trees in each size class to express the stand structure and composition in a numerically clear manner, which included the 8–10.9-cm thin pole wood stage, the 11–19.9-cm pole stage, the 20–35.9-cm thin timber stage, the 36–51.9-cm medium timber stage and the larger-than-52-cm-thick timber stage A Bray–Curtis dissimilarity matrix of the CAPs of the sampling plots was used in the clustering process. Five clusters were determined using FCM (Fuzzy C Means) according to the Normalized Partition Coefficient (PCN), Normalized Partition Entropy (PEN) values, and the cluster variance (Fig. 2). These clusters were initially created fuzzily and then defuzzified into hard clusters. To determine the cluster membership, the maximum membership value was used across the clusters.

To describe the composition and structure of the clusters, average density graphs belonging to each of the clusters were

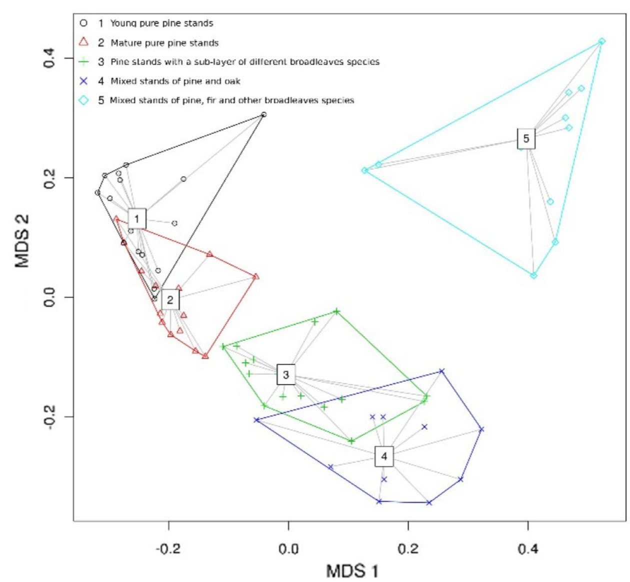

Fig. 2 Multidimensional scaling ordination of the dissimilarity matrix of the 69 sampling plots. We used a Bray–Curtis distance matrix of the tree layer CAPs to classify the sampling plots through the Fuzzy C-Means clustering method. Symbols correspond to the stand types given in Table 1. Each cluster center is shown with its corresponding number. Distances to centroids on the first two PcoA axes were drawn with gray line, and borders of each cluster were drawn with corresponding color

Table 1 Stand types assessed in this study and their descriptions

Stand types	Stand type description
Young pure pine stands	Black pines were generally seen in the pole stage and the thin timber stage. The average total number of every other mixed species was < 1
Mature pure pine stands	The Anatolian black pines were generally present in the thin and medium timber stages and were rarely present in the thick timber stages. Turkey oak and oriental beech could be found (in low number) in the thin pole and pole wood stages
Pine stands with a sub-layer of different broadleaves species	Anatolian black pines were represented by the thick, medium and thin timber stages. Hungarian oak and oriental beech trees were found in the thin timber stage and pole stage, and the Turkey oak was found in the thin pole wood stage and the pole stage. The abundance of the species was relatively low
Mixed stands of pine and oak	The size class of the Anatolian black pines was composed mainly of trees in the pole stage and the thin, medium, and thick timber stages. The oak species were represented in higher number in the pole stage through the thin pole stage
Mixed stands of pine, fir and other broadleaves species	Anatolian black pines generally appeared in the thick, medium, and thin timber stages. The Kazdağı fir trees were more abundant and mainly found in the thin pole stage, the pole stage and the thin timber stage. The other species were less represented and found in the thin pole wood stage and the pole stage, with an average of two trees

drawn for the five most dominant species within each cluster (Fig. 3). The average CAPs of the clusters were calculated with the "CAPmeans" function of the "vegclust" package using the cluster number as a factor parameter. The resulting density graphs provided numerically clearer definitions of the tree communities. After the clusters were determined,

