Dynamics of humus forms and soil characteristics along a forest altitudinal gradient in Hyrcanian forest

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Humus forms are good indicators of environmental conditions and thus important in forest ecological processes. Altitudinal gradients are considered as natural laboratory for evaluating soil ecological processes and humus form distribution. The objective of this study was to evaluate the macromorphology of humus forms along an altitudinal gradient (0-2000 m a.s.l.) covered with plain forest, mixed and pure forests and forest-grassland ecotone, in Alborz Mountains in northern Iran. In total, 225 humus profiles were evaluated. Forest stand variables including tree density, basal area, crown density, and height, forest floor and soil eco-chemical properties along with biological features were measured. We found that altitudinal gradients influence both humus forms distribution and soil properties but with different mechanisms. While soil properties (i.e., temperature, pH, CaCO₃, soil N content, soil C/N and microbial biomass N) were significantly correlated with altitude, the forest floor properties were more influenced by tree species composition. Particularly, the abundance of Mull was decreased in plain mixed forests compared to mountain pure forests, whereas the frequency of Amphi was increased. Moreover, Oligomull and Leptoamphi were abundant in mixed beech forests, while Eumacroamphi, Eumesoamphi and Pachyamphi were only observed in pure beech forests. Such a distribution influenced soil fertility where higher values of nitrogen (N), microbial biomass nitrogen (MBN) and pH were observed at lower altitudes under mixed forests compared to pure forests at higher altitudes.

Keywords: Altitude Gradient, Plant-humus-soil Relationships, Humus Systems, Soil Microbial Biomass

Introduction

Forest humus is an indicator of the existing environmental conditions (Ponge 2013), because it is the result of complex interactions between stand species composition (Labaz et al. 2014), soil properties (Ponge et al. 2011), soil micro- and macro-organisms’ activities and environmental factors (Badía-Villas & Girona-García 2018). Since humus forms show specific morphological patterns (layering and structure – Jabiol et al. 2013), they are useful tool for assessing the health status of forests and the overall soil fertility (Salmon 2018). The current classification systems enabled to distinguish five humus systems and sixteen humus forms in terrestrial ecosystems (Jabiol et al. 2013, Zanella et al. 2018). Humus forms can be directly identified in field without the need for expensive laboratory tools (Zanella et al. 2018). According to Zanella et al. (2011), temperature, precipitation and vegetation composition are the three most important factors affecting biological degradation of organic residues and contributing in the formation of different humus forms. On the other hand, altitude through changes in temperature and precipitation, affects the distribution of forest species, forest floor quality and quantity (Bayranvand et al. 2017b), soil characteristics (Ponge et al. 2011), micro-organism types and activities (Zhang et al. 2013, Xu et al. 2015), thus contributing in humus forms (Ascher et al. 2012, Salmon 2018). Altitudinal gradients are considered as natural laboratories for evaluating soil ecological processes (Labaz et al. 2014, Bojko & Kabala 2017). Understanding the complex interactions between soil and plant communities along altitude gradients can be used for the prediction of soil microbial activity and forest floor decomposition (Bojko & Kabala 2017, Xu et al. 2015).

The natural broadleaf forests in northern Iran are similar to those in central Europe, northern Turkey and the Caucasus. In these forest ecosystems, composition of tree species changes with elevation (Bayranvand et al. 2017a). Due to their unique topographical conditions compared to the oldest forest in Asia, Alborz mountains offers the potential to assess changes in forest types and humus forms with altitude (Naqinezhad et al. 2013). So far, few studies investigated the pattern of humus forms, forest floor features and soil microbial biomass along altitudinal gradients (Bayranvand et al. 2017b, Waez-Mousavi

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In this study, we described humus morphology, forest floor, soil quality, microbial biomass carbon (MBC) and nitrogen (MBN) in five different forest types along an altitudinal gradient from 0 to 2000 m a.s.l. (i.e., plain forest, low, medium and high mountainous mixed and pure forests, and forest-grassland ecotone). We hypothesized that:

1. increased beech species abundance and decreased soil temperature along altitudinal gradient strongly affect the pattern of humus forms and organic layer thickness;

2. forest floor and soil characteristics correlate with humus forms and vegetation characteristics;

3. specific soil chemical and biological features correlate with humus forms and vegetative characteristics.

