Functional turnover from lowland to montane forests: evidence from the Hyrcanian forest in northern Iran

Seyed Mohammad Jafari [(1)], Shahin Zarre [(1)], Seyed Kazem Alavipanah [(2)], Farrokh Ghahremaninejad [(3)]

Plant functional traits and functional diversity play a key role in forest ecosystems. Altitudinal patterns of plant functional diversity are poorly investigated in the Hyrcanian relict forest, northern Iran. In this study, differences in trait composition between lowland and montane forest types were analyzed. Variation of plant functional traits along a 2400 m altitudinal gradient was examined in 67 vegetation sampling plots established at different elevations along the gradient. Eight plant functional traits related to plant physiognomy, competitive ability and dispersal were considered for 174 recorded vascular plants. We used generalized linear model, principal coordinate analysis and functional diversity metrics to investigate functional changes along the gradient. The importance of different traits such as the chamaephyte life form, tiny leaves, dry indehiscent fruits and small seeds increase with altitude. In contrast, other traits including large leaves, maximum height of plants, fleshy fruits, anemophily as well as medium to large seeds decrease with increasing elevation. Our findings support the existence of strong functional differences between lowland and montane forest vegetation types. Trait associations, different environmental parameters, disturbances and especially elevation were discussed as important predictors of functional changes. Vegetation type is a key factor affecting functional diversity variation in temperate forests. Therefore, we strongly recommend exploring and considering functional diversity in forest management practices.

Keywords: Functional Diversity, Gradient, Hyrcanian Forest, Multivariate Analysis, Vegetation

Introduction

Exploring the heterogeneous distribution of biological diversity and ecological communities in the biosphere has long been a core objective in ecological studies (Gaston 2000). Plant functional traits, as link factors of biological diversity to ecosystem functioning, are attributes with significant influence on establishment, survival and fitness of plant species in the ecosystem (Diaz & Cabido 2001). Such traits vary both along the environmental gradients and among species occupying similar habitat conditions (Cornwell & Ackerly 2009). Some functional traits are advantageous under specific environmental conditions, and they are prevalently represented by species groups which grow under such conditions (Diaz et al. 1998, Pellissier et al. 2010).

Elevation gradients are among the most interesting tools for exploring the distribution patterns of biological diversity (Rahbek 1995), in that certain factors (such as general geological characteristics and evolutionary history of species) are constant, while others may abruptly change at short distance (*e.g.*, temperature, radiation, precipitation, season length, etc.), making elevation gradients an ideal test system for understanding the ecosystems responses to environmental changes (Körner 2000, Fischer et al. 2011).

Studies on the association between plant traits and habitat conditions along environmental gradients have a long history (Körner 1999, Duckworth et al. 2000), and may provide important hints on the processes and mechanisms governing species distribution, richness pattern, community assembly and ecosystem functioning (Lavorel & Garnier 2002). Due to complexity of the observed variation in plant traits, at least for elevation gradients, plant ecologists still debate over the generality of the patterns found (Körner et al. 2007). Some factors such as co-presence of environmental sub-gradients including temperature, precipitation and radiation, human interference including land use/land cover changes, phylogenetic bias in trait variation, surface area, season length, along with community composition, stand age, and competition are among the major causes of the aforementioned complexity (Körner 2000).

Lowland forests present significant differences in trait composition as compared with montane forest. We hypothesized that the vegetation type may play a key role in the functional turnover along the elevational gradient. Montane and lowland forest ecosystems represent either a different set of plant functional traits or similar traits with different importance values. Our aims were to answer the following key questions: (1) Does functional trait composition differs between lowland and montane forests? (2) Which ecological drivers, including forest compositional and physiognomic properties, cause functional differences between lowland and montane forest types? (3) How and why the distribution of different plant functional traits change with altitude?

Material and Methods

Study area and sampling

Hyrcanian forest is a temperate deciduous forest ecosystem in the southeastern part of the Caucasus biodiversity hotspot, northern Iran. This unique ecosystem belongs to Euro-Siberian floristic region (Takhtajan 1986) and hosts relict flora which has survived the Quaternary glaciations (Leroy & Arpe 2007). In spite of its limited extension, Hyrcanian forest along with adjacent mountains hosts about 44 % of the Iranian flora (more than 3000 *taxa* - Akhani et al. 2010).

Hyrcanian forest suffers from numerous

☐ (1) Department of Botany, School of Biology and Center of Excellence in Phylogeny of Living Organisms, College of Science, University of Tehran, P.O. Box 14155-6455, Tehran (Iran); (2) Department of Cartography, Faculty of Geography, University of Tehran, Enqelab Ave., Vesal St.,Tehran (Iran); (3) Department of Plant Biology, Faculty of Biological Sciences, Kharazmi University, 43 Dr. Mofatteh Avenue, Tehran (Iran)

