1   **Tree or soil? Factors influencing humus form differentiation in Italian forests.**

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12

13   Abstract

14   We aim to investigate the occurrence of forest humus forms (Moder, Amphi and Mull) in relation to
15   environmental factors describing parent material, climate and tree species. Boosted regression trees (BRT)
16   were applied as modelling tool to analyse data of 238 plots of the BioSoil database covering the whole
17   Italian forest territory. Though predictive ability was not very high, especially for the Amphi form, we could
18   gain significant insight into factors controlling humus form differentiation. In the BRT analysis, the diversity
19   of tree species was the most important predictor for Moder and Mull models and specific plant effects
20   were evidenced. However, our results showed that the geographic distribution of Italian forest species was
21   influenced by soil and climate conditions, partly explaining the high weight of tree species as factor. The
22   importance of the soil nutritional status, due to parent material properties, in driving humus form
23   differentiation was stated, highlighting the key role played by pH and calcium content, with the hitherto
24   understated importance of phosphorus. This study further clarified the functioning of the still poorly
25   understood Amphi form. Reduced effective soil volume (EfVol) combined with seasonality appeared to
26   constrain pedofauna activity in otherwise favorable and nutrient rich systems, favoring the evolution of
27   Amphi instead of Mull forms.

29

30   1. Introduction

31   Humus forms are the morphological expression of the pathways through which organic debris are either

32   incorporated within the mineral topsoil or accumulated on top of it, to form ectorganic horizons (Ponge,

33   2003, Zanella et al., 2011). Numerous studies (see Ponge, 2003, 2013 for reviews) have established that

34   humus forms result from composition, biomass, activity and behaviour of soil meso- and micro-fauna; in

35   turn, these biotic factors are controlled by nutrient availability and pedoclimate conditions (Wall et al.,

36   2008). Nutrient availability is conditioned by soil fertility, but also by complex feedbacks involving soil

37   microbiota, climate (Aerts, 2006) and plants (Hooper et al., 2000), through litter quality and quantity.

38   Further feedbacks were identified in relation to forest stand life cycle and development (Mulder et al., 2013;

39   Ponge and Chevalier, 2006; Schaefer and Schauermann, 1990; Scheu and Falca, 2000), influencing sign and

40   magnitude of soil-plant nutrient transfers and, also, pedoclimate, through control on soil insolation and

41   temperature exerted by stand density, LAI, continuity etc. Extensive knowledge of these relationships

42   brought Ponge (2003) to point to humus forms as keys to soil biodiversity and as indicators of ecosystem

43   nutrient management strategies. More recently, humus forms have been found to be significant indicators

44   of soil organic carbon storage (Andreetta et al., 2011; De Vos et al., 2015).

45   Existing data demonstrate how humus forms react punctually and rapidly to even small changes in soil

46   nature, forest life cycle and forest management (Ponge et al., 2014) and this, given their easy experimental

47   access, leads them to be proposed as practically useful keys to forest ecosystem surveys (Andreetta et al.,

48   2011; Ponge et al., 2014). In more general terms, humus forms might have a potential to represent what

49   soils, in their entirety, were expected to represent at the dawn of Pedology, i.e., a faithful "impression" of

50   the environment (climate, biota, drainage) on a portion of the Earth's crust, and are responsive enough to

51   change accordingly to environmental changes, thus offering an "integrating" view of ongoing environmental

52   processes and their results.

53   Recently, analysis of the factors driving humus form differentiation has received increasing attention

54   (Labaz et al., 2014; Ponge et al., 2011, 2014), but a basic issue in these analysis still requires more

55   investigation. This is the relative weight of different kind of factors, which may be alternately defined as

56   "distal" (geology, climate, main tree species) vs. "proximal" (topsoil conditions, litter quality, microbiota) or

57   as "truly independent" vs. "co-varying with humus". Ponge et al. (2011) showed that, for the French

58   territory, geology and climate were the major determinants of humus forms, while the influence of forest

59   canopies was negligible. Labaz et al. (2014) found that bedrock geology was the least influencing factor on

60   humus forms, though they pointed out that this result was possibly influenced by relatively homogeneous

61   geology in their sample. In Veneto (Northern Italy), Ponge et al. (2014) showed that the first canonical

62   component of the projection of environmental variables could be interpreted as a composite factor

63   embracing both geological, climate and soil gradients. They also showed that geology, climate, soil and

64   vegetation exert a prominent influence on the distribution of humus forms.

65   This study takes advantage of the existence of a database covering the entirety of Italy as produced by the

66   BioSoil project, to identify the environmental factors that mostly influence the occurrence of Moder, Amphi

67   and Mull forms, treated in three separated models, at national level. Differently from comparable studies

68   (Cools et al., 2014; Ponge et al., 2011, 2013) the central aim of this study is not to select covariates for

69   upscaling humus form observations at national or continental scale, but rather to get deeper into

70   elucidating factors controlling humus form development, involved processes, and soil-humus feedbacks.