Material and methods

Site description

With an area of about 14,000 hectares, the Vaz catchment forests are located in the northern Alborz mountain, beside the Caspian Sea, in northern Iran (36° 16′ N, 52° 48′ E – Fig. S1 in Supplementary material). The study area was located along an altitude gradient 0-2000 m a.s.l. Forest vegetation in this area largely depends on altitude gradient and therefore five different forest types could be distinguished (Khaleghi et al. 1997): (1) plain mixed forests (PMF – 0 m a.s.l.); (2) low mountainous mixed forests (LMMF – 500 m a.s.l.); Beech (Fagus orientalis Lipsky), Ash (Fraxinus excelsior L.), Parrotia persica C. A. Meyer, Acer (Acer velutinum Boiss) and Carpinus betulus; (3) middle mountainous mixed forests (MMMF – 1000 m a.s.l.): Beech (Fagus orientalis Lipsky), Ash (Fraxinus excelsior L.), Parrotia persica C. A. Meyer, Acer (Acer velutinum Boiss) and Carpinus betulus; (4) high mountainous pure forests (HMFP – 1500 m a.s.l.): Fagus orientalis Lipsky; (5) forest-grassland ecotone (F-GE – 2000 m a.s.l.): Hawthorn (Craetaegus sp.), Pear (Pyrus communis L.), Apple (Malus communis L.), Barberry (Berberis  crataegi), Maple-AC (Acer campestre L.).

The mean annual temperature at PMF, LMMF, MMMF, HMFP and F-GE are 8.98, 8.43, 8.76 and 8.44 mm in PMF, LMMF, MMMF, HMFP and F-GE, respectively (Karger et al. 2017). About 35-45% of the rainfall occurs in autumn (from September to November), 18-35% in winter (December to February), and the rest (10-20%) in summer (June to August; Noushahr city meteorological station, 1977-2010 – Fig. S2 in Supplementary material). Based on World Reference Basis (WRB) and USDA Soil Taxonomies, plain forest soils were classified as Cambisols (Inceptisols), low and medium altitudes as Luvisols (Alfisols), and higher altitudes as Phaeozems (Molisols) and Cambisols, developed on dolo- lime mounds belonging to the upper Jurassic and lower Cretaceous period (Khalighi et al. 1997, IUSS Working Group 2015).

Experimental design, tree investigation, humus identification, forest floor and soil sampling

At each altitude (0, 500, 1000, 1500 and 2000 m a.s.l.), three 1-ha plots with at least 1500 m distance were delimited. Elevation at each plot was recorded using a Garmin™ model GPSMAP® 60Cx (Olathe, KS, USA). Aspect values were assigned using angles from 0 to 360° given by a pocket compass. In each plot, three random subplots (400 m²) were chosen for sampling. All living trees were counted at each subplot. The diameter at breast-height (DBH, 1.3 m) and total height (> 1.3 m) of all living trees were measured with a diameter tape and Impulse® 200 Laser Hypsometer (Laser Technology Inc., Centennial, CO, USA), respectively (Tab. 1).

The experiment was conducted during April 2018. Humus profiles (Organic: OL, OF, OH; and organic-mineral: AH) and diagnostic horizons were described and sampled at the corners and at the center of each sub-plot using a metal frame (30×30 cm). The morphological characteristics of each humus profile were described according to Zanella et al. (2018). The basal elements of the adopted humus classifications are reported in Tab. S1 (Supplementary material). Humus layer thickness (HLT) was also measured with a tape from the forest floor surface to the top of the mineral soil. The earthworm ecological groups (i.e., Epi...
geic, Anecic and Endogeic) were also identified (Bohlen 2002). Forest floor samples including OL and OF layers were finely mixed before sampling. To remove soil, the forest floor samples were soaked gently in tap water for a few seconds (this is not recommended for samples dominated by OH layers) and then dried at 70 °C for 48 h. Dried forest floor samples were finely grounded/homogenized with an electric mixer and analyzed.