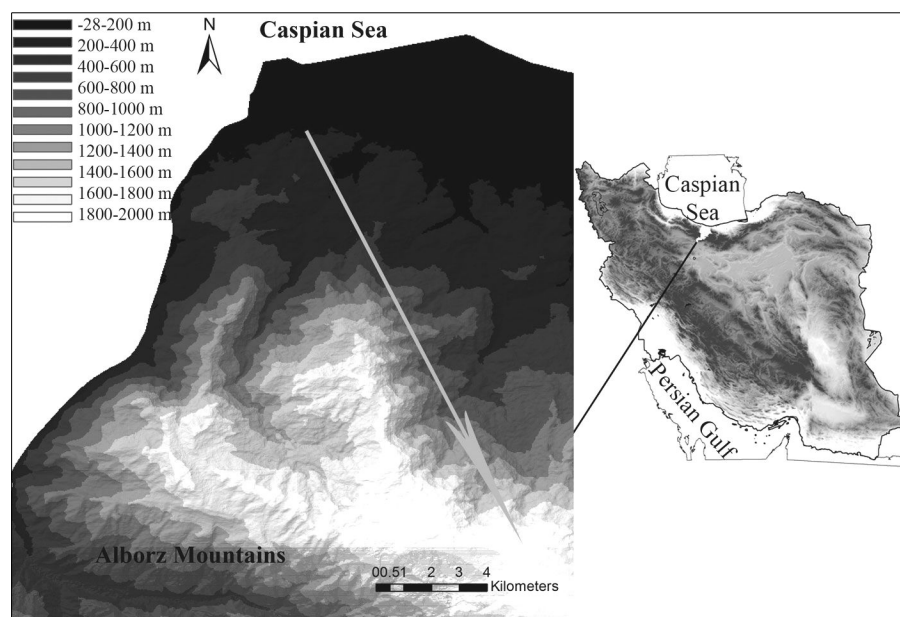@ Seyed Mohammad Jafari (smjafari@alumni.ut.ac.ir)

Fig. 1 - Geographic location of the study area in northern Iran, with the elevation transect (grey arrow) located on the Central Alborz Mountains.

natural and anthropogenic threats including improper management, wood harvesting activities, flood, fire, land use/land cover changes, husbandry and intense grazing (especially in the montane part). Currently, about 40 conservation areas are partly or completely located in this region.

Precipitation in this area decreases from about 1300 mm in the northern part to 800 mm at 2400 m elevation peak in the south (Bastl et al. 2008). The mean annual temperatur decreases from 16.1 °C in the northern part to 10 °C in southwest and to 12.2 °C in the southeastern part. General climatic conditions abruptly change from very humid at the northern limit to the Mediterranean-like climate in the southern part. Maximum precipitation occurs in September-December in the north and March-May in the south (IRI-MO 2012).

The study area is mainly covered by brown forest soils with relatively thick humus layer (Dewan & Famouri 1964). Based on the TAVO soil map (Straub 1988), northern lowlands is dominated by fluvisol formed by alluvial deposits, while cambisol is the most widespread soil type in the area. Bedrock is a late Quaternary (Maastrichtian) sedimentary rocks and limestones spread over most parts of the area.

In order to address our objectives, a 2400 m altitudinal gradient was selected in the Hyrcanian forest ecosystem in the Central Alborz Protected Area, northern Iran (Fig. 1). The selected gradient spans from the lowland deciduous forest at lower elevations to the montane deciduous forest at upper elevations. Lowland forests roughly extend from 0 to 800 m a.s.l. and is characterized by semi-tropical climatic conditions. It is dominated

by cold sensitive taxa such as *Parrotia persica* C.A.Mey, *Quercus castaneifolia* C.A. Mey., *Carpinus betulus* L., *Acer velutinum* Boiss., *Tilia platyphyllos* Scop. and evergreen broadleaf shrubs such as *Buxus hyrcana* Pojark. and *Prunus laurocerasus* L. Montane forests is more heterogeneous and dominates above 1600 m a.s.l. It is mainly characterized by the presence of *Fagus orientalis* Lipsky at mid-altitudes, *Quercus macranthera* Fisch. & C.A.Mey. at higher elevations, and a transitional *Fagus-Quercus* forest vegetation in between.

Major land use/land cover categories in lowlands are deciduous forest, orchards, agriculture and urban land cover classes. Mid-altitude habitats are characterized by deciduous forests, fragmented to some extent due to local husbandry and ranching activities in forest openings. Lowland forests have been subject to anthropogenic disturbance during last few decades due to easy accessibility (Poorzady & Bakhtiari 2009). Generally, disturbance intensity decreases from lowland to mid-altitudes, and increases again in montane forests (Jafari et al. 2013). The montane forests are characterized by a lower stem density, and gradually shifts into montane shrublands and rangelands, due to the increasing intensity of grazing with the elevation.

Sampling

Based on the results of former floristic and vegetation studies (Jafari et al. 2013), the selected gradient was split in three altitudinal zones (0-800 m, 800-1600 m, 1600-2400 m a.s.l.) covered by lowland (LoF), mid-altitude (MiF) and montane (MoF) forests, respectively. Each zone was further divided in four 200 m altitudinal belts, and 4 to 7 sampling plots (20 × 20 m - 400 m²) were established within each belt in homogenous, mature and undisturbed forest stands (Tab. 1). Overall, 67 sampling plots were established along the above gradient.

Vegetation and species composition for each plot were recorded during 2009-2010 vegetative seasons using the Braun-Blanquet approach (Braun-Blanquet 1932). Diameter at breast height (DBH) and tree ring width data were used to estimate the age of dominant forest species. Overall, 174 species of vascular plants were recorded (see Appendix 1). Taxonomic status of all *taxa* was double checked using published and online resources (Clayton et al. 2006).

Plant functional traits

Plant traits related to physiognomy, productivity, competitive ability, dispersal and reproduction were considered in this analysis (Tab. 2). For each species in each plot three mature leaves were collected, and the leaf area measured by scanning using the image analyzer CAMPU EYE LSA software (Bakr

Tab. 1 - Characteristics of the elevational belts considered along the main altitudinal gradient in the Hyrcanian forest. (LoF): Lowland Forest; (MiF): Mid-altitude Forest; (MoF): Montane Forest.

