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The optimization of typical species inventory of habitat types of a NATURA 2000 site using a phytosociological approach

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Abstract

The definition of typical species inventories of the 92/43/EEC Directive habitat types is a valuable information for the optimization of the conservation status assessment. Habitat-specific assessment protocols and predefined local inventories of typical species provide a method for a relatively fast and accurate assessment of the criterion "structures and functions". Habitat types are often defined and described on the basis of a phytosociological description of vegetation units, mainly at the syntaxonomical level of alliance. Therefore, the definition of typical species inventories can be based on phytosociological approaches. Within this concept we surveyed the vegetation of a NATURA 2000 Special Area of Conservation in northern Greece in order to optimize and downscale the existing region-wide inventories of typical species. In total, we sampled 164 relevés in beech and in thermophilous deciduous broadleaved forests. The relevés were assigned to vegetation units and habitat types using numerical approaches and their differential and constant taxa were defined. We used these taxa to draw up the optimized, site-specific inventories of typical species for seven habitat types of community interest and one habitat type of national interest.

Keywords

Constant taxa, differential taxa, GR1240002, Greece Habitats Directive, Mt. Tzena

Introduction

Among the main research questions in vegetation science is the description and typification of plant communities, in a way that recognizable and reproducible units are identified wherever similar ecological conditions are met (Pott 2011). Phytosociology, through analysis of species composition and structure, defines vegetation units that express historical, sociological and site conditions (Blasi and Burrascano 2013). This approach offers a multipurpose, hierarchical vegetation classification scheme in which the description of plant communities is based on their floristic composition and the identification of dominant, constant and diagnostic species (Dengler 2016). It is not surprising, therefore, that this scheme has been applied to a number of applications in resource management (Biondi 2011). The characteristics of phytosociological classification allow for its use in the assessment of the ecological value of a site (Loidi 1994; Loidi 1999), as well as for a number of indicators of sustainable forest management (Blasi and Burrascano 2013). Moreover, the information regarding the successional stage of vegetation, a parameter that can be deducted through phytosociological analysis, allows for the elaboration of targeted management plans (Velev and Vassilev 2014).

Phytosociological analysis and classification of plant assemblages has also strong relations with nature conservation (Loidi 1994; Loidi 1999). It has been used in a number of vegetation typologies including the biotype differentiation of the UNESCO convention on biodiversity (Pott 2011), the EUNIS habitat classification (Chytrý et al. 2020), the European red list of habitats (Janssen et al. 2016) and, especially, the identification, description and assessment of habitat types of the 92/43/EEC Directive (Rodwell et al. 2018). The relationship between vegetation syntaxa and habitat types of the 92/43/EEC Directive is well demonstrated in the interpretation manual of Habitat types (European Commission 2013), as well as in the published guidelines for the assessment and reporting under Article 17 of the Habitats Directive (DG Environment 2017; Evans and Arvela 2011). The description of habitat types in the interpretation manual largely depends on the phytosociological description of vegetation units, mainly at the syntaxonomical level of alliance (Tsiripidis et al. 2018). Moreover, numerous crosswalks aiming in matching habitat types to one (or more) vegetation types and vice versa exist (Biondi et al. 2012; Biserkov et al. 2015; Chytrý et al. 2010; Rodwell et al. 2002; Schaminée et al. 2012) and serve as the main manuals for the description of habitat types at the European or at the member-state level.

Similarly in Greece, a first attempt for the development of a crosswalk between habitat types and phytosociological syntaxa is presented by Papastergiadou et al. (1997) and was further elaborated in the national interpretation manual of habitat types (Dafis et al. 2001). New data have emerged since then. Analyses of nation-wide data sets reviewed the syntaxonomical classification of large vegetation groups (Bergmeier and Dimopoulos 2001; 2008; Tsiripidis et al. 2007), but there was not any critical review for this crosswalk even when new habitat types (European Commission 2013) were included in the national inventory. Recent studies demonstrating the strong links between vegetation science and the Habitat types Directive (Attorre et al. 2018, Gennai et al. 2022) show that the potential of using phytosociological concepts for the optimum implementation of Habitats Directive are still to be exploited. Phytosociological concepts and methods can be used for the typification and description of habitat types. The identification of typical species (Bonari et al. 2018; Bonari et al. 2021; Gennai et al. 2022; Tsiripidis et al. 2018), the assessment of the conservation status of structure and functions (Dimopoulos et al. 2018; Tsiripidis et al. 2018) or the study of impacts of climate change, as a threat to habitat types through the analysis of historical relevés (Evangelista et al. 2016), are only some examples that show the important role of phytosociology in the implementation of Habitats Directive.

The assessment of typical species is included as a sub-criterion for the assessment of 'structures and functions' (DG Environment 2017) of habitat types. Although typical species play an important role in the assessment, they are not clearly defined in the Directive. The explanatory notes regarding the evaluation of the conservation status of habitat types (DG Environment 2017), or the elaboration of the standard data forms (SDF) (European Commission 2011), clearly indicate the need to assess the conservation status of typical species, yet there is not a clear inventory of typical species of each habitat type or a method to identify them. Typical species should reflect favourable structure and functions, meaning that they should be: (a) indicative of good habitat quality, (b) tightly related with the habitat types over large areas, and (c) sensitive to changes in the conditions of the habitat (Angelini et al. 2018; Evans and Arvela 2011). Until recently, a few member states had compiled inventories of typical species for some habitat types (Ellwanger et al. 2018) and even fewer for all habitat types (Angelini et al. 2018; Ellwanger et al. 2018; Gennai et al. 2022; Tsiripidis et al. 2018). The lack of a clear definition of typical species has allowed for the development of a number of methods to use them as an assessment criterion. Some approaches for the compilation of typical species inventories include expert judgment (Dalle Fratte et al. 2022) or numerical, analytical methods (Bendali and Godron 2021; Dalle Fratte et al. 2022; Gennai et al. 2022; Tsiripidis et al. 2018). Recent studies showed the agreement of experts that plant sociology methods should be used in the conservation status assessment of habitat types (Gigante et al. 2016) and that the use of diagnostic and characteristic species provides valuable information of the conservation status of habitat types (Bonari et al. 2021).

In Greece, phytosociological methods and concepts were applied to elaborate habitat-specific protocols for the assessment of the habitat types of the 92/43/EEC Directive (Dimopoulos et al. 2018; Tsiripidis et al. 2018). These protocols have been derived from a large, nation-wide data set of phytosociological relevés and the inventory of typical species for each habitat type has been developed at a broad geographical scale: at the level of phytogeographical region (Strid and Tan 1997) or at groups of adjacent Natura 2000 sites. On the one hand, this generalization offers the flexibility to use these evaluation protocols across a considerably large region, yet the assessment of habitat types and especially the assessment of the conservation status of typical species requires more detailed information at the level of a Natura 2000 site. That is because habitat type features may vary locally when, for example, different vicariant habitat have been identified (Tsiripidis et al. 2018). The adjustment of the evaluation protocols at a local spatial scale can support the efforts of local conservationists and managers of the Natura 2000 network to optimally assess the conservation degree and the conservation status. There is a link, for example, between the assessment criteria "representativity" and "conservation status" of the SDF and the typical species inventory list (European Commission 2011). A site-specific typical species inventory will facilitate the update of these assessment criteria. Moreover, a typical species list that is compiled at the local scale can assist in the selection of species during restoration practices.

In this paper we describe and classify the forest vegetation of a Natura 2000 site, applying phytosociological concepts and methods that ensure objectivity. The identified vegetation units are then assigned to habitat types, and site-specific inventories of typical species are formed. These adapted floristic inventories are to replace the existing, large-scale typical species lists of evaluation protocols, and used as the basis for the assessment of the criterion "structures and functions". This substantially supports the optimization of the implementation of the 92/43/EEC Directive.

Methods

Study area

The study area consists of Mt. Tzena, which is a mountain situated in central Macedonia, Greece, at the borders with the Republic of North Macedonia (Fig. 1). Its highest peak rises at 2,182 m a.s.l. The main geological substrates of the area are acidic. Schists dominate, but calcareous elements like marbles and sipoline marbles cover a significant part of the area (Mountrakis 1985) (see Suppl. Material 1, Figure S1). The area, depending on the elevation under consideration, can be classified in the classes BSk (Arid, steppe, cold), Csa (Temperate, dry summer, hot summer), Csb (Temperate, dry summer, warm summer), Dsb (Cold, dry summer, warm summer), Dsc (Cold, dry summer, cold summer), Dfb (Cold, no dry season, warm summer) and Dfc (Cold, no dry season, cold summer) of the Köppen-Geiger classification (Beck et al. 2018) (see also Suppl. Material 1, Figure S1). At low elevations, a distinct warm-dry period can be observed during the summer months, in contrast to the high elevations where such period is not observed.

The vegetation of the mountain has been recently described and mapped at an area of 5,326.75 ha by Chasapis et al. (2013). Twelve natural and human-induced land use/land cover units have been identified in the area. In total, deciduous, broad-leaved woodlands cover more than 50% of the mountain area extending to the altitude of 1,800 m a.s.l. The dominant vegetation is the beech forest that covers 30% of the surface area. Heath and gorse of the subalpine and alpine zone also cover a significant surface area, reaching 16% of the total area. Similarly, a recent survey by Chasapis et al. (2020) showed that the flora of the mountain consists of 1,254 taxa.

Regarding the protection regime of the study area, Mt. Tzena is part of the Special Area of Conservation (SAC) of the 92/43/EEC Directive of the European Natura 2000 network under the code GR1240002 – Ori Tzena. It largely coincides with the Special Protection Area (SPA) of the bird's Directive GR1240007 – Ori Tzena kai Pinovo. SAC GR1240002 consists of two distinct mountains, Mt. Tzena and Mt. Pinovo, the former covering the eastern half of the SAC.