Top mineral soils (depth 0-10 cm) were collected after removal of the organic layers. Using a standard soil auger (5 cm inner diameter). Soil temperature (ST) was measured at a depth 0-10 cm with a portable temperature probe (model TA-288). Since no rainfall occurred during the sampling time, temperature was quite constant during the day.

To determine microbial biomass, the soil samples were immediately transferred to sterile bags, placed in a cooled and insu- lated container, transferred to the laboratory and stored at 4 °C. Soil samples used for physico-chemical analyses were air-dried and passed through a 2-mm sieve. In total, 225 samples were analyzed in this study (5 altitude levels × 3 plots × 3 sub-plots × 5 profiles). The soils and forest floors collected from five elevation level were mixed and the mean of the humus layers and percentage of humus form were used to compute humus layer thickness and humus form classification, respective- ly.

Laboratory analysis of forest floor and soil physico-chemical and biological properties

Forest floor carbon (FFC) and nitrogen (FFN) contents were determined through fumigation-extraction method with a conversion factor of 0.45 for microbial C and 0.54 for microbial N (Brookes et al. 1985, Sparling et al. 1998).

Statistical analysis

The normality of data was checked by the Shapiro-Wilk test. For non-normally distributed data, the Spearman’s correlation analysis was performed. All statistical analyses were conducted using SPSS® v. 16 (IBM Corp., Armonk, NY, USA). Multivariate correlations were analyzed using factor analysis based on principal components analyses (PCA) performed by the software PC-Ord v. 5.0 (McCune & Mefford 1999).

Results

PCA revealed significant changes in all studied soil and humus characteristics along the altitudinal gradient (Tab. 2, Fig. 1A-B), with greater than 45 percent of variations being explained. The left side of the

<table>
<thead>
<tr>
<th>Feaures</th>
<th>PC1</th>
<th>PC2</th>
<th>Features</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree density</td>
<td>-0.56 **</td>
<td>0.25</td>
<td>Eumacroamphi</td>
<td>-0.33</td>
<td>-0.20</td>
</tr>
<tr>
<td>Tree basal area</td>
<td>0.39 *</td>
<td>-0.40</td>
<td>Eumesamphi</td>
<td>-0.35 *</td>
<td>-0.37 *</td>
</tr>
<tr>
<td>Tree crown density</td>
<td>0.60 **</td>
<td>-0.67 **</td>
<td>Pachyamphi</td>
<td>-0.38 *</td>
<td>-0.25</td>
</tr>
<tr>
<td>Mean tree height</td>
<td>0.34 *</td>
<td>-0.76 **</td>
<td>FFC</td>
<td>-0.32</td>
<td>-0.50 **</td>
</tr>
<tr>
<td>OL</td>
<td>-0.65 **</td>
<td>-0.63 **</td>
<td>FFN</td>
<td>0.16</td>
<td>0.07</td>
</tr>
<tr>
<td>OF</td>
<td>-0.75 **</td>
<td>-0.32</td>
<td>FFC/N</td>
<td>-0.24</td>
<td>-0.23</td>
</tr>
<tr>
<td>OH</td>
<td>-0.67 **</td>
<td>-0.50 **</td>
<td>SM</td>
<td>-0.35 *</td>
<td>-0.26</td>
</tr>
<tr>
<td>AH</td>
<td>0.57 **</td>
<td>-0.43 *</td>
<td>ST</td>
<td>0.89 **</td>
<td>-0.25</td>
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<tr>
<td>Eumull</td>
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<td>0.04</td>
<td>pH</td>
<td>0.23</td>
<td>-0.61 **</td>
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<tr>
<td>Mesomull</td>
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<td>0.03</td>
<td>CaCO3</td>
<td>0.20</td>
<td>-0.32</td>
</tr>
<tr>
<td>Oligomull</td>
<td>0.54 **</td>
<td>-0.09</td>
<td>SOC</td>
<td>-0.42 *</td>
<td>-0.75 **</td>
</tr>
<tr>
<td>Rhizo Mesomull</td>
<td>-0.12</td>
<td>0.25</td>
<td>SN</td>
<td>0.24</td>
<td>-0.55 **</td>
</tr>
<tr>
<td>Rhizo Oligomull</td>
<td>-0.24</td>
<td>0.54 **</td>
<td>SC/N</td>
<td>-0.63 **</td>
<td>-0.23</td>
</tr>
<tr>
<td>Rhizo Dysmull</td>
<td>-0.24</td>
<td>0.54 **</td>
<td>MBC</td>
<td>-0.004</td>
<td>-0.47 **</td>
</tr>
<tr>
<td>Leptooamphi</td>
<td>-0.04</td>
<td>-0.22</td>
<td>MBN</td>
<td>0.70 **</td>
<td>-0.02</td>
</tr>
</tbody>
</table>