Elevational belt	Altitudinal range (m)	Surface Area (m²)	Plots	No. Species	Vegetation Type
Belt1	0-200	52 192 295.40	5	92	LoF
Belt2	200-400	59 860 284.44	7	87	LoF
Belt3	400-600	56 189 891.22	7	89	LoF
Belt4	600-800	54 236 731.49	5	81	LoF
Belt5	800-1000	54 298 613.78	5	70	MiF
Belt6	1000-1200	56 390 235.12	7	71	MiF
Belt7	1200-1400	60 473 692.62	7	73	MiF
Belt8	1400-1600	65 444 387.42	7	71	MiF
Belt9	1600-1800	39 392 717.61	5	69	MoF
Belt10	1800-2000	20 546 466.74	4	64	MoF
Belt11	2000-2200	10 217 539.31	4	52	MoF
Belt12	2200-2400	2 856 641.13	4	40	MoF

Tab. 2 - Plant functional traits related to plant physiognomy, competitive ability and dispersal in Hyrcanian forest (Assadi et al. 1988, Kleyer et al. 2008, Klotz et al. 2002, Rechinger 1963, Royal Botanical Gardens Kew 2008). (a): Quantitative traits were transformed to multi-class traits for GLM analysis.

Trait group	Trait Type	Traits
Life form	Categorical	Phanerophyte (LFPhan), Chamaephyte (LFCham), Hemicryptophyte (LFHemi), Geophyte (LFGeop), Therophyte (LFTher), Fern (LFFern), Liana/Climber (LFLian), Hydrophyte (LFHydr)
Maximum Height	Quantitative	MH (m) [Categories: MH1 (<0.5 m), MH2 (0.5-1 m), MH3 (1-6 m), MH4 (6-20 m), MH5 (>20 m)
Leaf Type	Categorical	Simple leaves (LTSimp), Compound leaves (LTComp)
Mean Leaf Area	Quantitative	MLA (cm^2) [Categories: MLA1 (<1 cm^2), MLA2 (1-2 cm^2), MLA3 (2-4 cm^2), MLA4 (4-6 cm^2), MLA5 (6-8 cm^2), MLA6 (8-10 cm^2), MLA7 (10-15 cm^2), MLA8 (15-25 cm^2), MLA9 (25-40 cm^2), MLA10 (40-70 cm^2), MLA11 (70-100 cm^2), MLA12 (100-200 cm^2), MLA13 (>200 cm^2)
Seasonality	Categorical	Woody deciduous (SWDeci), Woody evergreen (SWEver), Perennial (SPere), Biennial (SBien), Annual (SAnnu)
Fruit type	Categorical	Fleshy (FTFles), Dry Dehiscent (FTDDe), Dry Indehiscent (FTDIn), Without Fruit (FTNone)
Pollination	Categorical	Entomophily (PEnto), Anemophily (PAnem), Hydrophily (PHydr), Self-Pollination (PSelf)
Seed Weight	Quantitative	SW (mg of 1000 seeds). Categories: SW1 (<1 mg), SW2 (1-2 mg), SW3 (2-3 mg), SW4 (3-4 mg), SW5 (4-5 mg), SW6 (5-10 mg), SW7 (10-20 mg), SW8 (20-50 mg), SW9 (50-100 mg), SW10 (100-200 mg), SW11 (>200 mg), SW12 (No seeds)

2005). Maximum plant height was assessed for each species in each plot using standard stick methods, and then averaged over plots to obtain a mean value for each species in each belt. As for pollination mechanism, species were assigned to the categories listed in Tab. 2 based on the information obtained from available databases (such as Biol·Flore plant trait database - Klotz et al. 2002, and Interaction Web Database), except for 7 species for which it was determined based on field observations. For 5 species no information was available at all. Mean seed weight for each species was obtained from the Seed Information Database (Royal Botanical Gardens Kew 2008) and LEDA Traitbase (Kleyer et al. 2008). The seed weight trait represents the weight of 1000 seeds in gram. For plant *taxa* not listed in the above databases, the mean value of the closest relative species (when available) was considered. Each species was assigned to life form categories based on the authors' field experience and checked *a posteriori* using online resources (Klotz et al. 2002, Kleyer et al. 2008).

Data analysis

Values for quantitative traits were grouped into categorical classes. Categorization was primarily implemented using frequency of range values within our dataset.

Data collected were arranged in two "state" matrices of 174 species × 12 belts and 174 species × 60 traits, and then combined to obtain a 12 belts × 60 traits state matrix, according to the method proposed by Diaz et al. (1998). Cover-abundance values for each species were averaged over plots in each belt and used as belt-wise weighting factor in that belt. After weighting species in each belt, the frequency of each trait category was calculated and converted to proportion, and then transformed by the arcsine function prior to analysis (Sokal & Rohlf 1995).

A generalized linear model function (normal distribution with identity link) was applied by the software package SPSS 20.0 (IBM Corp 2011) using the proportion of the trait states as dependent variable, and the mean elevation of each belt as predictor.