Thirteen habitat types of the 92/43/EEC Directive have been described in the SAC, with one of them, 6230*- Species-rich *Nardus* grasslands, on siliceous substrates in mountain areas (and submountain areas in Continental Europe), being a priority habitat type. Among these

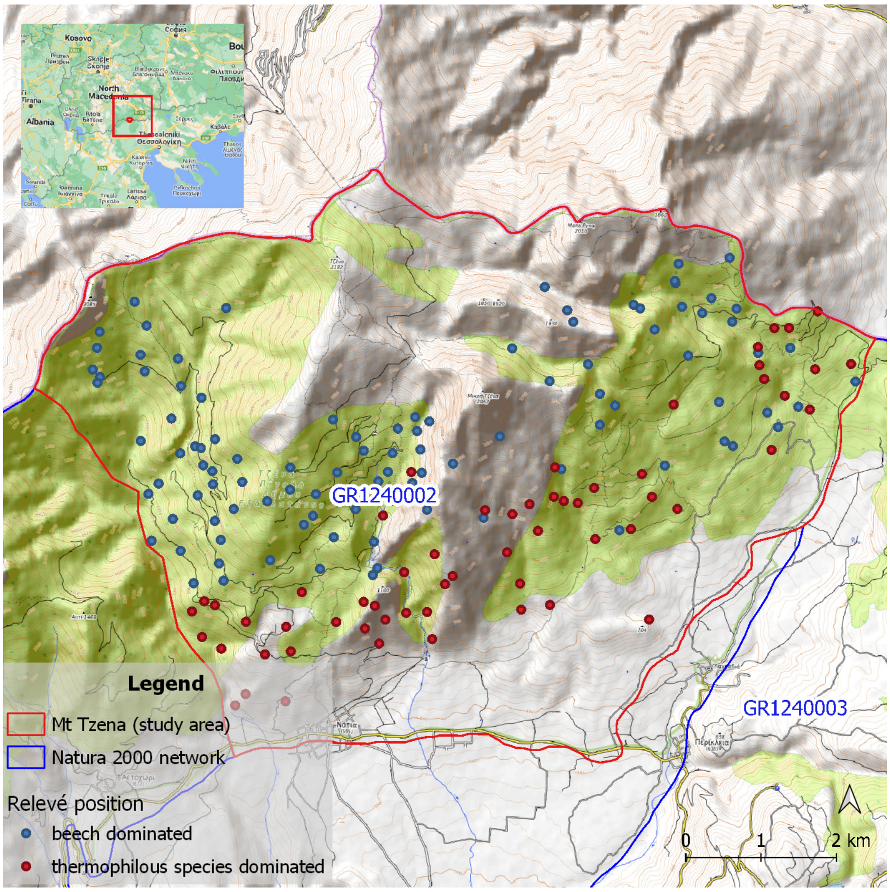

Figure 1. Mt. Tzena, as part of the SAC GR1240002 and SPA GR1240007 of the Natura2000 network.

thirteen habitat types, seven are forest habitat types and five of them, 9110 (*Luzulo-Fagetum* beech forests), 9130 (*Asperulo-Fagetum* beech forests), 9150 (Medio-European limestone beech forests of the *Cephalanthero-Fagion*), 91M0 (Pannonian-Balkanic turkey oak –sessile oak forests) and 9280 (*Quercus frainetto* woods) are under consideration in this paper. The other two, 9270-Hellenic beech forests with *Abies borisii-regis* and 92C0-*Platanus orientalis* and *Liquidambar orientalis* woods (*Platanion orientalis*), cover a relatively small surface area and were not considered in the analysis. In addition to these aforementioned habitat types, a forest habitat type of national interest that includes the extended *Carpinus orientalis* and *Ostrya carpinifolia* forests has been considered. It is coded under the 4-digit code 9254 and described as "Forests of *Ostrya*, *Carpinus orientalis* and mixed thermophilous forests" (Dafis et al. 2001) (see Suppl. Material 1, Figure S1).

Data collection

To study the vegetation of Mt. Tzena, 105 relevés were recorded in beech-dominated stands and 59 relevés were recorded in thermophilous deciduous forests, i.e. pure or mixed stands of *Quercus pubescens*, *Q. petraea* subsp. *polycarpa*, *Q. frainetto*, *Carpinus orientalis* and *Ostrya carpinifolia*. The location of the relevés is shown in Figure 1. A preferential sampling was performed, as this is commonly used in phytosociological research and, in certain cases, it is preferable to randomized sampling schemes (Dengler 2016). Especially for the identification of typical species, the preferential sampling on typical localities of each vegetation unit ensures that taxa that indicate degraded conditions will not be included in the typical species inventory. Sampling size was 200 m^2 (Chytrý and Otýpková 2003). All vascular taxa were recorded in each relevé and their cover-abundance values were estimated using the extended 9-class Braun-Blanquet scale (van der Maarel 2005). All taxa were assigned to three vegetation layers: tree (>5 m), scrub (0.5-5 m) and herb (up to 0.5 m). Additionally, auxiliary variables were recorded in the field, including slope (o), elevation a.s.l. (m), total vegetation cover (%), vegetation cover at each layer (%), maximum vegetation height (m), average height of each layer (m), maximum breast-height diameter (m), and bedrock and orographic position (top, middle or bottom slope).

Vegetation analysis

To distinguish vegetation units, we applied agglomerative hierarchical clustering. Firstly, relevés were separated into two distinct vegetation data sets on the basis of species dominance: beech and thermophilous broad-leaved forests. These two main datasets reflect the two major groups of forest habitat types that occur in the study area: the temperate beech-dominated forests and the thermophilous *Quercus* spp. and *Carpinus/Ostrya* dominated forests. In each data set, we removed taxa that occur in less than 3% of the total number of plots in order to reduce the effect of rare species (McCune and Grace 2002). Plots with less than 5 taxa were also excluded, since plots with a small number of taxa are often identified as outliers in statistical analyses. Cover values of taxa appearing in more than one layer were merged. Species' cover values were square-rooted to reduce the prominent effect of dominant taxa and allow for taxa with lower cover values to affect the outputs (McCune and Grace 2002). This was decided because the different habitat types, especially beech forest, would have otherwise been identified based only on a few dominant taxa. The vegetation groups were defined by means of a hierarchical cluster analysis. We used the clustering algorithm included in the R package[1] 'cluster' (Maechler et al. 2019) using the Bray-Curtis dissimilarity matrix of the square-rooted cover values and the flexible beta as clustering method with the value a=0.625 (McCune and Grace 2002). The choice of this clustering method is based on its compatibility with the Bray-Curtis dissimilarity measure, which shows good results with vegetation data (McCune and Grace 2002). Dissimilarity matrix was calculated by means of the R package 'vegan' (Oksanen et al. 2019). An important choice in cluster analysis is the assessment of the optimum and meaningful number of clusters (groups) to be formed, and there is a variety of methods that have been proposed for that (Borcard et al. 2011; Kassambara 2017; Tavakoli et al. 2020). Among them, we decided to apply a method presented in McCune and Grace (2002) and it is considered to be well suited for vegetation data. This approach firstly defines the maximum number of clusters (fn) that can be formed running a hierarchical cluster analysis under the restriction that each cluster should include at least three plots. Then, a series of hierarchical cluster analyses is performed, gradually increasing the number of groups to be formed from n=2 to fn. For each step, the number of statistically significant indicator (differential) taxa is calculated using the 'indicspecies' package in R (De Cáceres and Legendre 2009; De Cáceres et al. 2010). The hierarchical level with the highest number of indicator taxa was then accepted as the most informative in terms of vegetation differentiation power.

Having selected the final number of clusters, we identified the diagnostic/differential taxa of vegetation units applying: (a) the multilevel analysis for the identification of indicator taxa presented in De Cáceres et al. (2010) using the group adjusted IndVal from the R package 'indicspecies' (De Cáceres and Legendre 2009; De Cáceres et al. 2010), and (b) the differential taxa applying the method presented by Tsiripidis et al. (2009). The latter was performed by means of R package 'goeveg' version 0.4.2 (Goral and Schellenberg 2018). Applying both methods allow us to take advantages of each method's features, as shown by Xystrakis (2009).

1 R scripts for the aforementioned analyses, as well as for all the analyses presented here, are available upon request.

Assignment to syntaxa

Each relevé was assigned to an already described syntaxon at the association level. We used the works of Bergmeier and Dimopoulos (2001), and of Tsiripidis et al. (2007), as the basis to assign relevés of beech forests. Similarly, the works of Bergmeier and Dimopoulos (2008) provided the basis to assign relevés of thermophilous broadleaved forests. In order to assign each relevé in a syntaxon, we adopted a similar approach with the one proposed by Tsiripidis et al. (2018) for the assignment of relevés in habitat types of the 92/43/EEC Directive. Taxa in relevés were relativized on the basis of their abundance values, i.e. abundances of taxa were divided by the sum of abundances in each relevé. Then, the phi coefficient of diagnostic/differential taxa for beech syntaxa was obtained by Tsiripidis et al. (2007) and was calculated for the diagnostic taxa identified by Bergmeier and Dimopoulos (2001) and by Bergmeier and Dimopoulos (2008). For comparison, we used the original version of the phi coefficient (Bruelheide 2000) because this version was applied by Tsiripidis et al. (2007). Having relativized the relevé data and having estimated the phi coefficients of diagnostic taxa for each syntaxon, a weighted averaging was performed using the relativized abundance values of taxa in each and every relevé in our data set, as well as the phi coefficient of every diagnostic/differential species of each syntaxon described by Bergmeier and Dimopoulos (2001), Tsiripidis et al. (2007) and by Bergmeier and Dimopoulos (2008). The sum of phi coefficients for all of the aforementioned combinations was then calculated. Each relevé was finally assigned to the syntaxon with the highest weighted averaged summary of phi coefficient. All calculations were performed in R (R Core Team 2021). Taxonomic nomenclature follows Bergmeier and Dimopoulos (2001) for beech associations, Bergmeier and Dimopoulos (2008) for thermophilous associations and Mucina et al. (2016) for syntaxa of higher rank.