Tab. 2 - Correlation of vegetation, humus forms and soil features with PCA components. (*): p < 0.05; (**) p < 0.01.
PC axis 1 reflects low quality of forest floor (i.e., high FFC, FFC/N and thickness), and soil (i.e., higher values of SOC and C/N) which resulted in the formation of Amphi humus forms under high mountainous pure forests (Fig. 1B). The right side of PC axis 1, instead, corresponds to conditions with higher forest productivity (tree basal area, tree crown density and mean tree height), improved forest floor (i.e., N) and soil characteristics (N content, MBN, pH and CaCO₃). In these conditions, the frequency of the null humus forms was higher (plain mixed and low mountainous mixed forests – Fig. 1B). Middle mountainous mixed forests showed intermediate conditions with regard to the forest floor and soil properties and thus a strong relationship with leptoamphi humus and MBC (Fig. 1B). In addition, the forest-grassland ecotone with Rhizo-Mull humus forms did not show any relationship with soil properties (Fig. 1B).

As expected, canopy composition, stand features, humus forms and their characteristics changed with altitude (Tab. 1, Tab. 2). In the plain forest, ironwood was the dominant species followed by oak and hornbeam. However, ironwood density decreased with altitude and this species was totally absent at altitudes above 1500 m a.s.l. At intermediate altitudes (500 and 1000 m), beech, ash and maple were the dominant species, while at higher altitude (1500 m) only beech was present. Above 2000 m a.s.l., Hawthorn was the most common species. Total tree density significantly increased with altitude (R = 0.54, p < 0.01), while basal area (R = -0.39, p < 0.01), crown density (R = -0.79, p < 0.01) and mean tree height (R = -0.53, p < 0.01) decreased.

Alitudinal gradient significantly affected the abundance of the humus systems (p < 0.001) and humus forms (p < 0.001 – Fig. 2A). Mull was the dominant system below 1000 m a.s.l.; Amphi appeared at 1000 m and dominated at 1500 m; Rhizo Mull was dominant under F-GE at 2000 m a.s.l. Oligomull was the most common form at 0 and 1000 m and Eumull at 500 m (Fig. 2B). At higher altitudes, no dominant humus form was detected. In fact, Eumacro, Eumusco and Pachyamphi humus forms were equally represented at 1500 m, while at 2000 m Rhizo Mesomull, Rhizo Oligomull and Rhizo Dymull were equally abundant (Fig. 2B).

The thickness of the organic layers including OL, OF, OH significantly increased with altitude (R = 0.36, p < 0.05; R = 0.53, p < 0.01; R = 0.36, p < 0.05; respectively), whereas the organic-mineral thickness (AH) decreased (R = -0.62, p < 0.01 – Tab. 3, Fig. 3). The thickness of OL and OF at 1500 m was approximately 2.5 times greater than that at the other altitudes (p < 0.001); the highest thickness of OH was recorded at 1500 m a.s.l., while this layer was not observed at 0, 500 and 2000 m altitudes (Tab. 3, Fig. 3).