In order to analyze the variation in the composition of functional traits along the elevation gradient, principal coordinate analysis (PCoA - Gower 1966) was applied on a pairwise belt-to-belt dissimilarity matrix based on Gower's coefficients (because of the categorical nature of the dataset – Gower 1971) using the PAST software package (Hammer et al. 2001). UPGMA clustering method using the Gower's coefficient matrix was adopted to re-test the PCoA results. In addition, several functional metrics, such as the modified attribute functional diversity (*MFAD* - Schmera et al. 2009) and the community based functional diversity index (*FDc* - Petchy & Gaston 2006), were calculated for each altitudinal belt using the FD-versity software (Casanoves et al. 2011) and then compared. *MFAD* may take values in the range 0-1 and it was calculated as follows (Pla et al. 2012 - eqn. 1):

$$MFAD = \frac{\sum_{i=1}^{N} \sum_{j>1}^{N} d_{ij}}{N}$$

where d_{ij} is the Gowers' dissimilarity between functional units i and j, and N is the number of functional units. This index reduces the matrix dimensions by summarizing similar species as functional units, providing a simple numerical index to compare communities in the functional space (Schmera et al. 2009). *FDc* is a dendrogram-based index, and equals the total length of the branches of the dendrogram constructed from information on species functional traits (Petchy & Gaston 2006). Moreover, Shannon's index

of taxonomic diversity (H') was calculated for each belt as follows (eqn. 2):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i is the relative importance value of the i-th species and S is the total number of species.

Results

Leaf size and type

Despite the prevalence of species with simple leaf type in comparison with compound leaf type in both lowland and montane forests, the proportion of both leaf types showed negligible changes with altitude and forest type (Tab. 3, Fig. 2a). The relative abundance of medium and large leaf classes (MLA8, MLA10, MLA11, MLA12 and MLA13) showed a meaningful negative correlation with altitude (Tab. 3, Fig. 2m, n). The proportion of small leaved species significantly increased from lowland to montane forests (MLA1: B=3.921, P<0.05; MLA2: B=4.835, P<0.05; MLA3: B=4.119, P<0.05; MLA4: B=5.667, P<0.05) (Fig. 2k, l). Patterns of change at mid-altitudes for mean leaf area trait differed from the patterns at the gradient extremes. For example, an increase in the frequency of classes MLA8, MLA9 and MLA13 was observed at mid elevations, as well as a reduction in proportion for classes MLA3, MLA4 and MLA11 (Fig. 2k, l, m, n).

Life form, seasonality and maximum height

As for life form traits, the importance of geophytes and ferns showed a non-significant decrease with elevation (B = -2.180, P = 0.107; B = -3.331, P = 0.183, respectively - Fig. 2b, c). Moreover, ferns do not produce

fruits and the proportion of the "FTNone" class decreased non-significantly with altitude (B = -3.331, P = 0.183). On the contrary, the proportion of chamaephytes significantly increased with altitude along the gradient (B = 4.187, P < 0.05). Generally, phanerophytes showed non-significant (or marginally signi-

ficant) relationship with altitude (B = -4.509, P = 0.061). However, a significant decrease of woody deciduous *taxa* (B = -3.854, P < 0.05) was observed from lowland to high altitude forests (Fig. 2f). Furthermore, a non-significant variation in the proportion of woody evergreens (usually shrubs, *e.g.*, pha-

nerophyte or chamaephyte life forms) was detected along the altitudinal gradient (B = -3.397, P = 0.338 - Fig. 2f).

Annual species or therophytes showed a non-significant but non-negligible increase in proportion from lowland to montane forests (B = 3.718, P = 0.130). Hemicryptophytes (including forbs and non-rhizomatous grasses) were dominant in both vegetation types and their importance rises from lowland to montane type (0.372 *vs.* 0.403 WMP - Tab. 3, Fig. 2d, e). Generally, the proportion of herbaceous *taxa* (including annual, biennial and perennial species) increased non-linearly with altitude, while perennials and annuals showed an opposite pattern of change at mid-altitudes. In contrast to perennials, annuals decreased in proportion at mid-altitude sites, then rise up again in the montane forest type (Fig. 2e).

Concerning maximum height, all classes showed a significant correlation with altitude (Fig. 2g, h), except MH2 (0.5 to 1 m). For example, herbaceous plants (class MH1) increase their importance along the altitudinal gradient (B = 4.186, P < 0.05). Shrub species (MH3, 1-6 m of maximum height) presented a small decrease from low to high altitudes (0.296 to 0.256 WMP). As expected, tall woody plants (MH4 and MH5) significantly decrease in importance with altitude (Fig. 2h, Tab. 3).

Tab. 3 - Generalized linear model correlation between proportion of plant functional traits and altitude in the Hyrcanian forest. (WMP): Weighted mean proportion; (LF): Lowland forest; (MF): Montane forest. (*): p<0.05; (**): p<0.01; (***): p<0.001.