Assignment to habitat types

In order to refine the typical species inventory, vegetation relevés have to be first assigned to a habitat type, or eventually to one of the vicariants of habitat types that were identified by Tsiripidis et al. (2018). The assignment was achieved through the estimation of floristic similarity of the vegetation relevés with one of the existing field-sheets that were prepared by Tsiripidis et al. (2018). Each elaborated field sheet by Tsiripidis et al. (2018) has a unique typical species inventory and each of the taxa in this inventory is attributed a mean cover-abundance class at the Braun-Blanquet scale. Therefore, each protocol can be considered as a vegetation relevé and (dis-)similarity indices can be applied. We thus estimated the similarity between each vegetation relevé and each evaluation protocol by applying the Bray-Curtis dissimilarity index, which takes into consideration the square rooted cover-abundance values of taxa. Moreover, each relevé was assigned to the habitat type protocol with the highest weighted averaged summary of phi coefficient, estimated with the same procedure that was followed in the affiliation with existing syntaxa, and which is described by Tsiripidis et al. (2018). To minimize potential errors, an initial draft elimination of habitat types that cannot possibly occur in the area took place. Analyses were performed using the R package 'vegan' (Oksanen et al. 2019). Each relevé was assigned to that habitat type reflecting the minimum dissimilarity.

Typical species inventory

To refine the typical species inventory and form site-specific evaluation protocols, we (a) narrowed down the typical taxa in the assessment protocol proposed by Tsiripidis et al. (2018) by deleting those that do not occur at the site, and (b) added to the inventory taxa of high constancy values (III-V), taxa with high indicator values (De Cáceres and Legendre 2009; De Cáceres et al. 2010; Dufrene and Legendre 1997) and taxa identified as differential by the algorithm developed by Tsiripidis et al. (2009). Taxa with high indicator values were estimated by means of the package 'indicspecies' R package (De Cáceres and Legendre 2009; De Cáceres et al. 2010) applying the method with group and without group combinations. Combining different methods to conclude over the differentiation significance of taxa allows for taking advantage of the various positive aspects of each method. To illustrate this, on the one hand the algorithm proposed by Tsiripidis et al. (2009) has a sound phytosociological background but on the other hand, indicator taxa as estimated by De Cáceres et al. (2010) take advantage of abundances, and not only presence/absence. Taxa that characterize degraded ecosystems were manually excluded from the typical species inventory, even if the analyses identified them as constant or differential.

Results and discussion

Vegetation survey resulted in 509 plant taxa in 164 relevés (see Suppl. Material 2, Table S1). Out of them, 260 taxa are found in 105 relevés of beech dominated units and 342 plant taxa are found in 59 relevés in the thermophilous deciduous broadleaved forests.

Beech dominated units

The outputs of the cluster analysis allowed for the identification of four vegetation groups in the beech dominated forests of the study area (Table 1). The sorted vegetation table of beech dominated units, in which differential species using the approaches described in the methods section is shown, can be found in Suppl. Material 3, Table S2.

Table 1. Indicator (differential) and constant species (>25% constancy) of beech-dominated forests (applying Tsiripidis et al. (2009) algorithm). Abbreviations: p= positive, n= negative differential taxa. Red-shaded cells indicates that taxa are negative differential. Green shaded cells indicate that taxa should be considered as "typical species" for the respective habitat type either because they are constant or because they are positive differential .

taxon	group 1	group 2	group 3	group 4	group 1	group 2	group 3	group 4
	indicator				constancy			
Constant taxa								
Fagus sylvatica subsp. *sylvatica*	-	-	-	-	100	100	100	100
Euphorbia amygdaloides	-	-	-	-	79	65	38	57
Lactuca muralis	-	-	-	-	57	97	59	65
Neottia nidus-avis	-	-	-	-	71	35	54	70
Poa nemoralis	-	-	-	-	100	94	97	83
Luzula sylvatica	-	-	-	-	29	19	54	39
Cystopteris fragilis	-	-	-	-	7	29	14	17
Saxifraga rotundifolia	-	-	-	-	21	35	8	26
Veronica urticifolia	-	-	-	-	7	29	5	26
Prenanthes purpurea	-	-	-	-	14	29	30	13
Abies borisii-regis	-	-	-	-	14	13	14	30
Differential taxa								
Campanula trachelium	p	n	n	n	71	16	14	0
Doronicum orientale	p	n	n	n	64	0	11	0
Galium mollugo aggr.	p	n	n	n	36	3	5	4
Galium pseudaristatum	p	n	n	n	57	0	16	0
Juniperus oxycedrus subsp. *deltoides*	p	n	n	n	36	3	3	4
Lathyrus laxiflorus	p	n	n	n	64	13	11	0
Lathyrus niger	p	n	n	n	21	0	0	0
Lathyrus venetus	p	n	n	n	50	0	3	0
Platanthera chlorantha	p	n	n	n	36	0	0	0
Primula veris	p	n	n	n	57	10	8	13
Quercus frainetto	p	n	n	n	36	3	0	0
Quercus pubescens	p	n	n	n	21	0	0	0
Rosa arvensis	p	n	n	n	64	13	3	0
Silene atropurpurea	p	n	n	n	21	0	0	0
Silene italica subsp. *italica*	p	n	n	n	50	3	5	4
Silene viridiflora	p	n	n	n	29	0	3	0
Sorbus torminalis	p	n	n	n	21	0	0	0
Trifolium pignantii	p	n	n	n	57	3	16	0
Festuca koritnicensis	p	n	n	-	21	0	0	4
Hippocrepis emerus subsp. *emeroides*	p	n	n	-	36	0	3	13
Campanula sparsa	p	n	-	n	21	0	3	0
Carex flacca subsp. *serrulata*	p	-	n	n	21	3	0	0
Cyclamen hederifolium	p	-	n	n	29	10	0	4
Dactylis glomerata subsp. *glomerata*	p	-	n	n	64	29	0	13
Potentilla micrantha	p	-	n	n	79	45	22	13
Fraxinus ornus	p	-	n	-	43	16	8	22
Silene vulgaris	p	-	n	-	29	10	3	22
Viola alba subsp. *alba*	p	-	n	-	50	23	11	17
Primula acaulis	p	-	n	n	29	19	3	0
Dioscorea communis	p	-	-	n	21	6	3	0
Poa bulbosa subsp. *bulbosa*	p	-	-	n	21	3	3	0
Sedum cepaea	p	-	-	n	21	3	5	0
Campanula persicifolia	p	n	p	n	43	3	27	0
Campanula spatulata	p	n	p	n	50	3	41	4
Festuca heterophylla	p	-	p	n	79	45	89	26
Hieracium racemosum	p	n	p	n	71	16	54	13
Luzula forsteri	p	n	p	n	93	13	54	0
Polypodium vulgare	p	-	p	n	29	19	41	0
Veronica vindobonensis	p	-	p	n	93	45	78	17
Hieracium murorum	p	n	p	p	93	16	62	52
Aremonia agrimonoides subsp. *agrimonoides*	p	p	n	p	43	48	8	48
Cephalanthera rubra	p	n	n	p	71	13	8	52
Acer hyrcanum	p	-	n	p	36	13	8	43
Sanicula europaea	p	p	n	n	36	35	0	4
Hedera helix subsp. *helix*	p	p	n	n	64	35	5	9
Brachypodium sylvaticum subsp. *sylvaticum*	p	p	n	n	21	23	0	0
Aegopodium podagraria	n	p	n	n	14	48	8	4
Anemone ranunculoides	n	p	-	n	0	42	14	0
Calamintha grandiflora	n	p	-	-	0	55	32	13
Dactylorhiza saccifera	-	p	-	n	7	29	16	0
Dryopteris filix-mas	n	p	n	n	0	52	3	13
Epilobium montanum	n	p	n	n	0	65	5	17
Galeobdolon montanum	n	p	n	n	14	77	16	13

Table 1. Continuation.

taxon	group 1	group 2	group 3	group 4	group 1	group 2	group 3	group 4
	indicator				constancy			
Geranium robertianum	n	p	n	n	0	61	8	13
Geum urbanum	n	p	n	-	0	23	0	4
Hordelymus europaeus	n	p	n	n	0	45	3	0
Moehringia trinervia	-	p	n	n	29	39	8	9
Polystichum aculeatum	n	p	n	-	0	26	0	4
Pteridium aquilinum	-	p	-	n	36	45	35	9
Pulmonaria rubra	n	p	n	n	7	42	0	0
Rubus hirtus	n	p	n	n	7	77	14	0
Salvia glutinosa	n	p	-	-	0	23	3	4
Scilla subnivalis	-	p	n	n	21	42	11	4
Symphytum tuberosum subsp. *angustifolium*	n	p	-	n	7	48	27	9
Urtica dioica	n	p	n	n	0	23	0	0
Viola reichenbachiana/riviniana	-	p	-	n	36	61	32	13
Cardamine bulbifera	n	p	p	n	7	71	38	0
Galium odoratum	n	p	p	n	0	65	30	0
Melica uniflora	-	p	p	n	14	42	38	9
Lilium martagon	-	p	n	p	14	32	5	39
Avenella flexuosa	n	-	p	-	0	13	22	9
Hypopitys monotropa	-	-	p	n	14	3	22	0
Luzula luzuloides subsp. *luzuloides*	n	-	p	n	14	29	57	9
Arabis turrita	-	n	n	p	21	13	3	48
Carex digitata	n	-	-	p	7	13	11	39
Cotoneaster nebrodensis	n	n	n	p	0	0	0	26
Doronicum columnae	n	-	n	p	0	19	3	35
Orthilia secunda	n	n	-	p	0	0	11	30
Polygonatum odoratum	-	-	n	p	14	6	3	26
Rosa villosa	n	n	n	p	0	0	0	30
Rubus idaeus	n	-	n	p	0	19	0	26
Sesleria robusta	-	n	-	p	29	0	11	52
Solidago virgaurea	-	n	-	p	21	6	16	39
Sorbus aria	-	n	n	p	7	3	0	26
Sorbus X thuringiaca	n	n	n	p	0	0	0	22

The assignment of the relevés to the syntaxa (units) that are described by Tsiripidis et al. (2007) and by Bergmeier and Dimopoulos (2001) for beech forests is shown in Table 2.