No clear relationship was observed between forest floor properties (C, N and C/N ratio) and altitude (Tab. 3), though some significant differences among forest types were detected (Fig. 4). The highest value of forest floor C was found in high mountainous pure forests (Fig. 4A), while the forest floor N was significantly higher at the plain mixed forests (Fig. 4B). The plain mixed forests, however, showed the lowest forest floor C/N ratio (Fig. 4C), while low and high mountainous mixed forests showed the highest forest floor C/N ratio (Fig. 4C).

Soil properties, however, significantly changed with altitude (Tab. 3, Fig. 5). Soil temperature differed among forest types and decreased with altitude (R = -0.94, p < 0.01). The lowest soil moisture was measured in plain mixed forests, while the high-

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**Table 3**: One-way analysis of variance (ANOVA) and Pearson’s correlation coefficients (R_{corr}) of forest floor and soil characteristics along the altitudinal gradients. (*): p < 0.05; (**): p < 0.01.

<table>
<thead>
<tr>
<th>Humus and soil properties</th>
<th>Variables</th>
<th>Abbr.</th>
<th>F test</th>
<th>P value</th>
<th>R_{corr}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humus layers thickness</td>
<td>Organic litter (cm)</td>
<td>OL</td>
<td>81.86</td>
<td>&lt;0.001</td>
<td>0.36*</td>
</tr>
<tr>
<td></td>
<td>Organic fragmentation (cm)</td>
<td>OF</td>
<td>21.73</td>
<td>&lt;0.001</td>
<td>0.53**</td>
</tr>
<tr>
<td></td>
<td>Organic humus (cm)</td>
<td>OH</td>
<td>40.81</td>
<td>&lt;0.001</td>
<td>0.36*</td>
</tr>
<tr>
<td></td>
<td>Organic-mineral layer (cm)</td>
<td>AH</td>
<td>11.32</td>
<td>&lt;0.001</td>
<td>-0.62**</td>
</tr>
<tr>
<td>Forest floor properties</td>
<td>Forest floor carbon (%)</td>
<td>FFC</td>
<td>3.74</td>
<td>0.012</td>
<td>0.093</td>
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<tr>
<td></td>
<td>Forest floor nitrogen (%)</td>
<td>FFN</td>
<td>15.84</td>
<td>&lt;0.001</td>
<td>-0.09</td>
</tr>
<tr>
<td></td>
<td>Forest floor C/N</td>
<td>FFC/N</td>
<td>5.80</td>
<td>&lt;0.001</td>
<td>0.11</td>
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<td>Soil physical properties</td>
<td>Soil moisture (%)</td>
<td>SM</td>
<td>3.24</td>
<td>0.021</td>
<td>0.25</td>
</tr>
<tr>
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<td>Soil temperature (°C)</td>
<td>ST</td>
<td>219.97</td>
<td>&lt;0.001</td>
<td>-0.94**</td>
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<td>Soil chemical properties</td>
<td>Soil pH</td>
<td>pH</td>
<td>75.08</td>
<td>&lt;0.001</td>
<td>-0.51**</td>
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<tr>
<td></td>
<td>Calcium carbonate (%)</td>
<td>CaCO₃</td>
<td>16.04</td>
<td>&lt;0.001</td>
<td>-0.45*</td>
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<tr>
<td></td>
<td>Soil organic carbon (%)</td>
<td>SOC</td>
<td>30.25</td>
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<td></td>
<td>Soil nitrogen (%)</td>
<td>SN</td>
<td>11.11</td>
<td>&lt;0.001</td>
<td>-0.39**</td>
</tr>
<tr>
<td></td>
<td>Soil C/N</td>
<td>SC/N</td>
<td>19.14</td>
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<td>0.53**</td>
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<tr>
<td>Soil biological properties</td>
<td>Microbial biomass carbon (mg kg⁻¹)</td>
<td>MBC</td>
<td>24.22</td>
<td>&lt;0.001</td>
<td>-0.007</td>
</tr>
<tr>
<td></td>
<td>Microbial biomass nitrogen (mg kg⁻¹)</td>
<td>MBN</td>
<td>44.08</td>
<td>&lt;0.001</td>
<td>-0.70**</td>
</tr>
</tbody>
</table>
Humus and soil dynamics along a forest altitudinal gradient