Trait group	Trait	Altitude B	Altitude P-value	LF	MF
Leaf type	Simple leaf (LTSimp)	2.093	0.150	0.800	0.820
	Compound leaf (LTComp)	-2.093	0.150	0.200	0.180
Life form	Phanerophyte (LFPhan)	-4.509	0.061	0.432	0.366
	Chamaephyte (LFCham)	4.187	0.005**	0.017	0.037
	Hemicryptophyte (LFHemi)	2.146	0.323	0.372	0.403
	Geophyte (LFGeop)	-2.180	0.107	0.073	0.052
	Therophyte (LFTher)	3.718	0.130	0.053	0.083
	Fern (LFFern)	-3.331	0.183	0.027	0.023
	Liana/climber (LFLian)	6.124	0.806	0.024	0.033
Maximum height	Maximum Height <0.5 m (MH1)	4.186	0.045	0.126	0.351
	Maximum Height 0.5-1 m (MH2)	9.721	0.563	0.193	0.216
	Maximum Height 1-6 m (MH3)	-6.315	0.055	0.294	0.204
	Maximum Height 6-20 m (MH4)	-4.260	0.038*	0.173	0.054
	Maximum Height > 20 m (MH5)	-6.750	0.061	0.241	0.198
Mean leaf area	Mean Leaf Area < 1 cm² (MLA1)	3.921	0.000***	0.031	0.213
	Mean Leaf Area 1-2 cm² (MLA2)	4.835	0.002**	0.042	0.097
	Mean Leaf Area 2-4 cm² (MLA3)	4.119	0.031*	0.034	0.123
	Mean Leaf Area 4-6 cm² (MLA4)	5.667	0.022*	0.065	0.164
	Mean Leaf Area 6-8 cm² (MLA5)	9.998	0.835	0.048	0.051
	Mean Leaf Area 8-10 cm² (MLA6)	2.931	0.051	0.050	0.081
	Mean Leaf Area 10-15 cm² (MLA7)	8.789	0.221	0.113	0.115
	Mean Leaf Area 15-25 cm² (MLA8)	-6.002	0.048*	0.211	0.125
	Mean Leaf Area 25-40 cm² (MLA9)	5.128	0.128	0.109	0.111
	Mean Leaf Area 40-70 cm² (MLA10)	-5.660	0.001**	0.357	0.114
	Mean Leaf Area 70-100 cm² (MLA11)	-2.732	0.019*	0.182	0.0.91
	Mean Leaf Area 100-200 cm² (MLA12)	-6.543	0.030*	0.110	0.070
	Mean Leaf Area > 200 cm² (MLA13)	-2.211	0.004**	0.029	0.033
Seasonality	Woody deciduous (SWDeci)	-3.854	0.028*	0.375	0.327
	Woody evergreen (SWEver)	-3.397	0.338	0.065	0.040
	Perennial (SPere)	1.276	0.580	0.485	0.502
	Biennial (SBienn)	3.678	0.025*	0.025	0.047
	Annual (SAnnu)	3.718	0.130	0.052	0.085
Fruit type	Fleshy (FTFles)	-7.730	0.016*	0.230	0.146
	Dry dehiscent (FTDDe)	2.447	0.923	0.266	0.262
	Dry indehiscent (FTDIn)	5.595	0.001**	0.475	0.567
	Without fruit (FTNone)	-3.331	0.183	0.027	0.023
Pollination mechanism	Entomophily (PEnto)	5.485	0.926	0.612	0.582
	Anemophily (PAnem)	-5.923	0.052	0.330	0.250
	Hydrophily (PHydr)	4.387	0.623	0.027	0.015
	Self-pollination (PSelf)	-5.148	0.052	0.032	0.017
Seed weight (mg x 1000 seeds)	Seed weight < 1 mg (SW1)	5.442	0.002**	0.107	0.162
	Seed weight 1-2 mg (SW2)	-8.663	0.518	0.132	0.120
	Seed weight 2-3 mg (SW3)	4.854	0.030*	0.060	0.010
	Seed weight 3-4 mg (SW4)	-6.981	0.021*	0.010	0.052
	Seed weight 4-5 mg (SW5)	-4.421	0.000***	0.077	0.047
	Seed weight 5-10 mg (SW6)	4.558	0.012*	0.052	0.080
	Seed weight 10-20 mg (SW7)	-9.338	0.776	0.067	0.065
	Seed weight 20-50 mg (SW8)	-3.489	0.056	0.087	0.070
	Seed weight 50-100 mg(SW9)	-5.038	0.830	0.082	0.087
	Seed weight 100-200 mg (SW10)	-1.529	0.556	0.112	0.105
	Seed weight > 200 mg (SW11)	5.667	0.701	0.095	0.100
	No seeds (SW12)	-8.427	0.101	0.027	0.025

Fruits, pollination and seed traits

Fleshy fruit species significantly decreased (B = -7.730, P < 0.05) along the gradient from lowland to montane forests, while dry indehiscent fruit showed a significant increase (B = 5.595, P < 0.05 - Fig. 2i).

As for pollination types, the percentage of the anemophilous and self-pollinating species showed a significant decrease with altitude (B = -5.923, P < 0.05; B = -5.148, P < 0.05, respectively). As for the latter category (PSelf), this could be due to low number of self-pollinating species (7) found in the lowland forest type (Fig. 2j). On the other hand, the proportion of insect-pollinated species decreased from lowland to mid-altitude forests (0.612 to 0.602 WMP), and increased from mid-altitude up to the timberline forests (0.602 to 0.750 WMP).