The site characteristics of the relevés forming each group are shown in Figure 2.

Group 1 is associated with vegetation units that are characterized by thermophilous species (Table 1 and Table 2). Relevés of this group are not clearly associated with a single vegetation unit from those described by Tsiripidis et al. (2007). They are distributed between units 14-thermophytic beech forests of Mt. Cholomon, in the south-western part of NE Greece and 11-forests on calcareous substrate at lower elevations (subcom. with *Fraxinus ornus* of the *Lathyro alpestris-Fagetum sylvaticae*). In contrast, relevés of this group are tightly associated with unit 13-Rubus canescens-Fagus sylvatica comm. described by Bergmeier and Dimopoulos (2001) of the alliance *Geranio striati-Fagion* Gentile 1970 of the order *Fagetalia sylvaticae* Pawłowski 1928 of the class *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968.

Among the indicator species of this group, taxa of the alliance *Quercion frainetto* such as *Primula veris*, *Quercus frainetto*, *Trifolium pignantii* are in abundance. Furthermore, it can be observed that relevés of this group occur in the lowest elevational zone of the examined *Fagus* forests (Figure 2). Thus, the assignment of all relevés of group 1 to the habitat type 9280 (*Quercus frainetto* woods) is expected. This habitat type includes the thermophilous beech forests appearing in the transition between *Fagus*- and *Quercus*-dominated forests and are characterized by significant presence of *Quercion frainetto* species (Dafis et al. 2001). The updated typical species inventory of habitat type 9280 that includes constant and differential species of this group is shown in Suppl. Material 4, Table S3

Group 2 Group 2 is related to unit 7 of Tsiripidis et al. (2007) which includes the association Lamiastro montani-Fagetum sylvaticae Bergmeier et Dimopoulos 2001 of the alliance Fagion sylvaticae Luquet 1926, of the order Fagetalia sylvaticae Pawłowski 1928 of the class Carpino-Fagetea sylvaticae Jakucs ex Passarge 1968. This association includes the mesophilous beech forests of Mt. Tzena and Mt. Voras, growing on moist, nutrient-rich soils. Tree height in these relevés is considerably high, when compared to other groups (Figure 2).

Relevés of this group should be included in the habitat type 9130 (Asperulo fagetum beech forests) (European Commission 2013). This habitat type includes beech forest at considerably high elevation on neutral or near-neutral soils with mild mull-type humus that form a considerably rich herb layer (European Commission 2013). Seven relevés from this group are assigned to habitat type 9280, indicating the relatively thermophilous character of this group as well. The updated typical species inventory of habitat

Table 2. Number of relevés of beech dominated forests assigned to each syntaxonomic unit described by Tsiripidis et al. (2007) and by Bergmeier and Dimopoulos (2001). Green-shaded cells indicate the cumulative assignment of more than 50% of relevés in each group.

	Number of relevés			
Unit (Tsiripidis et al. 2007)	**group 1**	**group 2**	**group 3**	**group 4**
u2: mesophytic beech forests of NE Greece	.	.	2	1
u3: acidophytic forests (on gneiss) of NE Greece	.	.	1	.
u7: mesophytic beech forests of Mt. Voras on humid nutrient-rich soils (*Lamiastro montani-Fagetum sylvaticae*)	.	18	5	2
u8: forests of Mt. Voras occurring in warmer and drier sites (*Galium odoratum-Fagus sylvatica*)	.	.	4	2
u10: forests on calcareous substrate at high elevations (*Cardamine graeca-Fagus sylvatica*)	.	2	4	6
u11: Forests on calcareous substrate at lower altitudes (subcom. with *Fraxinus ornus* of the *Lathyro alpestris-Fagetum sylvaticae*)	5	9	6	11
u12: *Lathyro alpestris-Fagetum sylvaticae*	2	1	13	1
u13: thermophytic beech forests of Mt. Chortiatis (southwestern part of NE Greece) (*Rubus canescens-Fagus sylvatica*)	.	.	1	.
u14: thermophytic beech forests of Mt. Cholomon (southwestern part of NE Greece)	7	1	1	.
sum	**14**	**31**	**37**	**23**
Unit (Bergmeir and Dimopoulos 2001)	**group 1**	**group 2**	**group 3**	**group 4**
u2: *Galium odoratum-Fagus sylvatica* comm.	.	.	1	.
u3: *Lamiastro montani-Fagetum sylvaticae*	.	20	4	3
u5: *Orthilio secundae-Fagetum* (subcom. with *Luzula luzuloides*)	2	3	23	16
u6: *Orthilio secundae-Fagetum* (subcom. with *Abies borisii-regis*)	.	.	.	1
u11: *Lathyro alpestris-Fagetum sylvaticae* (subcom. with *Galium odoratum*)	2	5	2	3
u13: *Rubus canescens-Fagus sylvatica* comm.	10	3	7	.
sum	**14**	**31**	**37**	**23**

type 9130 that includes constant and differential species of this group is shown in Suppl. Material 4, Table S3. *Urtica dioica* has been removed from the typical species inventory of habitat type 9130 because it is often associated with degraded habitats.

Group 3 is a large, rather heterogeneous group. It consists of 37 relevés, the majority of which (36) occurs on siliceous bedrock. It reflects an intermediate character between cool and warm habitats. Relevés of this group are associated with various units described by Tsiripidis et al. (2007), but their majority is associated with units 12 and 11 (units of the *Lathyro alpestris-Fagetum sylvaticae*) (Table 2). On the other hand, when units by Bergmeier and Dimopoulos (2001) are considered, this group shows tight affiliation with the *Orthilio secundae-Fagetum* (subcom. with *Luzula luzuloides*). The latter unit includes beech forests of north central Greece on acidic bedrock, which are characterized by the presence of species like *Avenella flexuosa* and *Luzula luzuloides*. These two taxa have also been identified as indicators of this group in our data set (Table 1). Based on the tighter and clearer relation of this group with the association *Orthilio secundae-Fagetum* Bergmeier 1990, we propose the inclusion of our relevés to this association. This association belongs to the alliance *Fagion sylvaticae* Luquet 1926 of the order *Fagetalia sylvaticae* Pawłowski 1928 of the class *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968. Forests of the *Orthilio secundae-Fagetum* often border and form transitional communities with the acidophilous vicariants of *Lathyro alpestris-Fagetum* which generally occur at lower elevations than the former alliance (Bergmeier and Dimopoulos 2001). This could explain the observed similarity with

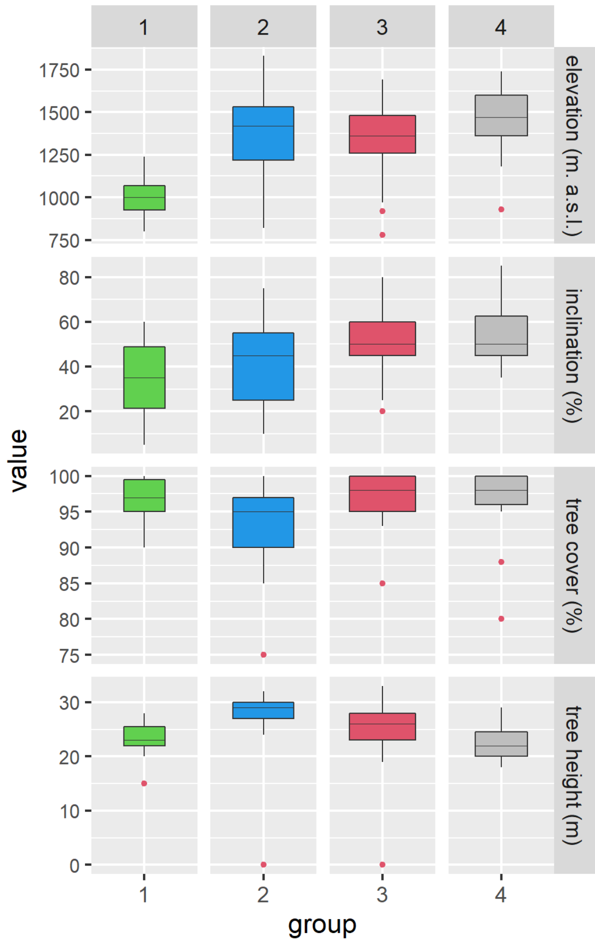

Figure 2. Site characteristics of the identified groups of the *Fagus* forests. Abbreviations: a.s.l. = above sea level.

the *Lathyro alpestris* units described by Tsiripidis et al. (2007).

Likewise in group 1 and group 2, a considerable number of relevés are similar to habitat type 9280, which includes beech forests with a significant presence of floristic elements of the alliance *Quercion frainetto* (Dafis et al. 2001; European Commission 2013). Nevertheless, some of the most characteristic species of the *Quercion frainetto* forests like *Quercus frainetto* or *Q. pubescens* are negative differential of group 3 (Table 1). Therefore, we preferred to assign this group to the habitat 9110 (*Luzulo-Fagetum* beech forests) because (a) a significant percentage of relevés of this group (38%) is assigned to the habitat type 9110 that includes mountainous acidophilous beech forest of Greece, (b) stands of the association *Ortillio secundae-Fagetum* Bergmeier 1990, in which the relevés of this group are assigned, are included in this habitat (Dafis et al. 2001). The updated typical species inventory of habitat type 9110 that includes constant and differential species of this group is shown in Suppl. Material 4, Table S3.