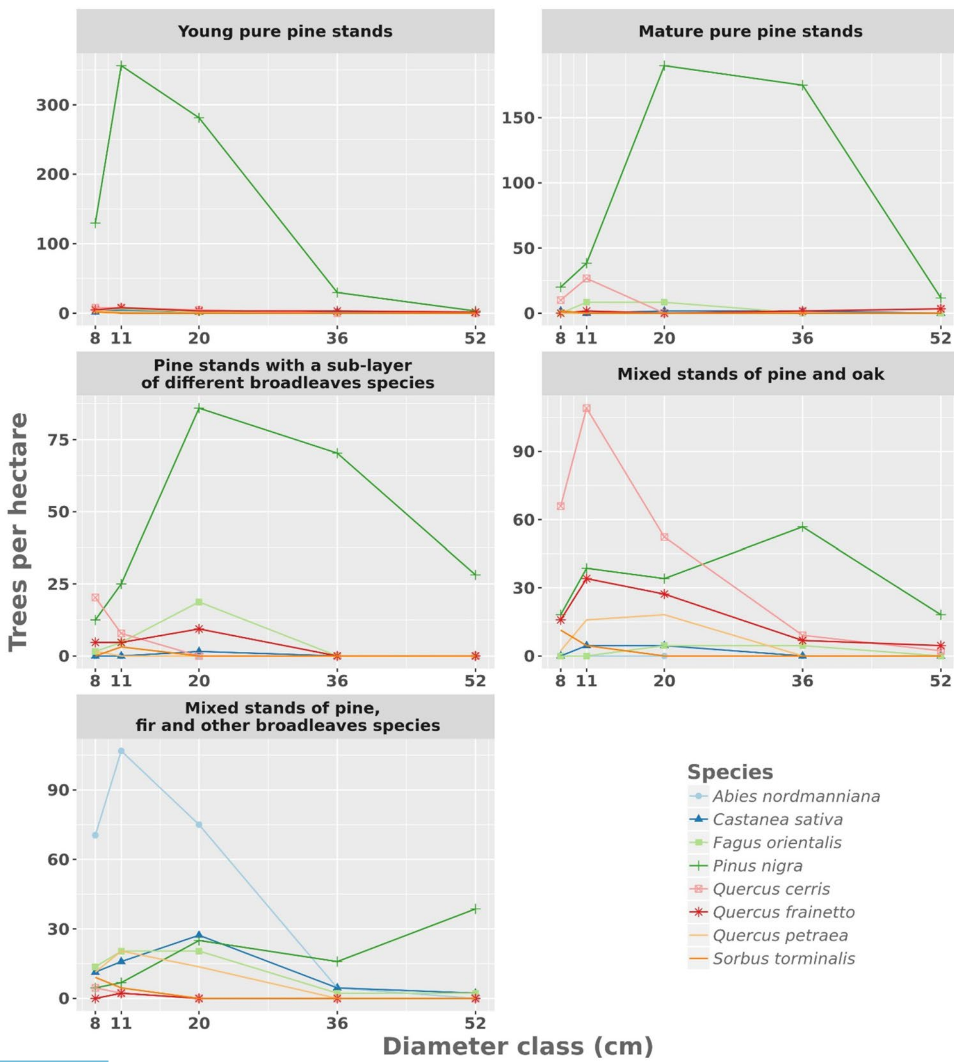

Fig. 3 Average number of trees per hectare depending on tree diameter within each stand type. The stand types are given in the top of each plot. Species color and shape codes are drawn in the right bottom of grid

the homogeneity of the cluster dispersions (variances) were tested in R using the 'betadisper' function of the vegan package. 'betadisper' is a multivariate analog of Levene's test for the homogeneity of variances (Oksanen et al. 2012). Species accumulation curves were used to compare the species richness of the herb and shrub layers for the stand types because they allow the comparison of the species richness between groups of plots, particularly when the sample sizes of the groups are not equal (Kindt and Coe 2005). Accumulation curves were calculated using the "specaccum" function of the "vegan" package with the "exact" method using presence–absence data. Moreover, the rank abundance analysis was performed using the "BiodiversityR" package (Kindt and Coe 2005), and the ten most abundant species of stand types are listed. We used proportional abundance to compare the stand types due to the unequal numbers of sampling plots within each cluster.

To determine the relationship between the understory species and the overstory composition, we use an indicator species analysis originally described by Dufrene and Legendre (1997) and improved later by De Cáceres et al. (2010b). This method allows for the combination of groups of sites, and identifies the species that serve to indicate either a single group or a combination of several groups. The indicator species were determined using the '*multipatt*-multi-level pattern analysis' function of the R package 'indicspecies' (De Cáceres and Jansen 2013). Because of the unequal sample size of the clusters, the sum of the mean overall clusters in the A component was included (De Cáceres and Legendre 2009; Vilches et al. 2013). Presence–absence data were used for the analysis of the indicator species, as this allows adjustments to be made for the low weight values of rare plant species which are often considered good indicators of vegetation types (De Cáceres and Legendre 2009). Based on the indicator species analysis, the indicator species for one cluster only or combinations of clusters were calculated. Only significant species at the 0.05 level with 'IndVal' values greater than 0.5 were assessed further.