est was recorded in high mountainous pure forests (Fig. 5A, Tab. 3). On the contrary, soil pH (R = -0.51, p < 0.01), calcium carbonate (R = -0.45, p < 0.01), soil N (R = -0.39, p < 0.01) and microbial biomass nitrogen (R = -0.70, p < 0.01) decreased with altitude, while soil C/N ratio increased (R = 0.53, p < 0.01). The highest soil pH and CaCO3 concentration were observed in plain mixed forests and high mountainous pure forests and the lowest in forest-grassland ecotone (Fig. 5B). The highest concentrations of soil C, C/N ratios and BMC values were measured under high and middle mountainous forests, whereas plain mixed forests showed the highest soil N concentrations and BMN values (Fig. 6).

Discussion
We showed that there exist significant associations between altitudinal gradient and forest characteristics including tree composition, stem density, tree height in Hycranian forest in northern Iran, consistently with findings of other studies previously published (Naqinezhad et al. 2013, Bayranvand et al. 2018). The distribution of humus forms also changed with altitudinal gradient. Particularly, Mull humus forms decreased with altitude, while Amphi forms increased. With respect to the forest type, our results showed that Oligomull and Lep-toamphi were dominant in mixed beech

![Fig. 3 - Organic (OL, OF and OH) and organic-mineral (AH) humus layers thickness along the altitudinal gradient. Error bars indicate standard error (n = 45).](image-url)

![Fig. 4 - Mean floor carbon (A), nitrogen (B), and C/N ratio (C) among the altitude levels. Different letters indicate significant differences (p < 0.05) according to the ANOVA and Tukey HSD test. Error bars indicate standard error (n=9). (PMF): plain mixed forests; (LMMF): low mountainous mixed forests; (MMMF): middle mountainous mixed forests; (HMPF): high mountainous pure forests; (F-GE): forest-grassland ecotone.](image-url)

![Fig. 5 - Mean soil moisture and soil temperature (A), pH and CaCO3, (B) among the altitudes. Different letters indicate significant differences (p < 0.05) based on ANOVA and Tukey HSD test. Error bars indicate standard error (n=9). (PMF): plain mixed forests; (LMMF): low mountainous mixed forests; (MMMF): middle mountainous mixed forests; (HMPF): high mountainous pure forests; (F-GE): forest-grassland ecotone.](image-url)
forests, while in pure beech forests Eu-
macroamphi, Eumesoamphi and Pachyam-
phi were the dominant forms. Previous
study by Waez-Mousavi (2018) also re-
ported that Mull and Amphi are the most
dominant humus systems in the Hycanian
forests. In mixed beech stands, Waez-Mou-
savi & Habashi (2012) reported the domi-
nance of Mull and Amphi humus systems.

Both environmental conditions and tree
species composition influence humus for-
mation and its characteristics. A significant
change in soil temperature, moisture and
species composition was noted in our alti-
tudinal gradient. Previous study revealed
that a decrease in mean temperature asso-
ciates with a decline in Mull humus form
and an increase in Amphi humus (Ponge et
al. 2015). In agreement to our finding in
plain mixed forest, Ponge et al. (2011)
noted that Mull systems are more frequent
at higher tree species diversity and under
rich trophic conditions. In contrary, under
low tree species richness and in colder en-
vvironments, Moder and Amphi humus sys-
tems with OF and OH layers are dominant
(Badía-Villas & Girona-García 2018). Labaz
et al. (2014) showed that Amphi humus
forms can be found in cold conditions
where organic matter decomposition is slower. Previous study by Waez-Mousavi &
Habashi (2012) indicated that Mull humus
forms are abundant under forest types
with higher floor quality and decomposi-
tion rate, while Amphi and Moder humus
forms are observed under beech forest type
with low floor quality (high C and low
N – Bayranvand et al. 2017a). Mull humus
forms are biologically active (Endogeic and
Anecic with high activity) with fine-granular
structure, which have low SOC content
compared to humus forms with OF and OH
layers (Jabiol et al. 2013, Labaz et al. 2014).
Moder forms are abundant in beech domi-
nated forest with low soil pH (< 5.5), while
Mull forms are absent in non-beech stands
(Bayranvand et al. 2018). The increased