Group 4 consists of 23 relevés, the majority of them being located on calcareous substrate. It is strongly affiliated with units 10-forests on calcareous substrate at high elevations (*Cardamine graeca-Fagus sylvatica*) and 11-forests on calcareous substrate at lower elevations (subcom. with *Fraxinus ornus* of the *Lathyro alpestris-Fagetum sylvaticae*)) of Tsiripidis et al. (2007) (Table 2). Interestingly, it is associated with the acidophilous unit 5-*Orthilio secundae-Fagetum* (subcom. with *Luzula luzuloides*) described by Bergmeier and Dimopoulos (2001). Among the indicator species of group 4, some calcicolous taxa like *Arabis collina*, *Cotoneaster nebrodensis*, *Euonymus verrucosus* and *Carex humilis* are found. This demonstrates that group 4 is differentiated by calcicolous plant taxa. Nevertheless, units 10 and 11 by Tsiripidis et al. (2007) are vegetation units that are endemic to Mt. Olympus, corresponding to the *Cardamine graeca-Fagus sylvatica* community by Bergmeier and Dimopoulos (2001). The latter mostly includes the calcareous beech forests in the association *Lathyro alpestris-Fagetum sylvaticae* Bergmeier 1990. It is argued here that the calcicolous beech forests of north central Greece are understudied from a phytosociological perspective and further research is required. The assignment of the relevés of group 4 to an association should be a result of a broader research including relevés from extended geographical regions that will include adjacent mountain ranges.

The majority of the relevés of this group are associated with the habitat types 9150 (Medio-European limestone beech forests of the *Cephalanthero-Fagion*) that include a large part of beech forests developing on calcareous substrates in Greece (Dafis et al. 2001). The updated typical species inventory of this habitat type that includes constant and differential species of this group is shown in Suppl. Material 4, Table S3.

Comparing the updated typical species inventories with the respective inventories presented in the original protocols, it is made obvious that substantial changes took place. Out of 29 typical species in the existing evaluation protocol of the habitat type 9110, only 11 are also included in the new inventory, which counts 26 taxa. Regarding habitat type 9130, out of 36 species, 19 are also present in the updated protocol (in these taxa *Urtica dioica* is also included). Thirty-five taxa are considered as new addition to the updated inventory. Regarding habitat type 9150, 16 out of 44 taxa of the existing evaluation protocol are considered in the updated inventory while 20 more taxa have been included additionally. Finally, in habitat type 9280, 31 out of 53 taxa are included in the updated inventory while 28 new taxa are added. These changes are mostly related to the extended sampling that took place in this NATURA 2000 area. The existing typical species inventories were compiled using a limited number of relevés from each NATURA 2000 site.

Thermophilous deciduous broadleaved forests

The outputs of the cluster analysis justified the acceptance of three groups in the data set that includes the relevés dominated by thermophilous deciduous broadleaved species (Table 3). The sorted vegetation table of the thermophilous deciduous broadleaved forests, in which differential species using the approaches described in the methods section is shown, can be found in Suppl. Material 5, Table S5.

These three groups correspond to the i) *Ostrya carpinifolia-Carpinus orientalis-Quercus pubescens*, ii) *Quercus pubescens-Carpinus orientalis*, and iii) *Quercus frainetto* and *Q. petraea* forest formations respectively. The assignment of the relevés to the syntaxa (units) identified in Greece by Bergmeier and Dimopoulos (2008) for the thermophilous deciduous forests is shown in Table 4.

In terms of site characteristics (Figure 3), the identified groups show a clear gradient in tree height and cover of the tree layer. There is a remarkable homogeneity regarding the cover of the tree layer and slope's inclination in group 3. In contrast, values of elevation, tree cover for group 1 and of slope inclination in group 2 reflect high variability.

Group 1 consists of *Ostrya carpinifolia-Carpinus orientalis* mixed stands, with the former taxon being rather dominant in most relevés. *Quercus pubescens* is a constant species in this group, but it participates in the tree cover with considerably low values. Relevés of this group are assigned to the *Dryopterido pallidae–Ostryetum carpinifoliae* Bergmeier 1990 association (Bergmeier and Dimopoulos 2008) of the *Carpinion orientalis* Horvat 1958 alliance. This alliance includes the low-elevation calcareous thermophilous oak and oriental hornbeam forests (Mucina et al. 2016). This alliance belongs to the *Quercetalia pubescenti-petraeae* Klika 1933 order of the *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959 class. Bergmeier and Dimopoulos (2008) consider this alliance to be synonym with *Fraxino orni-Ostryion* but Čarni et

Table 3. Indicator (differential) and constant species of thermophilous deciduous broadleaved forests (applying Tsiripidis et al. (2009) algorithm). Abbreviations: p= positive, n= negative differential taxa. Red-shaded cells indicates that taxa are negative differential. Green shaded cells indicate that taxa should be considered as "typical species" for the respective habitat type either because they are constant or because they are positive differential .

	group 1	group 2 indicator	group 3	group 1	group 2 constancy	group 3
Constant taxa						
Asplenium ceterach	-	-	-	41	16	17
Hypericum perforatum	-	-	-	36	16	17
Pilosella piloselloides/bauhini	-	-	-	27	11	11
Thymus longicaulis/sibthorpii	-	-	-	45	16	17
Acer hyrcanum	-	-	-	73	95	67
Arabis turrita	-	-	-	77	89	56
Brachypodium sylvaticum subsp. *sylvaticum*	-	-	-	82	42	44
Carex flacca subsp. *serrulata*	-	-	-	59	89	61
Carpinus orientalis	-	-	-	86	89	44
Cephalanthera longifolia	-	-	-	50	32	72
Cephalaria flava	-	-	-	27	53	28
Clinopodium vulgare subsp. *orientale*	-	-	-	86	74	72
Cyclamen hederifolium	-	-	-	50	53	33
Dactylis glomerata subsp. *glomerata*	-	-	-	82	89	100
Dioscorea communis	-	-	-	41	42	56
Euphorbia amygdaloides	-	-	-	59	89	72
Fagus sylvatica subsp. *sylvatica*	-	-	-	45	32	78
Festuca valesiaca	-	-	-	41	37	61
Fraxinus ornus	-	-	-	100	95	83
Juniperus oxycedrus subsp. *deltoides*	-	-	-	86	95	89
Physospermum cornubiense	-	-	-	27	26	39
Potentilla micrantha	-	-	-	55	68	89
Primula veris	-	-	-	32	63	33
Prunus divaricata	-	-	-	41	26	44
Rosa arvensis	-	-	-	59	63	44
Scorzoneroides cichoriacea	-	-	-	41	63	44
Silene italica subsp. *italica*	-	-	-	77	74	94
Veronica vindobonensis	-	-	-	50	47	89
Viola alba subsp. *alba*	-	-	-	91	84	50
Arabis sagittata	-	-	-	27	32	17
Cornus mas	-	-	-	45	53	17
Festuca koritnicensis	-	-	-	41	47	17
Cardamine graeca	-	-	-	36	21	33
Galium aparine	-	-	-	55	21	44
Rosa canina/corymbifera	-	-	-	27	11	33
Muscari neglectum	-	-	-	32	26	17
Anthoxanthum aristatum	-	-	-	5	11	28
Quercus petraea subsp. *polycarpa*	-	-	-	18	11	28
Campanula trachelium	-	-	-	14	37	17
Lithospermum purpurocaeruleum	-	-	-	18	47	17
Sorbus torminalis	-	-	-	23	47	33
Neottia nidus-avis	-	-	-	14	5	28
Pteridium aquilinum	-	-	-	23	16	44
Rubus sanctus	-	-	-	23	11	28
Verbascum xanthophoeniceum	-	-	-	14	5	28
Differential taxa						
Ostrya carpinifolia	p	-	n	91	42	28
Asplenium trichomanes	p	n	-	50	5	28
Clematis vitalba	p	n	n	73	16	17
Ruscus aculeatus	p	-	n	41	16	6
Poa bulbosa subsp. *bulbosa*	p	n	-	36	5	22
Hieracium murorum	p	n	-	32	5	22
Asplenium onopteris/adiantum-nigrum	p	n	n	55	0	17
Medicago sativa subsp. *falcata*	p	-	n	27	11	0
Viola reichenbachiana/riviniana	p	n	n	32	0	0
Achillea holosericea	p	-	n	23	11	0
Solidago virgaurea	p	n	-	27	0	6
Hedera helix subsp. *helix*	p	n	p	41	0	33
Aremonia agrimonoides subsp. *agrimonoides*	p	n	p	68	11	44
Quercus pubescens	p	p	n	95	100	33
Teucrium chamaedrys subsp. *chamaedrys*	p	p	n	82	95	28
Sesleria robusta	p	p	n	41	58	6
Asperula purpurea	p	p	n	50	32	6
Carex halleriana	p	p	n	27	58	0
Euonymus verrucosus	p	p	n	36	37	0
Hippocrepis emerus subsp. *emeroides*	p	p	n	59	79	11

Table 3. Continuation.