71   Studies that have previously applied the same model tool of the present work to determine the main

72   factors explaining forest floor parameters such as C/N ratio (Cools et al., 2014) and C stock (De Vos et al.,

73   2015), found that the diversity of tree species was clearly the most important predictor. Due to the close

74   link between humus forms and carbon-related parameters (Andreetta et al., 2011, 2013a, 2013b; Bonifacio

75   et al., 2011; De Nicola et al., 2014), we hypothesized that tree species were also associated to humus forms

76   with high relative influence score. A specific objective was then to deeply analysed interactions between

77   tree species and other environmental factors.

78   2. Materials and methods

79   2.1 Study area

80   Studied sites were made up by the Level I sites of the European ICP-Forests network, based on a 16 km × 16

81   km grid (Van Ranst et al., 1998), modified to 15 by 18 km in Italy. Sites are located across the whole Italian

82   territory. Sampling was carried out according to standard ICP-Forests protocols (FSCC, 2006). At each site,

83   composite samples were made from samples collected at five different points. Organic horizons OF and OH

84   were sampled together by a 25 × 25 cm frame, as OFH layer, due to their inconsistent and, in some cases,

85   small thickness. Mineral soil was sampled to represent fixed soil depth intervals (0-10 cm; 10-20 cm; 20-40

86   cm; 40-80 cm).

87   2.2. Humus form classification

88   Humus forms were classified according to the structure (IUSS Working Group WRB, 2006) of the first

89   mineral horizon (Fao et al., 2006) and the presence/absence of the OH horizon. Classification corresponds

90   to the higher hierarchical level of the European Humus Group proposal (Zanella et al., 2011), namely:

91   -   Moder, with massive E-AE or bio-microstructured (peds $\emptyset \leq 1$ mm) A horizon and organic horizons

92   (OL, OF and OH) present;

93   -   Amphi, with either bio-mesostructured (1 mm < $\emptyset \leq 5$ mm) or bio-macrostructured ($\emptyset$ >5 mm) A

94   horizon and the presence of organic horizons (OL, OF and OH);

95   -   Mull, with bio-mesostructured (1 mm < $\emptyset \leq 5$ mm) or bio-macrostructured ($\emptyset$ >5 mm) A horizon and

96   OH horizon absent.

97   Due to their rare occurrence in Italy, Mor forms were not considered in this study.

98   2.3 Soil analysis

99   Analytical methods followed the ICP Forests Manual on sampling and analysis of soil (FSCC, 2006; ICP-

100   Forests, 2010). Specifically, soil pH was measured in the supernatant suspension of a 1:2.5 soil:water

101   mixture, exchangeable cations were determined after exchange with an unbuffered 0.1M $BaCl_2$ solution,

102   while extractable elements were determined in *aqua regia* extracts.

103   *2.4 Statistical analyses*

104   In order to evaluate differences in all parameters between humus forms and tree species populations, a

105   non-parametric statistical test (Kruskal–Wallis) was applied due to non-normal distribution of some

106   properties.

107   *2.4.1 Predictor variables*

108   Selection of predictor variables was derived from the forementioned main objectives. Environmental

109   factors such as climate/pedoclimate, parent material and vegetation were selected as primary predictor

110   variables as they have a one-way relation to humus forms, i.e. they are true "independent" variables. Tree

111   species has been considered as partially dependent (Ponge et al., 2011) but there is a shortage of physical

112   hypotheses on such dependence.

113   Climatic data were obtained from the WorldClim database (http://www.worldclim.org/current), a

114   gridded climate database with the very high resolution of 30 arc-seconds ($\approx$1Km^2 or ~0.09°). Data layers are

115   generated through interpolation of average monthly climate measurements from 1950 to 1990, using thin

116   plate splines with climate data from meteorological stations and a digital elevation model to spatially model

117   various climatic variables (Hijmans et al., 2005). For our models, we selected those variables that may affect

118   biological activities, such as the mean temperature of warmest quarter seen as climatic limiting factor, and

119   the range between the precipitation of the wettest quarter and the precipitation of the driest quarter, to

120   represent seasonality.

121   Data from the ICP Forests database do not allow full model estimates of soil water availability; as a proxy

122   data, we used effective soil volume, i.e. the plant- (and earthworm-) available soil volume, in $m^3 \cdot m^{-2}$ of

123   surface area, obtained by subtracting coarse fragment percent volume from soil depth. This parameter is

124   referred to as EfVol.