Permutational multivariate analysis of variance (PERMANOVA) tests based on the Bray–Curtis ecological distance similarity indices were performed to test the statistical significance of the understory community composition variances. We also conducted Mantel test between the Bray–Curtis dissimilarity matrix of the tree layer and the Bray–Curtis dissimilarity matrices of the shrub and herb layers. The Bray–Curtis dissimilarity matrices were calculated using the abundance data for the herb and shrub species. All analyses were performed using the 'adonis' and 'mantel' functions of the "vegan" package of R (Oksanen et al. 2012).

Although this study mainly investigated the relationships between the overstory (i.e., the five stand types) based on the CAPs and its effects on the understory, we additionally investigated the relationships between the environmental variables, and shrub and herb layer composition. To identify these relationships, we used topographic, solar, bioclimatic, dendrometric, and geologic environmental variables (Table 2S) in the Constrained Correspondence Analysis (CCA) (Ter Braak 1986; Legendre and Legendre 2012). Topographic and solar variables were derived from the ASTER DEM with a 30-m resolution using the SAGA GIS terrain analysis and potential incoming solar radiation functions (Conrad et al. 2015). Bioclimatic variables were obtained from WorldClim database (http://www.worldclim.org). Overstory dendrometric variables, as completed by Barbier et al. (2009), were calculated from tree diameter values. A bedrock-type variable was extracted from a 1/25.000 scale geological map prepared by the General Directorate of Mineral Research and Exploration (MTA). Automatic stepwise model building with 999 permutations for CCA was used for selecting and reducing the large set of explanatory variables in each set of environmental variables separately. After performing 'ordistep' ten times, variables which were significant $p<0.05$ more than five times were considered in the subsequent analysis to produce the most parsimonious ordinations. CCA analyses were conducted once both with environmental and CAP variables, and once with only environmental variables to see the CAP's effect on the shrub and herb layer composition.

All of the statistical analyses were performed using the statistical software R 3.0.1 (R Development Core Team 2014), and all of the GIS functions were realized with SAGA (Conrad et al. 2015) and Quantum GIS (QGIS Development Team 2014).

Results

In the study area, 17 tree species were identified in the tree layer of the Anatolian black pine-dominated forests. Moreover, 52 species in the shrub layer and 315 species in the herb layer were identified.

The overstory structure and composition were classified into five clusters (Fig. 2). Descriptions of these five clusters, hereafter referred to as stand types with the names mixed stands of pine and oak ($n=11$), young pure pine stands ($n=16$), mixed stands of pine, fir and other broadleaves species ($n=11$), pine stands with a sub-layer of different broadleaves species ($n=16$), and mature pure pine stands ($n=15$), are given in Table 1.

The influence of tree layer on the diversity and composition of herb and shrub layer

Accumulation curves of the understory herb and shrub layer

The species richness of the five stand types was compared using 11 samples. The accumulation curves of the shrub layer showed that young pure pine stands had the highest shrub species richness levels, while pine stands with a sub-layer of different broadleaves species and mature pure pine stands had similar shrub species richness levels that were higher than those of mixed stands of pine and oak (Fig. 4). Considering the species richness of the herb layer of these stand types, pine stands with a sub-layer of different broadleaves species were the most diverse, followed by mature pure pine stands, then by young pure pine stands and mixed stands of pine and oak, which were almost equal. The mixed stands of pine, fir and other broadleaves species had the lowest species richness in both the herb and shrub layers. The young pure pine stands had the highest shrub species richness compared to the other stand types and had higher diversity than the mixed stands yet the lowest herb layer diversity among the pure stands.

Rank abundance of the understory

The ten most common herb layer species seen in the stand types are shown in Table 1S in the supplementary materials. *Rubus canescens* DC. occurred in all stand types with different ranks. *Luzula forsteri* (Sm.) DC. was found in the top ten species in all stand types except for young pure pine stands, whereas *Euphorbia amygdaloides* L. was found in all stand types with the exception of mixed stands of pine, fir and other broadleaves species. The species composition of the understory herb layer of the mixed stands of pine, fir and other broadleaves species stand was different from that of the other four stand types (Table 1S in the supplementary materials).

Homogeneity of the overstory and variance of the understory composition

The homogeneity of the five stand-type dispersions was tested using a permutational test. In these stand types, the cluster internal variances were demonstrated to be different ($F = 11.0698$, P value $= 0.01$) for the following reason: The pine stands with a sub-layer of different broadleaves species and mature pure pine stands showed more homogeneity than the other stand types. The young pure pine stands and mixed stands of pine, fir and other broadleaves species were more heterogeneous (Fig. 2).