Amphi humus form under pure beech for-
est (1500 m) could likely be due to high soil
pH (> 7.5) resulted from high CaCO3-concen-
trations (Li et al. 2018). The CaCO3 concen-
tration has probably a positive impact on the
forest floor decomposition rate and soil microbial activity (Guo et al. 2019) and
could likely facilitate the transition from
Moder to Amphi form (Labaz et al. 2014, Bonificacio et al. 2018).

Previous studies showed that climatic
(moisture and temperature) and biotic fac-
tors (species type and richness) are impor-
tant factors influencing humus accumula-
tion (Zanella et al. 2011, Labaz et al. 2014,
Badía-Villas & Girona-García 2018). In our
study, the thickness of OL, OF, OH layers
significantly were increased, while that of
AH was decreased. The more favorable
conditions for organic matter decomposi-
tion in plain mixed forests (i.e., high tem-
perature, good soil moisture and high litter
quality) is likely the cause (Salmon 2018).
Similarly, Bonificacio et al. (2018) also
showed that the OH layer thickness in beech forests with a low litter quality is
higher than in hornbeam, maple and ash
forests (Labaz et al. 2014). Thus, the higher
OH layer thickness at 1500 m a.s.l. found in
this study can be attributed to the low
temperature in this elevation level, which
slow down mineralization rates (Badía-Vil-
as & Girona-García 2018), decrease litter
quality under beech (Bayranvand et al.
2017a) and higher soil moisture (Zanella et
al. 2011).

The chemical composition of humus and
soil are the result of the interaction of
many factors including topography, cli-
mate, tree cover and soil microbial commu-
nities (Ponge et al. 2011). Shedayi et al.
(2016) showed that altitude has a low im-
pact on soil organic carbon and nitrogen,
while vegetation cover explains most of
the measured variations. Bayranvand et al.
(2017a) reported that, although tree spe-
cies affect soil chemical properties (i.e., pH,
C, and N content), earthworm and microb-
ial activity were mostly controlled by cli-
mate. Our results support the idea that soil
properties including temperature, pH,
CaCO3, soil N content, soil C/N and microb-
ial biomass N are significantly correlated
with altitude, while most forest floor prop-
erties are not directly influenced by tem-
perature, but affected by tree species com-
position. In fact, litter quality influences
both decomposition rates and the dynamic
of nutrient mineralization (Lucas-Borja et
al. 2019). Previous studies have argued that
higher forest floor N concentrations are as-
associated with faster litter decomposition
rates (Kooh & Bayranvand 2017, Lucas-
Borja et al. 2019). A decrease in forest floor
quality (high C content and high C/N ratio)
was reported to associate with a higher hu-
mus layer thickness and a decreased de-
composition rate in beech dominated for-
est at high altitudes (Bayranvand et al.
2017b). In fact, litter is known for having a high lignin/N ratio and a relatively low
contents of basic cations and N (Bonif-
cacio et al. 2018). In agreement with our
findings, low humus layer thickness is re-
lated to high quality floors in maple, iron-
wood, alder and hornbeam (Kooh & Bay-
Forest floor C/N ratio and N content are
the two most important factors influencing
litter decomposition and nutrient release
(Lucas-Borja et al. 2019).