The proportion of tiny seed species (classes SW1 to SW3) showed a positive correlation with elevation, increasing significantly from low to high altitudes (Fig. 2o). The proportion of small-medium sized and medium sized seeds decreased along the gradient (*e.g.*, SW4: B = -6.981, P < 0.05; SW5: B = -4.421, P < 0.05; SW8: B = -3.489, P < 0.05 - Fig. 2p, q). The importance of large seeds decreased (though not significantly) with elevation (Fig. 2r). On the contrary, mid-altitude pattern of variation for SW4 and SW7 was completely different, in that the proportion of seeds with 3-4 mg and 10-20 mg

Fig. 2 - Variation of trait proportions along the studied elevation gradient. The weighted proportions of traits (Y-axis) are plotted against elevation (X-axis).
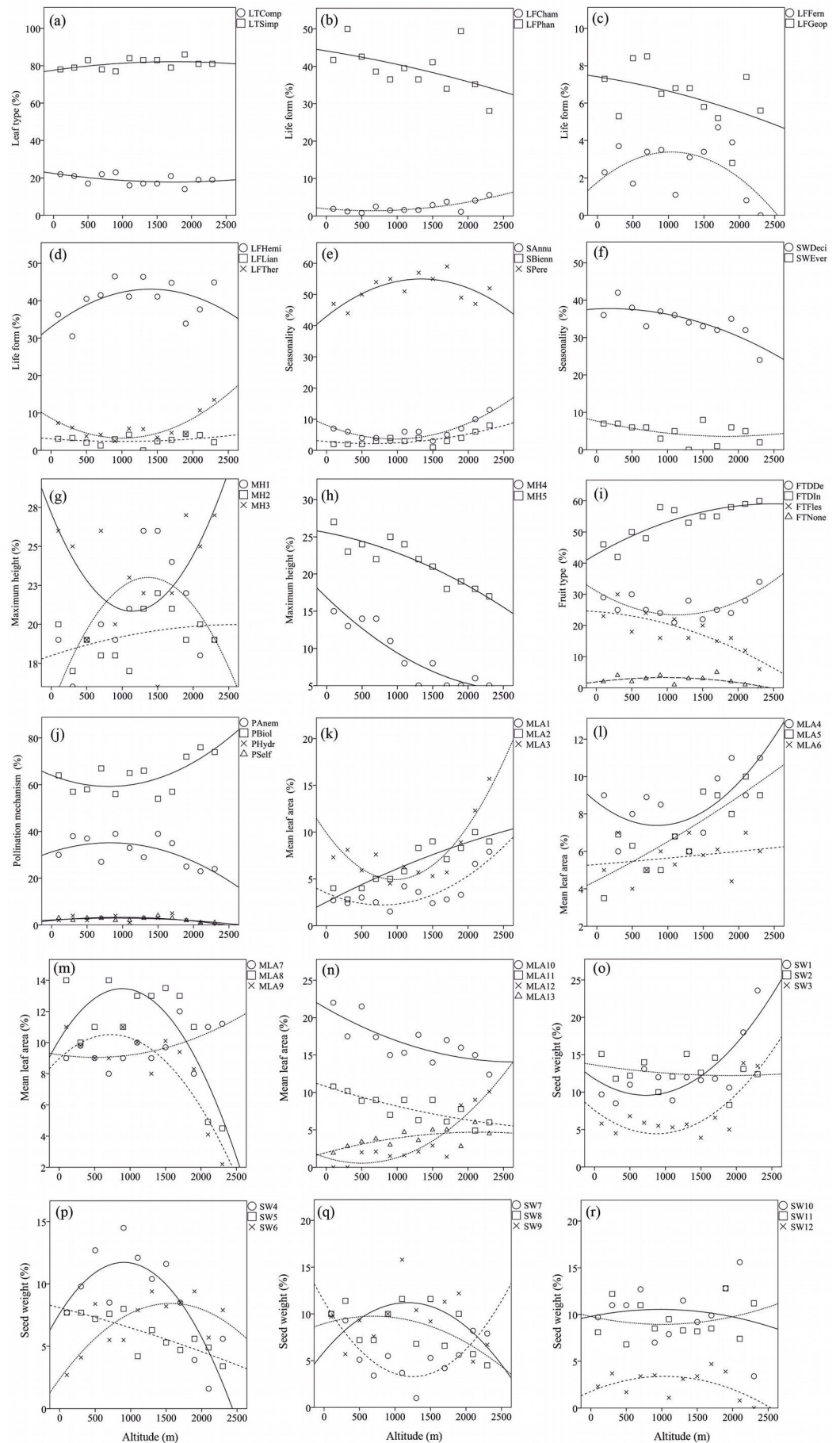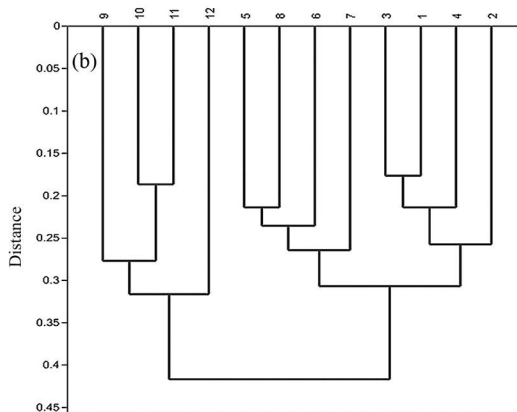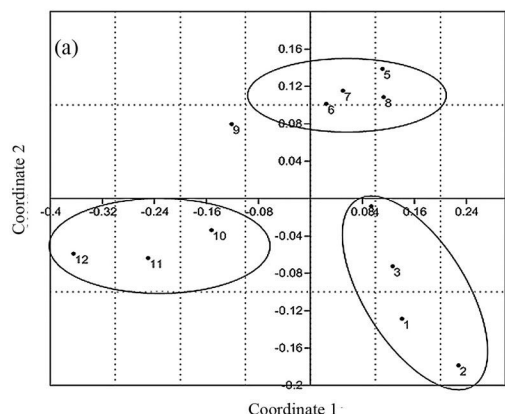
Fig. 3 - Multivariate analysis of functional turnover along the altitudinal gradient in Hyrcanian forest. Principal coordinate analysis (a) and cluster analysis (b) clearly revealed functional differences between lowland (belts 1-4) and montane (belts 9-12) forest types.