The analysis of the variance in the understory species composition of the five stand types was tested using the Bray–Curtis distance matrix. According to the dissimilarity matrix, the community composition of the herb layer showed significant differences in the compositional similarity (Bray–Curtis, $R^2_{\mathrm{ADONIS}} = 0.11$, $P = 0.001$). The community composition of the shrub layer also showed significant differences in the community compositional similarity (Bray–Curtis $R^2_{\mathrm{ADONIS}} = 0.24$, $P = 0.001$). The five stand types differed significantly in terms of their understory species composition.

A Mantel test with 999 permutations shows a significant association between the Bray–Curtis dissimilarity matrix of the overstory and the dissimilarity matrices of both the shrub and herb layers. The Mantel statistic and significance of the analysis between the overstory and shrub layer matrices were 0.35 and 0.01, respectively, while those of the analysis between the overstory and herb layer matrices were 0.25 and 0.01, respectively.

Indicator species for the stand types and stand type combinations

According to the multi-level pattern analysis, certain understory species were determined to be indicator species of some stand types and specific site combinations (Table 2). The young pure pine stands and mature pure pine stands were not assigned any individual indicator species and the mixed stands of pine, fir and other broadleaves species did not combine with any other stand types. Three species were selected as indicator species unique to the mixed stands of pine and oak, and two species unique to the pine stands with a sub-layer of different broadleaves species. The mixed stands of pine, fir and other broadleaves species had the highest number of indicator species of all of the stand types. The indicator species that best characterize this stand type are *A. nordmanniana* subsp. *equi-trojani, Festuca drymeja*, and *Dryopteris raddeana* (Fomin) Fomin. On the other hand, *Geranium lucidum* L. was identified as indicator species in the combination of mixed stands of pine and oak, and pine stands with a sub-layer of different broadleaves species, and *Doronicum orientale* Hoffm. was identified in the combination of mixed stands of pine and oak, and mature pure pine stands. Five indicator species—one of which is *Muscari latifolium*, an endemic species—were selected in the herb layer in combinations of mixed stands of pine and oak, mine stands with a sub-layer of different broadleaves species, and mature pure pine stands (Table 2). The highest number of indicator species appears in the herb and shrub layers in combinations of mixed stands of pine and oak, young pure pine stands, pine stands with a sub-layer of different broadleaves species, and mature pure pine stands. *Quercus cerris* was appointed as indicator species both in the herb and shrub layer. All species selected as indicator species for the last combination were common in the Anatolian black pine forests.

Environmental variables and the relationship between the shrub and herb layers

The correlations between the site variables, and herb and shrub layers were significant, but the *r*2 and especially

Table 2 Results of the indicator species analysis on the understory herb and shrub species of the stand types

Stand type	Indicator species	*A*	*B*	IndVal	*p* value
Herb layer					
Mixed stands of pine and oak	*Poa trivialis* L.	0.6554	0.5455	0.598	0.003**
	Epipactis helleborine (L.) Crantz	0.7379	0.3636	0.518	0.006**
	Ranunculus constantinopolitanus (DC.) d'Urv	1.0000	0.1818	0.426	0.049*
Mixed stands of pine, fir and other broadleaves species	*A. nordmanniana* subsp. *equi-trojani*	0.9106	0.6364	0.761	0.001***
	Festuca drymeia	0.7034	0.4545	0.565	0.001***
	Dryopteris raddeana	1.0000	0.2727	0.522	0.006**
	Turritis laxa (Sm.) Hayek	0.8136	0.2727	0.471	0.021*
	Cardamine bulbifera (L.) Crantz	0.7500	0.2727	0.452	0.043*
	Neottia nidus-avis (L.) Rich	1.0000	0.1818	0.426	0.036*
Pine stands with a sub-layer of different broadleaves species	*Sonchus asper* Mert. & W.D.J. Koch. subsp. *glaucescens* (Jord.) Ball ex Ball	0.8491	0.3750	0.564	0.003**
	Vulpia ciliata Dumort	1.0000	0.1875	0.433	0.044*
Mixed stands of pine and oak + pine stands with a sub-layer of different broadleaves species	*Geranium lucidum*	0.7391	0.4444	0.573	0.016*
Mixed stands of pine and oak + mature pure pine stands	*Doronicum orientale*	0.9065	0.3077	0.528	0.009**
Mixed stands of pine and oak + pine stands with a sub-layer of different broadleaves species + mature pure pine stands	*Muscari latifolium*	0.8751	0.5714	0.707	0.002**
	Pinus nigra	1.0000	0.4762	0.690	0.001***
	Trifolium campestre Schreb	0.9480	0.3810	0.601	0.008**
	Geranium purpureum Vill	0.9469	0.3810	0.601	0.008**
	Anemone blanda Schott Kotschy	0.9337	0.2857	0.517	0.031*
Young pure pine stands + pine stands with a sub-layer of different broadleaves species + mature pure pine stands	*Clinopodium vulgare* L.	0.9226	0.3617	0.578	0.036*
	Pilosella hoppeana (Schult.) F.W. Schultz & Sch. Bip	1.0000	0.2979	0.546	0.012*
Mixed stands of pine and oak + young pure pine stands + pine stands with a sub-layer of different broadleaves species + mature pure pine stands	*Quercus cerris*	1.0000	0.4828	0.695	0.012*
	Cistus creticus	0.9549	0.5000	0.691	0.045*
Shrub layer					
Mixed stands of pine, fir and other broadleaves species	*A. nordmanniana* subsp. *equi-trojani*	0.7822	1.0000	0.884	0.001***
	Carpinus betulus	0.8136	0.2727	0.471	0 0.017*
Young pure pine stands + pine stands with a sub-layer of different broadleaves species + mature pure pine stands	*Phillyrea latifolia*	*1.000*	*0.383*	*0.619*	*0.004***
Mixed stands of pine and oak + young pure pine stands + pine stands with a sub-layer of different broadleaves species + mature pure pine stands	*Quercus cerris*	*1.0000*	*0.7931*	*0.891*	*0.001****
	Erica arborea L.	*0.9658*	*0.6379*	*0.785*	*0.002***
	Arbutus unedo L.	*1.0000*	*0.5000*	*0.707*	*0.005***
	Quercus frainetto	*1.0000*	*0.4828*	*0.695*	*0.011**