	group 1	group 2 indicator	group 3	group 1	group 2 constancy	group 3
Trifolium alpestre	n	p	-	27	89	72
Galium mollugo aggr.	N	p	-	27	79	39
Centaurea napulifera	-	p	n	36	74	22
Orlaya daucoides	-	p	n	18	47	11
Origanum vulgare subsp. *vulgare*	-	p	n	18	42	11
Geranium sanguineum	n	p	n	5	74	11
Festuca hirtovaginata s.l.	-	p	n	18	37	6
Polygonatum odoratum	-	p	n	14	42	6
Veronica jacquinii	n	p	n	9	47	0
Campanula persicifolia	n	p	n	9	42	6
Inula conyzae	-	p	n	18	32	6
Campanula bononiensis	n	p	n	5	47	0
Tanacetum corymbosum	n	p	-	0	37	11
Calamintha nepeta	-	p	n	14	26	0
Astragalus monspessulanus	-	p	n	18	21	0
Sorbus aria	-	p	n	18	21	0
Sorbus aucuparia	n	p	-	0	26	17
Thalictrum minus subsp. *saxatile*	n	p	n	5	37	0
Erysimum cuspidatum	-	p	n	14	21	0
Lamium garganicum	-	p	n	5	21	0
Achnatherum bromoides	-	p	n	5	21	0
Allium macedonicum	-	p	n	5	21	0
Linum flavum subsp. *albanicum*	n	p	n	0	21	0
Brachypodium pinnatum	n	p	p	18	84	56
Vicia tenuifolia subsp. *dalmatica*	n	p	p	0	21	44
Chamaecytisus hirsutus	n	-	p	9	32	44
Festuca heterophylla	n	n	p	14	11	56
Geum urbanum	n	-	p	9	21	39
Galium pseudaristatum	-	n	p	18	0	50
Trifolium ochroleucon	n	n	p	5	11	44
Cephalanthera rubra	-	n	p	14	5	39
Silene viridiflora	n	n	p	0	11	44
Silene coronaria	n	n	p	0	5	50
Sedum cepaea	n	n	p	5	0	50
Lathyrus pratensis	n	n	p	0	5	44
Epipactis helleborine	n	-	p	0	11	39
Digitalis grandiflora	n	-	p	0	11	39
Anthemis tinctoria	n	-	p	0	16	28
Genista carinalis	-	n	p	14	0	28
Scutellaria columnae	n	n	p	5	0	39
Lathyrus niger	n	n	p	0	0	39
Verbascum nigrum subsp. *abietinum*	n	-	p	0	16	22
Hieracium lachenalii	n	-	p	0	5	28
Pilosella leucopsilon	-	n	p	5	0	22
Hieracium umbrosum	n	n	p	0	0	28
Silene atropurpurea	-	n	p	5	0	22
Vicia grandiflora	n	n	p	0	0	22
Poa nemoralis	-	n	p	59	37	100
Campanula spatulata	-	n	p	59	26	83
Luzula forsteri	-	n	p	41	26	94
Trifolium pignantii	n	n	p	27	16	78
Quercus frainetto	n	n	p	9	5	83
Rubus canescens	-	n	p	27	11	56
Lathyrus laxiflorus	n	n	p	18	11	61
Hieracium racemosum	-	n	p	18	5	39

al. (2009), Mucina et al. (2016) and Škvorc et al. (2017) treat these two alliances distinctly. Both alliances occur in the eastern Mediterranean region, and their distinction is mostly based on the fact that *Fraxino orni-Ostryion* has a more (sub)Mediterranean character than *Carpinion orientalis*, which is characterized by the abundance of heliophilous, montane-Mediterranean taxa (Čarni et al. 2009). Despite this, Bergmeier and Dimopoulos (2008) provide extensive argumentation against the use of macroclimatic gradients for the characterization of the thermophilous deciduous forest vegetation of Greece. One can argue that the presence of *Ostrya carpinifolia* is indicative of a submontane character, but the fact that (a) *Quercus pubescens* is also a positive differential of group 1 (Table 3), and (b) group 1 is characterized by a considerably open canopy and trees of low height (Figure 3), an indication of marginal conditions of dry and poor sites, allows for the inclusion of this group in the *Carpinion orientalis* Horvat

Table 4. Number of relevés ssigned to each syntaxonomic unit of thermophilous deciduous forests (Bergmeier and Dimopoulos 2008). Green-Shaded cells indicate the cumulative assignment of more than 50% of relevés in each group.

Association	Number of relevés group 1	group 2	group 3
DrO: *Dryopterido pallidae-Ostryetum carpinifoliae*	21	19	2
DiQ: *Digitali viridiflorae-Quercetum frainetto*	-	-	8*
GQp: *Genisto carinalis-Quercetum petraeae*	-	-	3
VeQ: *Verbasco glabrati-Quercetum frainetto*	-	-	5
TiC: *Tilio tomentosae-Castanetum*	1	-	-
sum	**22**	**19**	**18**

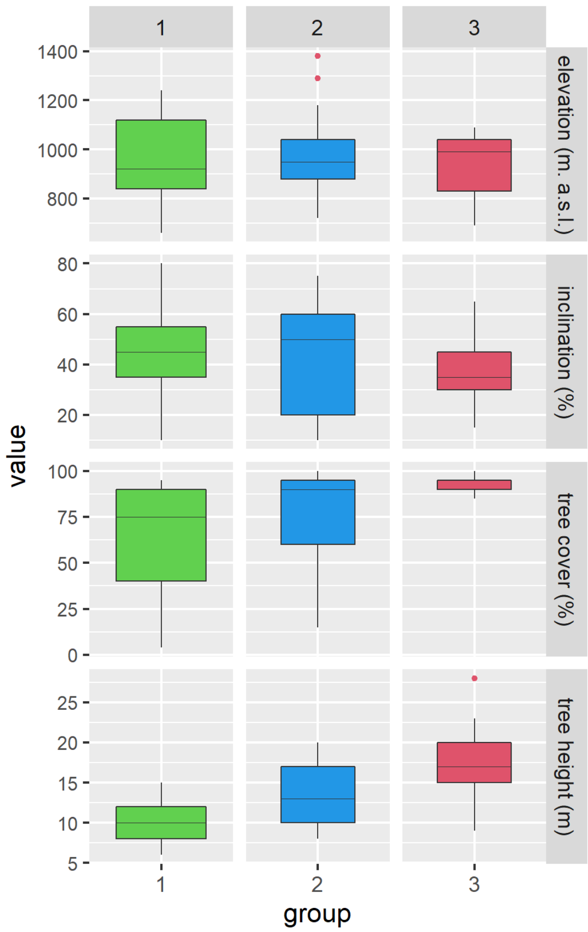

Figure 3. Ecological characteristics of the identified groups of the thermophilous broadleaved deciduous forests. Abbreviations: a.s.l. = above sea level.

1958 alliance (Mucina et al. 2016) with the strict sense. In any case, there is a clear need for a syntaxonomical revision of the thermophilous deciduous forests in the southern Balkan peninsula. The work of Bergmeier and Dimopoulos (2008) can form the basis for the classification, but it must be further ameliorated by new data from additional studies. These include data from local research (Gerasimidis and Korakis 2005; Korakis 2003) or data sets covering broader geographical areas (e.g. (Čarni et al. 2009; Stupar 2016).

Relevés of group 1 should be included in the habitat type 925A (forests of *Ostrya*, *Carpinus orientalis* and mixed thermophilous forests) (Dafis et al. 2001). This is a habitat type of national interest that includes forests of *Carpinion orientalis* dominated by *Carpinus* spp. and *Ostrya carpinifolia*. Since it is not a habitat type of community interest, an inventory of typical species does not exist, therefore the typical species shown in Suppl. Material 4, Table S4 is the first attempt to create one.

Group 2 has a similar character with group 1, but *Quercus pubescens* is rather dominant when compared with *Carpinus orientalis* and *Ostrya carpinifolia*, with the latter having low cover values (<3) in all relevés but three. Relevés of this group are assigned to the *Dryopterido pallidae-Ostryetum* association Bergmeier 1990 (Bergmeier and Dimopoulos 2008) of the *Carpinion orientalis* Horvat 1958. The inclusion of relevés of group 2 in the *Carpinion orientalis* (Mucina et al. 2016), in the strict sense, is even clearer when compared with relevés of group 1.

Relevés of group 2 should be included in the habitat type 91M0 (Pannonian-Balkanic turkey oak- sessile oak forests) due to the relative dominance of *Quercus pubescens*. Habitat type 91M0 has replaced the habitat type 924A-eastern Mediterranean and Balkan thermophilous oak-dominated forests (Dimopoulos et al. 2018). This habitat type included all Greek deciduous *Quercus* spp. formations with the exception of the (a) *Quercus trojana* subsp. *trojana* formations which are included in habitat type 9250 - *Quercus trojana* woods, (b) *Quercus ithaburensis* formations which are included in the habitat type 9350 - *Quercus macrolepis* forests, and (c) *Quercus brachyphylla* formations that are often associated with *Q. macrolepis* or *Q. ilex* in the Aegean islands which are included in the 9310 - Aegean *Quercus brachyphylla* forests (Dafis et al. 2001; European Commission 2013). The latter needs a critical revision because it is associated with *Quercus brachyphylla* Kotschy, which is a synonym for *Q. pubescens* Willd. There is a need to examine floristic and ecological differentiation between the 9310 and the *Quercus pubescens* dominated vicariants of 91M0 habitat type. Nevertheless, such a comparison is not within the scope of this paper.

The updated inventory of typical species that includes differential and constant taxa of group 2 is shown in Suppl. Material 4, Table S4. This should be considered as the typical species of the habitat type 91M0 (*Quercus pubescens* vicariant).