Multivariate analysis of functional diversity

Principal coordinate analysis revealed remarkable differences among the altitudinal belts (Fig. 3a). The first two axes accounted for 73 % of the total variation in functional trait composition. The first axis (variance accounted for: 52.9%) may be clearly interpreted as related to the elevation, since belts are fairly well-distributed along this axis following a forest altitudinal gradient (1-4: lowland > 5-8: mid-altitude > 9-12: montane forest vegetation types). Contrastingly, the second coordinate (variance accounted for: 20.1%) may be interpreted as related to both forest disturbance and diversity in structural parameters. Indeed, the second coordinate clearly separated lowland and montane forest types (belts 1-4 and 9-12) from mid-altitude plant communities (belts 5-8). Concerning belt 9, it is characterized by a transitional vegetation type, and this may explain its intermediate position in the space of the first two coordinates.

Cluster analysis using paired-group algorithm further supported the pattern observed by the principal coordinate analysis, clearly distinguishing the three forest types (Fig. 3b).

Based on the obtained results, lowland forest vegetation was more similar in functional trait composition to mid-altitude forest communities. Likely, this was due to the high number of "key" linking species shared by the mentioned vegetation types. Among shared key species with high importance values, *Fagus orientalis* and, to a lesser extent, *Acer velutinum* and *Quercus castaneifolia*, are worth to be mentioned. Generally, functional diversity decreased from lowland to montane forest vegetation types (Fig. 4a). Such trend fully agrees with the observed pattern for taxonomic diversity (Fig. 4b). Finally, average values of *MFAD*, *FDc* and Shannon's index clearly distinguished lowland, mid-altitude and montane forest types.

Discussion

Traits and altitude

The dominance of simple leaf type species at both lowland and high altitudes is probably due to taxonomic and historical reasons. Compound leaf trait is mainly represented in this study by three different functional groups: (1) woody *taxa* including *Albizia julibrissin* Durazz., *Pterocarya fraxinifolia* and *Gleditsia caspica* Desf.; (2) ferns, for which the fronds were considered as compound leaves; (3) herbaceous *taxa* of Fabaceae and Rosaceae. The high importance values of these groups in lowland forests may therefore be due by the higher proportion of such *taxa* in lowland forest. In this study, we did not find sufficient evidences to discuss about two major theories related to evolution of compound leaf trait (rapid growth and seasonal drought hypotheses - Malhado et al. 2010). General decrease of leaf size from lowland to montane forest is probably related to the warmer, more shady and humid conditions occurring in lowland forests. Moreover, considering the observed patterns for life form and seasonality traits under the Corner's rule scenario (Corner 1949), the observed decrease in leaf size with altitude was expected to some extent. Leaf size decreases in response to stressful condition of higher altitude as compared with the resource-rich condition and fertile soil of lowland forests (Anacker et al. 2011).

Generally, phanerophytes need more humidity, deeper soils and a longer vegetative season to complete their annual growth. In contrast, chamaephyte life form is a prominent adaptation to wind and grazing stresses, and shorter season length as well. Soil depth (Doležal & Šrutek 2002), length of the growing season (Körner 1999) and humidity (Khalili 1973) decrease with the altitude in the Hyrcanian forest. Moreover, forest openings above 1800 m a.s.l. imply higher wind speed and easy accessibility for grazing and trampling. As a consequence, the dominance of phanerophytes in lowland and an increasing frequency of chamaephytes along altitudinal gradients are expected based on the above ecological considerations. Altitudinal distribution of broad-leaved evergreen *taxa* is probably limited by the duration of low temperature period in winter which increases with altitude in the study area (Aerts 1995, van Ommen Kloeke et al. 2011). Herb layer of montane forest vegetation hosts higher proportion of therophytes, contrasting with
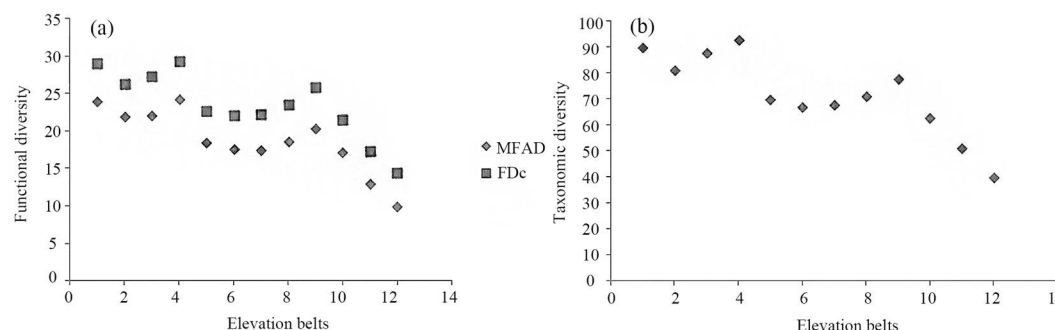

Fig. 4 - Pattern of functional (a) and taxonomic diversity (b) along the altitudinal gradient studied in the Hyrcanian forest. (*MFAD*): Modified Functional Attribute Diversity, (*FDc*): community based Functional Diversity.

the accepted trend for high altitude ecosystems (Körner 1999). Low competition for light and disturbances (*e.g.*, grazing and local timber harvesting) are factors favoring a higher proportion of therophytes in understory vegetation layer (McIntyre et al. 1995).