The specificity (*A*), sensitivity (*B*), indicator value (IndVal) and significance (*p* value) are given. '*A*' is the probability that the surveyed site belongs to the target site group, given that the species has been found. '*B*' is the probability of finding the species in sites belonging to the site group

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

adjusted R^2 values were low. Site variables explained the variation in the shrub layer ($r2=0.53$, adj $r2=0.32$) better than that in the herb layer ($r2=0.21$, adj $r2=0.09$) in the final model. Species composition was significantly associated with mean temperature of wettest quarter, elevation, terrain surface texture, duration of insolation, bedrock type, cumulative abundance profiles of five overstory tree species at the shrub layer, and with temperature seasonality, precipitation of wettest quarter, precipitation of coldest quarter, morphometric protection index, cumulative abundance profiles of three overstory tree species at the herb layer (Fig. 5). When CCA analysis was reperformed by removing CAP variables from above final model, $r2=0.41$ and adj $r2=0.23$ were found in the shrub layer, and $r2=0.12$ and adj $r2=0.04$ in the herb layer.

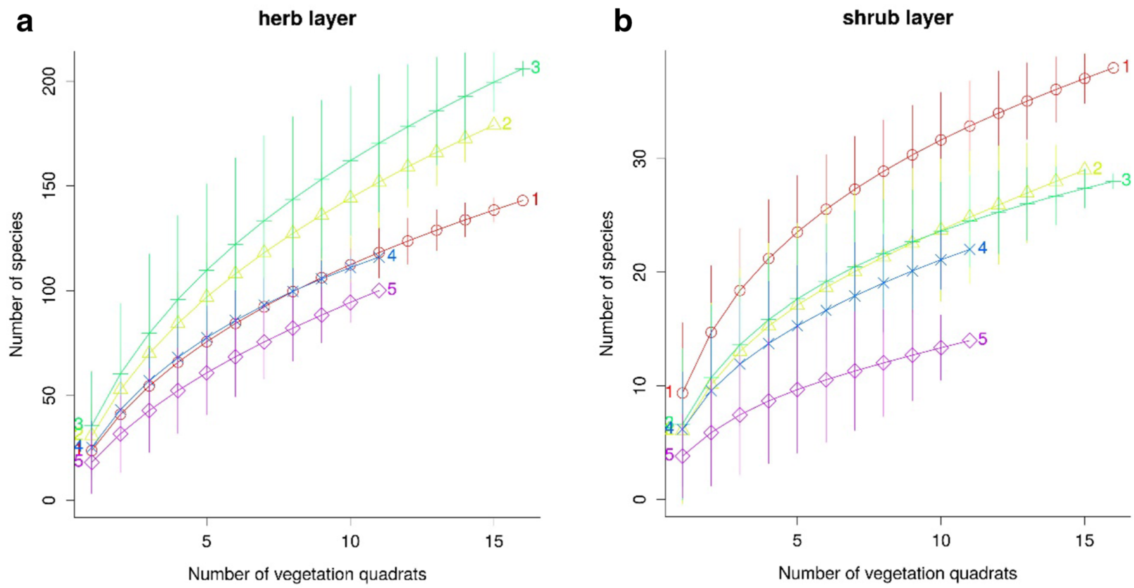

Fig. 4 Species accumulation curves of the **a** herb layer, and **b** shrub layer in the study area for comparing the species richness of the five stand types. Each point along the curve corresponds to an estimate of the mean species accumulation calculated from 100 random permutations of the sampling data. Error bars indicate the confidence intervals obtained from the standard deviation multiplied by 2. Stand type categories: (1) young pure pine stands, (2) mature pure pine stands, (3) pine stands with a sub-layer of different broadleaves species, (4) mixed stands of pine and oak, (5) mixed stands of pine, fir and other broadleaves species