Badía-Villas & Girona-García (2018) re-
ported that forest floor N in mountain for-
est in Spain is decreased during shift from
Mull to Amphi forms with increasing eleva-
tion. Ponge et al. (2011) measured lower C
content in Mull than in other humus forms.
It could be speculated that Mull forms de-
compose faster and introduce more N into
the soil. Zanella et al. (2011) argued that
forest floor and soil C/N ratios in Mull are
usually lower than in Amphi and the C/N is
an important indicator for the decomposi-
tion rate and nutrient cycling in the humus
Humus and soil dynamics along a forest altitudinal gradient

and soil. Our data also showed a significant decrease in soil MBN under different canopy compositions along the elevation gradient. MBN was significantly higher in mixed forest types (i.e., PMF) at the lowest elevation than in pure stands at the highest elevation levels (i.e., HMPF). This may be the result of a greater and a more diverse litter input in stands with a higher species richness or diversity (Wang & Wang 2011). Many investigations have also documented that soil microbial community structure is primarily driven by soil pH and C:N ratio as the altitude increases. Thus, higher levels of pH, such as those at low elevations, may be related to increased microbial biomass and bacterial diversity (Xu et al. 2015). Higher levels of soil temperature and N content, such as those at low elevations, may contribute to a larger microbial biomass (Xu et al. 2015, Bojko & Kabala 2017, Gou et al. 2019).

Beech litter quality, FFC accumulation and lower earthworm activity are main factors affecting soil quality in this forest system. PMF was correlated with Mull humus and higher forest floor and soil quality (high FFN and SN; low FFC and SN). In this condition, tree species composition along with high biological and microbial activities (i.e., high temperature and soil water content) speed up organic matter decomposition (Zaïets & Poch 2016). Mull humus forms are nutrient rich systems with fast nutrient cycling (Andreotta et al. 2011) which are associated to high earthworm activity and microbial biomass. In hornbeam and maple trees (MMMF) forest systems, higher forest floor quality and improved soil fertility support larger biological activities than in pure beech forests (Kooch & Bayramvand 2017).

Conclusion

Altitudinal gradient is a key factor determining the distribution of humus forms. Soil properties (temperature, pH, CaCO$_3$, N content, C:N and MBN) were significantly correlated with altitude, while forest floor properties were more influenced by tree species composition. Our data suggest that the abundance of Mull forms decrease from plain mixed forests to high mountain pure forests, whereas the frequency of Amphí humus forms increase. On the other hand, Oligomull and Leptooamphi are more abundant in mixed beech forests, while Eumacroamphi, Eumesooamphi and Pachyamphi are observed only in pure beech forests. In addition, plain mixed forests typically have higher quality of both forest floor (i.e., N) and soil (i.e., pH, CaCO$_3$, soil N content, soil C:N and MBN) than high mountainous pure one, while middle mixed forests show intermediate characteristics.

Abbreviations


Author contributions

MB and MA conceived and designed the experiment. MB performed the experiment. MB, GA and GS-J carried out the statistical analysis. MB, JC, GA and GS-J contributed to the data analysis and data interpretation. MB, JC, GS-J and CA wrote and edited the manuscript.

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References


Supplementary Material

Fig. S1 - (a) The Central Caspian region of northern Iran; (b) the study site at the Experimental Forest Station (Vaz watershed).

Fig. S2 - Mean monthly air temperature (°C) and precipitation (mm) at the study site based on the Noushahr city meteorological station report.

Fig. S3 - Two examples of humus profiles at the sea level (0 m a.s.l. - PMF).

Fig. S4 - Two examples of humus profiles at the 500 m a.s.l. (LMMF).

Fig. S5 - Two examples of humus profiles at the 1000 m a.s.l. (MMMF).

Fig. S6 - One example of humus profile at the 1500 m a.s.l. (HMPF).

Fig. S7 - Two examples of humus profiles at the 2000 m a.s.l. (F-GE).

Tab. S1 - Humus systems (Mull, Rhizo Mull and Amphi), Humus forms (Eumell, Mesomull, Oligomull, Rhizo Mesomull, Rhizo Oligomull and Rhizo Dymull; Leptoamphi, Eumacroamphi and Eumesoamphi and Pachyamphi) and their diagnostic horizons.

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