Taller plants may intercept more light in closed forest ecosystems (Ryan & Yoder 1997, Wright et al. 2007). A decrease in plant height with elevation has been observed in several regions (Kappelle et al. 1995). However, the use of elevation as an environmental predictor of plant height is still under debate (Moles et al. 2009). Indeed, Moles et al. (2009) found that the precipitation of the wettest month was an efficient predictor of plant height. Based on such evidence, we may expect taller plants in the lowland forest types analyzed in this study. Decrease in forest density lessens the competition for light and implies high wind speed and irradiance at higher altitudes. Such factors may trigger an overall reduction of plant height, even within life form classes.

Increasing pattern of dry indehiscent fruits is clearly influenced by dominant species in montane forests (*e.g., Fagus orientalis* Lipsky, *Carpinus orientalis* Mill., *Quercus macranthera* Fisch. and C.A.Mey. and *Acer hyrcanum* Fisch. and C.A.Mey.), which mostly produce dry indehiscent fruits, especially achenes. There are two hypotheses which may explain the evolution of fleshy fruits, including fruit shift and habitat shift theories (Bolmgren & Eriksson 2005). Central to both theories is that evolution of fleshy fruits coincides with the appearance of closed forest ecosystems in early Tertiary period. Proportion of fleshy fruits dramatically decreases from lowland closed forests to montane open forests. If the above theory holds, forest opening at higher elevations decreases the need of fruits to be a fleshy reward for dispersers. Genera belonging to the Rosaceae family, such as *Crataegus, Rubus, Mespilus* and *Prunus*, cladode-bearing plants such as *Ruscus* and *Danae* and some other groups such as *Diospyros, Cornus, Celtis* and *Frangula*, all producing fleshy fruits, are mostly abundant in lowland forests. Therefore, based on the above considerations and on the ecological costs of producing fleshy fruits, we can expect a lower frequency of such species at higher altitudes.

Anemophilous pollination depends on wind and subsequently increases with both altitude and latitude (Pallardy 2008). Pollination of anemophilous *taxa* in temperate deciduous forests occurs earlier than for non-anemophilous *taxa*, before leaf flushing (Whitehead 1984). In this study, lowland forests were dominated by anemophilous woody taxa, therefore a decreasing pattern of the wind pollination trait was observed along the elevation gradient (Friedman & Barrett 2009). Contrastingly, biotic pollination is

usually associated with closed habitats, though this trait showed non-significant changes with altitude in our study. The constant closeness of forest canopy along the elevation gradient may have contributed in this pattern.

It has been proposed that shaded environments such as tropical forest ecosystem may host species with larger seeds than less shaded habitats (Leishman & Westoby 1994). Lowland forests in in the study area area present semi-tropical conditions such as closeness, high temperature and moisture. In addition, parameters such as plant size (Baker 1972), growth form (Levin 1974), dispersal mechanism (Lord et al. 1997), length of the growing season and primary productivity (Moles & Westoby 2003) can influence seed mass and size. In the present study, overall larger size (*e.g.*, higher maximum height) and longer growing season in lowland forests may favor *taxa* with heavier seeds. Moreover, vertebrate-dispersed species such as those carrying fleshy fruits normally carry also larger seeds (Leishman et al. 1995), which are represented in higher proportion in the lowland forest type. In contrast, tiny seeds generally increase with altitude in our study, and this may be due to a shorter growing season, stressful conditions, dominance of smaller life forms and non-vertebrates dispersers in the montane forest vegetation type (Moles et al. 2007).

Functional diversity

Diversity along environmental gradients has often been investigated (Rahbek 1995) and vegetation types are usually considered as explanatory factors (Pellissier et al. 2010). In this study, we sought for differences in trait composition and functional diversity between lowland and montane forest vegetation types. Principal coordinate analysis revealed a remarkable difference in functional trait composition among the altitudinal belts considered (Fig. 3a). Elevation seems to explain fairly well the main functional trait variation in the study area, as it can be inferred from the distribution of belts along the first axis from lowland to montane forest types. The obtained dendrogram (Fig. 3b) corroborates these results. Along with species richness (Tab. 1), trait composition in both forest types remarkably differs. Functional diversity is an indicator of the complexity of relationships between species diversity and ecosystem processes (Petchy & Gaston 2006). Climax communities in a stable environment represent maximum capacity of interaction and complexity (Taylor 2005). In this study, lowland forests experience more stable conditions compared to the montane forest type, reflecting in a higher functional and taxonomic diversity in low altitude forests. Generally, frequency and intensity of perturbations or environ-

mental stability, stressful condition, competition for light, wind speed, irradiance, biotic interactions and human interference may play key role in the emergence of specific pattern of plant traits along altitude. Variation of the above factors may favor functional difference between habitats. For eample, logging and harvesting practices may remove key plant species and consequently important functional traits, deeply affecting the ecological functioning of the Hyrcanian forest ecosystem. Therefore, along with floristic and vegetation studies, the exploration of patterns of functional diversity in this ecosystems is of utmost importance.

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Supplementary Material

Appendix 1 - Species × trait matrix used for the analysis. Importance-values within the 12 elevational belts (B1-B12), trait states and values are reported.

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