The compositional variation in shrub layer species was associated with elevation, terrain surface texture, and duration of insolation. The shrub layer composition of mixed stands of pine, fir and other broadleaves species was associated with elevation, cumulative abundance profiles of two overstory tree species, and bedrock type (Fig. 5).

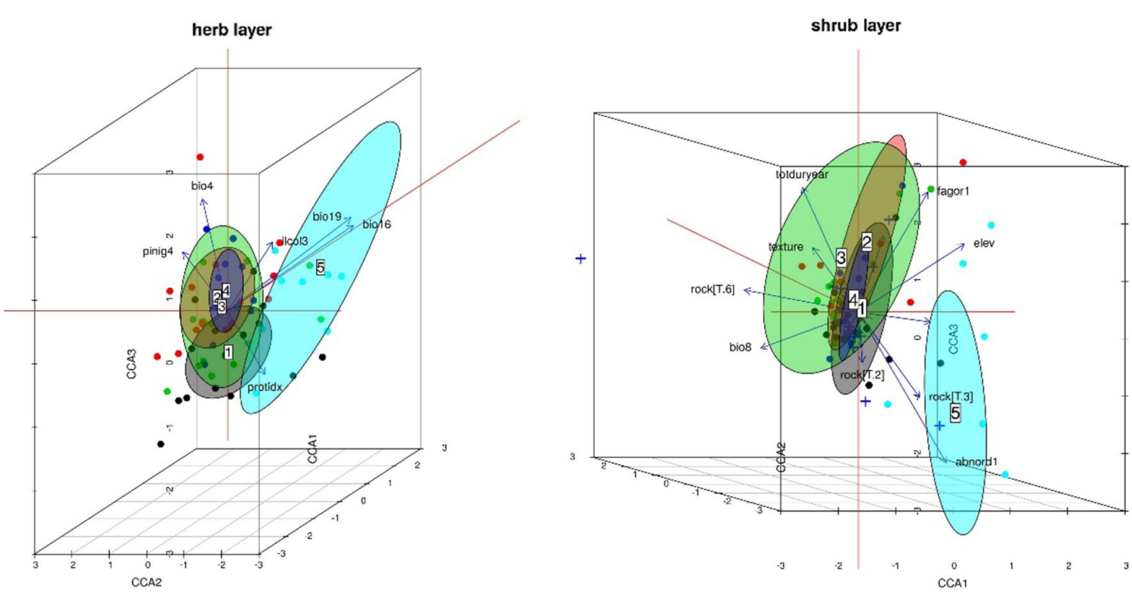

Fig. 5 Ordination diagram showing the result of CCA analysis between environmental variables, and shrub and herb layer composition in the study area. Abbreviations of environmental variables given in Table 2S in the supplementary materials

Discussion

The influence of the tree layer on the diversity and composition of the herb and shrub layer

We found obvious differences in the understory composition and diversity between stand types classified through CAP in the Anatolian black pine-dominated forests. Mature pure pine stands, pine stands with a sub-layer of different broadleaves species and young pure pine stands had similar overstory tree species composition, but different CAPs. Similarly, the herb and shrub layer diversity markedly differed among these stand types (Fig. 4). Although the young pure pine stands were the richest in terms of shrub layer diversity, they were ranked third in terms of herb layer diversity. This may be explained by the high density and diversity of the shrub layer. Regardless of the species, a high density of the shrub layer can lead to a low-herb layer diversity due to shade effect. While Huo et al. (2014) stated that the richness and diversity of the herb layer in coniferous forests were significantly related to the dominant canopy species but not related to the shrub layer, Klinka et al. (1996) stated that the herb layer diversity in a forest was instead influenced by both the overstory tree canopy and the shrub layer cover. We found maximum herb and shrub layer richness and abundance in pure or nearly pure forest stands, not in mixed stands.