Group 3 is clearly differentiated from the previous group. Quercus petraea subsp. polycarpa and *Q. frainetto* dominate the canopy and it is differentiated by a large number of taxa. When *Q. petraea* subsp. *polycarpa* dominates, relevés of this group are assigned to the *Genisto carinalis-Quercetum petraeae*. When *Q. frainetto* dominates, relevés of this group are assigned to the *Verbasco glabrati-Quercetum frainetto* Gamisans et Hebrard 1979, *Huetio cynapioidis-Quercetum frainetto* Raus ex Raus Bergmeir 2008, or the *Digitali viridiflorae-Quercetum frainetto* Gamisans et Hebrard 1980 associations (Table 4). We decided to affiliate relevés of group 3 to the association *Verbasco glabrati-Quercetum frainetto* Gamisans et Hebrard 1979 on the basis of its already recorded presence in the area by Bergmeier and Dimopoulos (2008). This association belongs to the alliance *Quercion confertae* Horvat 1958 of the class *Quercetalia pubescenti-petraeae* Klika 1933 of the order *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959. Nevertheless, there should be a critical analysis in order to eventually conclude over the presence of the association *Digitali viridiflorae-Quercetum frainetto* Gamisans et Hebrard 1980 in the area due to the large number of relevés from this study that are associated with this association. There is only one relevé which is assigned to the association *Huetio cynapioidis-Quercetum frainetto* Bergmeier et Dimopoulos 2008, probably due to the considerably high cover of *Fagus sylvatica* subsp. *sylvatica* and the accordingly low cover of *Q. frainetto* in the canopy. The geographical distribution (eastern Thessaly in central Greece in south-central Greece) and the ecological characteristics (pasture woods) of this association (Bergmeier and Dimopoulos 2008; Samaras et al. 2021) do not justify its occurrence in the area, therefore this relevé should be eventually assigned to the association *Digitali viridiflorae-Quercetum frainetto* Gamisans et Hebrard 1980, which is the syntaxon with the second largest sum of fidelity values for this plot.

Relevés of group 3 should be included in the habitat type 91M0 (Pannonian-Balkanic turkey oak- sessile oak forests), but a distinct vicariant of the *Quercus frainetto-Quercus petraea* subsp. *polycarpa* dominated formations should be formed. The updated inventory of typical species is shown in Suppl. Material 4, Table S4.

Since there is not an existing evaluation protocols for the habitat type 925A or the two vicariants of the 91M0 habitat type for the area, it is not possible to perform any comparisons with existing typical species inventories.

Conclusions

In this paper, we present a thorough methodology that aims to directly bridge some evaluation criteria of the conservation status of habitat types with the phytosociological background of description of habitat types in the 92/43/EEC Directive. Beginning with preferential data sampling, phytosociological analysis of relevés, and concrete, reproducible rules, we provided typical species inventories for all the forest habitat types that occur on Mt. Tzena in Greece. The preferential sampling ensured that degraded localities were avoided, thus typical species did not include differential or indicator taxa of disturbed sites. The latter is among the main properties of typical species. The numerical analyses are reproducible, repeatable in other sites and require data that are typically collected during standard phytosociological studies. The choice of constant and diagnostic/differential species ensures that the defined typical species are directly related with the habitat types, which is yet another important property of typical species. The method we proposed does not address the final property of typical species, which requires that typical species are sensitive to changes of habitat conditions. This can be addressed by considering specific structures that are related to the presence of specific taxa or groups of taxa. The criterion 'structures and functions' can include parameters that are directly related with the occurrence and cover of targeted species that indicate changes of the condition of the habitat. For example, Tsiripidis et al (2018) propose to record the occurrence of invasive or ruderal species as a distinct structural parameter, alongside the occurrence and cover of typical species.

Moreover, this method can be performed at various spatial scales. Large, national data sets can provide typical species inventories of wider regions that share similar phytogeographical conditions, provided that there is a balanced sampling. Typical species inventories that are compiled for wider phytogeographical regions allow for the consideration of 'dark diversity' species (Dalle Fratte et al. 2022), i.e. species that are expected to occur in the area but are not (yet) found. On the other hand, at the local scale, compilation of typical species inventories allows for the assessment of vicariants of habitat types that are rare and underrepresented in wider data sets. The outputs include typical species inventories that consist of taxa which are constant and highly probable to be observed in the field by evaluators, as well from taxa that differentiate each habitat type. Moreover, this method allows for the compilation of typical species inventories for habitat types that are not included in the Habitats Directive. These inventories will facilitate the responsible authorities for the optimal implementation of the 92/43/EEC Directive.

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Author contributions

F.X.: Conceptualization, data analysis, manuscript writing; M.C.: Conceptualization, data collection, data analysis, manuscript proof reading; E.E., D.S and K.T.: Conceptualization, manuscript proof reading.

Bibliography

Angelini P, Chiarucci A, Nascimbene J, Cerabolini BE, Dalle Fratte M, Casella L (2018) Plant assemblages and conservation status of habitats of Community interest (Directive 92/43/EEC): definitions and concepts. Ecological Questions 29: 87–97. https://doi.org/10.12775/EQ.2018.025

Attorre F, Pignatti S, Spada F, Casella L, Agrillo E (2018) Introduction: Vegetation science and the Habitats Directive: approaches and methodologies of a never-ending story. Rendiconti Lincei 29: 233–235. https://doi.org/10.1007/s12210-018-0716-5

Beck HE, Zimmermann NE, McVicar TR, Vergopolan N, Berg A, Wood EF (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific Data 5: 180214. https://doi.org/10.1038/sdata.2018.214

Bendali F, Godron M (2021) Non-inferential probabilistic method for designing typical species of northern Greece oak forest Natura 2000 habitat types. International Journal of Innovation and Applied Studies 32: 15-23.

Bergmeier E, Dimopoulos P (2001) *Fagus sylvatica* forest vegetation in Greece: Syntaxonomy and gradient analysis. Journal of vegetation science 21: 109–126. https://doi.org/10.1111/j.1654-1103.2001.tb02622.x

Bergmeier E, Dimopoulos P (2008) Identifying plant communities of thermophilous deciduous forest in Greece: Species composition, distribution, ecology and syntaxonomy. Plant Biosystems 142: 228–254. https://doi.org/10.1080/11263500802150357

Biondi E (2011) Phytosociology today: Methodological and conceptual evolution. Plant Biosystems 145: 19–29. https://doi.org/10.1080/11263504.2011.602748

Biondi E, Burrascano S, Casavecchia S, Copiz R, Del Vico E, Galdenzi D, Gigante D, Lasen C, Spampinato G, Venanzoni R, Zivkovic L, Blasi C (2012) Diagnosis and syntaxonomic interpretation of Annex I Habitats (Dir. 92/43/EEC) in Italy at the alliance level. Plant Sociology 49: 5–37. https://doi.org/10.7338/pls2012491/01

Biserkov VE-i-C, Gussev CDE-i-C, Popov V, Hibaum G, Roussakova V, Pandurski I, Uzunov Y, Dimitrov M, Tzonev R, Tsoneva SME (Eds) (2015) Red Data Book of the Republic of Bulgaria. Volume 3: Natural habitats. BAS & MoEW, Sofia, Bulgaria, 422 pp.

Blasi C, Burrascano S (2013) The role of plant sociology in the study and management of European forest ecosystems. iForest - Biogeosciences and Forestry 6: 55–58. https://doi.org/10.3832/ifor0913-006

Bonari G, Acosta ATR, Angiolini C (2018) EU priority habitats: rethinking Mediterranean coastal pine forests. Rendiconti Lincei Scienze Fisiche e Naturali 29: 295–307. https://doi.org/10.1007/s12210-018-0684-9

Bonari G, Fantinato E, Lazzaro L, Sperandii MG, Acosta ATR, Allegrezza M, Assini S, Caccianiga M, Di Cecco V, Frattaroli A (2021) Shedding light on typical species: implications for habitat monitoring. Plant Sociology 58: 157–166. https://doi.org/10.3897/pls2020581/08

Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. Springer, on-line version. 306 pp. https://doi.org/10.1007/978-1-4419-7976-6

Bruelheide H (2000) A new measure of fidelity and its application to defining species groups. Journal of vegetation science 11: 167–178. https://doi.org/10.2307/3236796

Čarni A, Košir P, Karadžić B, Matevski V, Redžić S, Škvorc Ž (2009) Thermophilous deciduous forests in Southeastern Europe. Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 143: 1–13. https://doi.org/10.1080/11263500802633881

Chasapis M, Samaras DA, Theodoropoulos K, Eleftheriadou E (2020) The vascular flora of Mt Tzena (northern Greece). Flora Mediterranea 30: 55–63. https://doi.org/10.7320/FlMedit30.055

Chasapis M, Theodoropoulos K, Eleftheriadou E (2013) Vegetation mapping of Mt.Tzena (N. Greece) [in Greek]. 16th Panhellenic Forestry Conference. Hellenic Forestry Society, Thessaloniki, Greece, 21–29 pp.

Chytrý M, Kučera T, Kočí M, Grulich V, Lustyk P (Eds) (2010) Katalog biotopů České republiky. Agentura ochrany přírody a krajiny ČR Praha, 445 pp.

Chytrý M, Otýpková Z (2003) Plot sizes used for phytosociological sampling of European vegetation. Journal of vegetation science 14: 563–570. https://doi.org/10.1111/j.1654-1103.2003.tb02183.x

Chytrý M, Tichý L, Hennekens SM, Knollová I, Janssen JAM, Rodwell JS, et al. (2020) EUNIS Habitat Classification: Expert system, characteristic species combinations and distribution maps of European habitats. Applied Vegetation Science 23: 648-675. https://doi.org/10.1111/avsc.12519

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of vegetation science 13: 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Dalle Fratte M, Caccianiga M, Ricotta C, Cerabolini BEL (2022) Identifying typical and early warning species by the combination of functional-based diagnostic species and dark diversity. Biodiversity and Conservation 31: 1735–1753. https://doi.org/10.1007/s10531-022-02427-4

Dafis S, Papastergiadou E, Lazaridou E, Tsiafouli M (2001) Technical manual for the interpretation, description and mapping of habitat types of Greece [in Greek]. Greek Biotope/Wetland Centre, Thessaloniki, Greece, 393 pp.

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90: 3566–3574. https://doi.org/10.1890/08-1823.1

De Cáceres M, Legendre P, Moretti M (2010) Improving indicator species analysis by combining groups of sites. Oikos 119: 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x

Dengler J (2016) Phytosociology. In: Richardson D, Castree N, Goodchild MF, Kobayashi A, Liu W, Marston RA (Eds) International Encyclopedia of Geography: People, the Earth, Environment and Technology: People, the Earth, Environment and Technology. John Willey & Sons, 1–6.