The mixed stands of pine and oak which are characterized by heterogeneous tree layer both in terms of age and species composition, were ranked fourth in terms of understory species richness. Previous studies (Saetre et all. 1997; Yu and Sun 2013) found that the conifer–deciduous mixed stands had a higher plant richness than the pure conifer stands. In contrast, this study revealed that in young pure pine stands or mature pure pine stands, the richness of the understory herb and shrub layers was markedly higher than those of the mixed stands of pine and oak, and mixed stands of pine, fir and other broadleaves species. Based on the results and field observations, this can be explained as follows: oak species in the Anatolian black pine–oak mixed stands were found in the herb and especially shrub layers, as well as the tree layer (i.e., in all layers) at high densities. This in turn leads to light, water and nutrient competition with other species. All of these effects negatively influence the diversity, particularly in the herb layer. Because of its frugality, pioneer qualities, and ecologic elasticity, *P. nigra* improves the soil properties and encourages colonization of many other broadleaved trees in *Pinus nigra* plantation areas in the Mediterranean region (Bussotti 2002). Although this study was performed in natural forests, the presence of oak species in both herb and shrub layer beyond the overstory in this stand type is related to the successional status of *Pinus nigra* forests, as described in Bussotti (2002). Oak species found in mixed stands of pine and oak are supported by forest managers, as oaks are considered to be filler trees (Özel 1999).

The mixed stands of pine and oak, and mixed stands of pine, fir and other broadleaves species are both coniferous and broadleaved mixed forests, but the majority of the canopy layer of mixed stands of pine, fir and other broadleaves species consists of two conifer tree species. The proportion of broadleaf and conifer trees in the overstory affects the diversity and composition of the understory vegetation (Berger and Puetmann 2000; Bartels and Chen 2013). The mixed stands of pine, fir and other broadleaves species showed significantly lower understory diversity in both the shrub and herb layers compared to the other stand types (Fig. 4). This may be explained by the shade effect caused by the canopy cover of the overstory trees. The herb species grown in the mixed stands of pine, fir and other broadleaves species stands were generally composed of shade-tolerant plants. In this stand type, the moisture and light, in addition to the foresters' interventions, have the most important effects on the overstory composition. While the Anatolian black pine's demand for light is high, the demand for moisture by fir and beech trees is also high. In terms of intra- and interspecific competition for above and below ground resources such as light, moisture and nutrients, the Anatolian black pine has advantages in moisture acquisition but disadvantages for light use (Ata 1989; Özel 1999).

Indicator species for the stand types and stand-type combinations

Indicator species are biological indicators representing the habitat types of plant combinations. These species can provide relevant ecological information, and support ecosystem management and protection (Legendre 2013). Such information is most important for relict forests and areas that must be protected (Vilches et al. 2013). Specific stand structure-based indicators were determined for particular stand types and stand-type combinations. These stand structure-based indicators are stand-level features of forests (Lindenmayer et al. 2000) that can be used to evaluate the stand structure and composition of Anatolian black pine forests across time. They can also be used to monitor the influence of management activities and to plan the conservation of the plant diversity of these forests.

Three herbaceous species were associated with the mixed stands of pine and oak (Table 2). *Epipactis helleborine* is a common semi-shade-tolerant plant species that usually grows in woodlands and scrubs. *Poa trivialis* generally grows in well-lit places but can also live in partly shady conditions (Hill et al. 1999). *Ranunculus* *constantinopolitanus* prefers damp places, such as swampy meadows (Davis et al. 1965–1985). The presence of these plants indicates that the forest in which they are found has a dense canopy. These mixed stands, which have their own group of indicator species, are important for sustainable biodiversity; thus, the management of these areas merits careful attention.

Mixed stands of pine, fir and other broadleaves species contain many specific indicator plants, which are significantly associated (Table 2) with this stand type. A high number of indicator species for mixed stands of pine, fir and other broadleaves species indicate this stand type's uniqueness (Vilches et al. 2013). The fact that mixed stands of pine, fir and other broadleaves species did not generate any combinations with the other stand types can be interpreted to show the floristic dissimilarity of mixed stands of pine, fir and other broadleaves species from the other stand types. Therefore, despite its lower diversity, this stand type contributes highly to the overall plant diversity. Also, these stands are specific to the Kazdağı Mountains as Kazdağı fir is an endemic subspecies. All indicator species in the understory layers, particularly the herb layer, of this stand type are moisture-demanding and shade-tolerant. Interventions to favor one of the species in these mixed stands may affect the structure and composition of the forest.