DG Environment (2017) Reporting under Article 17 of the Habitats Directive: Explanatory notes and guidelines for the period 2013-2018. Brussels, 188 pp.

Dimopoulos P, Tsiripidis I, Xystrakis F, Kallimanis A, Panitsa M (2018) Methodology for monitoring and conservation status assessment of the habitat types in Greece. National Center of the Environment and Sustainable Development, Athens, 128 pp.

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Ellwanger G, Runge S, Wagner M, Ackermann W, Neukirchen M, Frederking W, Müller C, Ssymank A, Sukopp U (2018) Current status of habitat monitoring in the European Union according to Article 17 of the Habitats Directive, with an emphasis on habitat structure and functions and on Germany. Nature Conservation 29: 57–78.

European Commission (2011) NATURA 2000 Standard Data Form Explanatory Notes 32 pp.

European Commission (2013) Interpretation Manual of European Union Habitats - EUR28. European Comission 144 pp.

Evangelista A, Frate L, Stinca A, Carranza ML, Stanisci A (2016) VIOLA-the vegetation database of the central Apennines: structure, current status and usefulness for monitoring Annex I EU habitats (92/43/EEC). Plant Sociology 53: 47–58. https://doi.org/10.7338/pls2016532/04

Evans D, Arvela M (2011) Assessment and reporting under Article 17 of the Habitats Directive - Explanatory Notes & Guidelines for the period 2007-2012 - Final Draft. European Topic Centre on Biological Diversity, 123 pp.

Gennai M, Angiolini C, Bertacchi A, Gabellini A, Sarmati S, Viciani D, Foggi B (2022) Studying local species assemblages of salt-affected vegetation for monitoring Natura 2000 habitats. Plant Sociology 59: 1–10. https://doi.org/10.3897/pls2022591/01

Gigante D, Attorre F, Venanzoni R, Acosta A, Agrillo E, Aleffi M, Alessi N, Allegrezza M, Angelini P, Angiolini C, et al. (2016) A methodological protocol for Annex I Habitats monitoring: the contribution of Vegetation science. Plant Sociology 53: 77–87. https://doi.org/10.7338/pls2016532/06

Gerasimidis A, Korakis G (2005) Formation of forest vegetation in relation to the abiotic factors in Mount Mitsikeli [in Greek]. Geotechnical Scientific Issues 16: 16–27.

Goral F, Schellenberg J (2018) goeveg: Functions for Community Data and Ordinations. R package version 0.4.2.

Janssen J, Rodwell J, Criado MG, Gubbay S, Haynes T, Nieto A, et al. (2016) European Red List of Habitats. Part 2. Terrestrial and freshwater habitats European Union, 38 pp. https://doi.org/10.2779/091372

Kassambara A (2017) Practical guide to cluster analysis in R. CreateSpace, North Charleston, SC, USA, 187 pp.

Korakis G (2003) Vegetation units of Mt Paiko and evaluation from a reforestation prespective [in Greek]. PhD Thesis, Aristotle University of Thessaloniki, Thessaloniki, Greece.

Loidi J (1994) Phytosociology applied to nature conservation and land management. In: Song Y, Dierschke H, Wang X (Eds) 36th IAVS Symposium East China Normal University Press, Shanghai, China, 17–30 pp.

Loidi J (1999) Preserving biodiversity in the European Union: the Habitats Directive and its application in Spain. Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 133: 99–106. https://doi.org/10.1080/11263509909381538

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K (2019) cluster: Cluster Analysis Basics and Extensions. R package version 2.1.0.

McCune B, Grace J (2002) Analysis of ecological communities. MjM Software Design, Oregon, U.S.A, 300 pp.

Mountrakis D (1985) Geology of Greece [in Greek]. University Studio Press, Thessaloniki, 207 pp.

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, et al. (2016) Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19: 3-264. https://doi.org/10.1111/avsc.12257

Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHM, Szoecs E, Wagner H (2019) vegan: Community Ecology Package. R package version 2.5-6

Papastergiadou E, Dafis S, Dimopoulos P, Lazaridou T (1997) Syntaxonomic typology of Greek habitats. Folia Geobotanica 32: 335–341. https://doi.org/10.1007/BF02804011

Pott R (2011) Phytosociology: A modern geobotanical method. Plant Biosystems 145: 9–18. https://doi.org/10.1080/11263504.2011.602740

R Core Team (2021) R: A Language and Environment for Statistical Computing. 4.1.0 ed. R Foundation for Statistical Computing, Vienna, Austria, pp.

Rodwell JS, Evans D, Schaminée JHJ (2018) Phytosociological relationships in European Union policy-related habitat classifications. Rendiconti Lincei Scienze Fisiche e Naturali. 29: 237–249. https://doi.org/10.1007/s12210-018-0690-y

Rodwell JS, Schaminée JHJ, Mucina L, Pignatii S, Dring J, Moss D (2002) The diversity of European vegetation; an overview of phytosociological alliances and their relationships to EUNIS habitats. Wageningen, 115 pp.

Samaras DA, Theodoropoulos K, Eleftheriadou E (2021) The plant communities of Hungarian oak (*Quercus frainetto* Ten.) forests of Mt Goulinas (Sterea Ellas, Greece) [in greek]. Geotechnical Scientific Issues 30: 40–58.

Schaminée JHJ, Chytrý M, Hennekens SM, Mucina L, Rodwell JS, Tichý L (2012) Development of vegetation syntaxa crosswalks to EUNIS habitat classification and related data sets. Alterra, 134 pp.

Škvorc Ž, Jasprica N, Alegro A, Kovačić S, Franjić J, Krstonošić D, Vraneša A, Čarni A (2017) Vegetation of Croatia: Phytosociological classification of the high-rank syntaxa. Acta Botanica Croatica 76: 200–224. https://doi.org/10.1515/botcro-2017-0014

Strid A, Tan K (1997) Flora Hellenica. Koeltz Scientific Books, Königstein, 547 pp.

Stupar V (2016) Phytosociological characteristics of thermophilous deciduous forests of the class *Quercetea pubescentis* in Bosnia and Herzegovina within the framework of the forest vegetation of the western Balkans. Ljubljana: University of Ljubljana.

Tavakoli S, Ejtehadi H, Esmailzadeh O (2020) Optimizing the classification of species composition data by combining multiple objective evaluators toward selecting the best method and optimum number of clusters. Phytocoenologia 50(2): 163–172. https://doi.org/10.1127/phyto/2020/0360

Tsiripidis I, Bergmeier E, Dimopoulos P (2007) Geographical and ecological differentiation in Greek *Fagus* forest vegetation. Journal of vegetation science 18: 743–750. https://doi.org/10.1111/j.1654-1103.2007.tb02589.x

Tsiripidis I, Bergmeier E, Fotiadis G, Dimopoulos P (2009) A new algorithm for the determination of differential taxa. Journal of vegetation science 20: 233–240. https://doi.org/10.1111/j.1654-1103.2009.05273.x

Tsiripidis I, Xystrakis F, Kallimanis A, Panitsa M, Dimopoulos P (2018) A bottom-up approach for the conservation status assessment of structure and functions of habitat types. Rendiconti Lincei Scienze Fisiche e Naturali 29: 267–282. https://doi.org/10.1007/s12210-018-0691-x

van der Maarel E (2005) Vegetation ecology - an overview. In: van der Maarel E (Ed) Vegetation ecology. Blackwell Science, 1-51

Velev N, Vassilev K (2014) Management regimes within syntaxa of semi-natural grasslands in west Bulgaria. Hacquetia 13: 191–204. https://doi.org/10.2478/hacq-2014-0003

Xystrakis F (2009) The drought tolerance limit of European beech (*Fagus sylvatica* L.) stands on Mt. Olympus, NC Greece. PhD Thesis, Albert-Ludwigs Universität, Freiburg, Germany.

Supplementary material 1

Figure S1

Authors: Fotios Xystrakis, Minas Chasapis, Eleni Eleftheriadou, Dimitrios Samaras, Konstantinos Theodoropoulos

Data type: maps

Explanation note: Maps including important ecological information for the study area: Substrate, Koeppen climate classification, elevation and habitat types.

Link: https://doi.org/10.3897/pls2022592/01.suppl1

Supplementary material 2

Table S1

Authors: Fotios Xystrakis, Minas Chasapis, Eleni Eleftheriadou, Dimitrios Samaras, Konstantinos Theodoropoulos

Data type: vegetation data

Explanation note: Vegetation data.

Link: https://doi.org/10.3897/pls2022592/01.suppl2

Supplementary material 3

Table S2

Authors: Fotios Xystrakis, Minas Chasapis, Eleni Eleftheriadou, Dimitrios Samaras, Konstantinos Theodoropoulos

Data type: vegetation table

Explanation note: Vegetation table of beech-dominated stands.

Link: https://doi.org/10.3897/pls2022592/01.suppl3

Supplementary material 4

Tables S3 and S4

Authors: Fotios Xystrakis, Minas Chasapis, Eleni Eleftheriadou, Dimitrios Samaras, Konstantinos Theodoropoulos

Data type: tables

Explanation note: Updated inventory both of typical species of beech dominated habitat types in GR1240002 and of typical species of thermophilous forest habitat types in GR1240002.

Link: https://doi.org/10.3897/pls2022592/01.suppl4

Supplementary material 5

Table S5

Authors: Fotios Xystrakis, Minas Chasapis, Eleni Eleftheriadou, Dimitrios Samaras, Konstantinos Theodoropoulos

Data type: Vegetation table

Explanation note: Vegetation table of thermophilous forests.

Link: https://doi.org/10.3897/pls2022592/01.suppl5