Young pure pine stands and pine stands with a sub-layer of different broadleaves species do not have any indicator species unless combined with other stand types. This shows us that the two stand types are at the transitional stage. Our results confirm the structural and floristic affinities of mixed stands of pine and oak, pine stands with a sub-layer of different broadleaves species, and mature pure pine stands. Because five species were identified as indicators of the herb layers for the combination of these stands, it seems likely that there was a high degree of similarity between these stand types.

Cistus laurifolius L., which had been noted to be an indicator species of Anatolian black pine in several studies (Güner et al. 2011; Özkan 2002), was not present in our sample plots. However, several shrub species that are common to Anatolian black pine forests, such as *Cistus creticus, Arbutus unedo, Erica arborea, Quercus cerris* and *Quercus frainetto*, were assigned as indicator plants for the combination of mixed stands of pine and oak, young pure pine stands, pine stands with a sub-layer of different broadleaves species, and mature pure pine stands. The presence of *Q. frainetto* in shrub layer and *Q. cerris* in both herb and shrub layers as indicator species in the four stand-type combination indicates that these oak species are the main components of these forest types.

The influence of site variables

The constrained ordination shows that the compositional variation in shrub layer and herb layer species was associated with different environmental variables. However, the low correlation between the herb and shrub layer, and the site variables used in the study was not enough to explain the compositional variation in the understory, especially in the herb layer. This could be explained with the environmental variables that we did not take into account while conducting CCA, such as soil and litter properties, and past disturbances (Chang et al. 2013). Lower explained variation in the herb layer composition could be caused by local site conditions' and shrub layer's effect. CAP variables were found significant both in herb and shrub layer ordination models. When we excluded CAP variables from the models explained compositional variation was reduced.

Some environmental variables, such as the elevation, cumulative abundance profiles of two overstory tree species, and bedrock type were correlated with mixed stands of pine, fir and other broadleaves species shrub layer composition. The Kazdağı fir has a narrow ecological amplitude and grows in mixed forests with *Pinus nigra, Castanea sativa, Quercus* sp., and *Fagus orientalis* at an altitudinal range of between 500 and 1700 m on north-facing aspect, but optimum growing sites of species begin at approximately 1000 m elevation (Ata 1989).

Mantel tests show a significant association between the overstory and both the shrub and herb layers. It can be said that the influence of the overstory structure and composition on understory plant diversity is greater than the effect of local site variables (Brosofske et al. 2001).

The understory diversity and composition of Anatolian black pine forests were not directly related to environmental factors, but may instead be due to the temporal variability in the site. Because of its frugality and ecological elasticity, *Pinus nigra* is able to adapt ecologically and physiologically to different conditions and takes a leading role in the different stages within forest succession in various ecological niches (Zaghi 2008). The current and past management systems (Montes et al. 2005) were regarded as the most important parameters among the many other environmental factors that affect the composition and diversity of the understory vegetation. Although the site variables had some important influences on plant diversity variation in the understory structure, the composition and diversity of the Anatolian black pine forests on the Kazdağı Mountains could not be explained by the site variables and were instead determined primarily by the overstory structure and composition.

In conclusion, this manuscript presents a study of the plant diversity and the relationship between the overstory and understory in Anatolian black pine-dominated stands. We found that both the understory herb and shrub layer diversity were related to the composition and structure of the overstory. We found that the herb and shrub layer diversity of the young pure pine stands and mature pure pine stands is higher than other three stand types. At the same time, some understory plants occurred exclusively in a particular stand type, and specific indicator species were also associated with certain stand types and some stand combinations. Therefore, maintaining a range of overstory stand types is critical to sustain understory plant diversity in a forest. These results suggest that the loss of a particular overstory stand type could result in the loss of some herb and shrub layer species. Therefore, it can be inferred that the maintenance of forest stands composition and structure affect understory diversity and composition in managed forest.

Pinus nigra subsp. *pallasiana*-dominated forests in Turkey cover large areas with different climatic and edaphic conditions. Therefore, further studies should be conducted in different parts of Turkey for a better understanding of the understory diversity in the Anatolian black pine forests. While conducting such studies, stand structure, composition, degree of mixture, and development stages should be determined precisely. Such precise determinations can be made through CAP and clustering methods. Autoecological knowledge of understory plant species is crucial both for the maintenance of plant diversity in a forest, and to understand the ability of species establishment, tolerance to disturbances, and persistence under various effects of management operations.

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