125   Parent material (p.m.) was recorded according to FSCC (2006); this is a simplified way, often derived

126 from available geological maps. As such, it is equivalent to "Geology" as in Ponge et al. (2011) and De Vos et

127 al. (2015); it is one of the most useful variables for upscaling geographical distribution of humus forms and

128 carbon stocks, but not as much to understand relationships between p.m. and humus forms. In the models,

129 we included subsoil extractable Ca (sub.Ca), subsoil total P (sub.P) and pH (sub.pH) as properties indicative

130 of p.m. These parameters were those obtained from the deepest samples. Sub.Ca and sub.P were included

131 in the model after being log transformed to improve readability of the partial dependence plots.

132   The 'Tree' variable was taken from the dominant tree species recorded in ICP Forests crown condition

133 survey (Lorenz et al., 2004). Frequency of individual tree species was quite variable. According to Cools et

134 al. (2014), species were grouped to obtain groups of no less than 20 sites (Table 1). The most frequent

135 species (Norway spruce, *Picea abies* (Pabi)*,* European beech*, Fagus sylvatica* (Fsyl)*,* sweet chestnut,

136 *Castanea sativa* (Csat)*,* Turkey oak, *Quercus cerris* (Qcer)) were analysed as pure groups. Other species were

137 grouped according to physiological and ecological similarities, as follows: Conif included all conifers except

138 *P. abies*; this group is dominated by black pine *(Pinus nigra*) and European larch (*Larix decidua*). "Other"

139 grouped all broadleaved trees except *F. sylvatica*, *C. sativa* and oaks. Qpub included all strictly deciduous

140 oaks, i.e. excluding *Q. cerris*; this group is dominated by downy oak (*Quercus pubescens*). Med grouped all

141 sclerophyll oaks, mostly holm oak (*Quercus ilex*); in this group we also included other Mediterranean

142 species such as *Pinus halepensis* and *Eucalyptus* spp*.*

143

144   *2.4.2 Model Building*

145   Boosted Regression Trees (BRT) were applied as a modelling tool to explore the influence of

146 environmental factors on the occurrence (as presence/absence) of humus forms. BRT are a relatively new

147 statistical method, based on techniques from both statistical and machine learning methods (Friedman et

148 al., 2000; Elith et al., 2008), and are increasingly applied in spatial modelling of species or environmental

149 variables, including soil parameters. BRT are very flexible and capable of dealing with complex responses,

150 including nonlinearities and interactions (Elith et al., 2008). BRT performed well in soil modelling (Ciampalini

151 et al., 2014; Cools et al., 2014; De Vos et al., 2015) and have been applied in various study domains, from

152 predicting the distribution of organisms (Elith et al., 2008) to comparing the factors of cropland

153 abandonment (Müller et al., 2013). Regression trees predict a response from observations and one or more

154 continuous or categorical predictor variables, and boosting uses a forward stagewise procedure to gradually

155 add regression trees to the model. BRT show several advantages, since they can accommodate any type of

156 variable (continuous, categorical, nominal), missing and non-independent data and can also deal with many

157 distribution types (Gaussian, binomial, Poisson etc.). Additionally, a BRT model allows the derivation of

158 partial dependence plots, which indicate how the response is affected by a certain predictor after

159 accounting for the average effects of all other predictors in the model. These plots can be used for

160 interpreting model behaviour (Elith et al., 2008).

161 We built three different models, one for each humus form, applying the BRT using the R version 3.0.2 (R

162 Development Core Team, 2013), package ''dismo'' version 0.9–3 (Hijmans et al., 2013). We applied the

163 gbm.step function of the dismo package, which assesses the optimal number of boosting trees using cross

164 validation. We tested various combinations of the learning rate (0.01 to 0.001), which controls the

165 contribution of each tree to the growing model, and tree complexity (3 to 5), the number of splits levels of

166 each tree. By changing these two parameters the number of trees (nt) required for optimal model fit was

167 calculated. Bag fraction, used to control model stochasticity, was set at 0.5. The most effective parameters

168 for our data set were 0.001 for the learning rate and 5 for the tree complexity. The model was fit with a

169 Bernoulli distribution, since we evaluated the presence-absence of each humus form. Cross-validation was

170 performed to estimate the optimal number of trees producing the best predictive performance, which was

171 evaluated by predictive deviance and area under the receiver operator characteristic curve (ROC AUC).

172

173 *2.5 Soil variables*

174 "Soil" variables, relative to actual topsoil properties, which, of course, are linked to humus forms by two-

175 way interactions, were not included as predictors in the models, but were analysed statistically and

176 considered in the discussion. The selected parameters were those linked to the subsoil properties: topsoil

177 (0-10 cm) pH, Ca and P content; exchangeable aluminum (Exc_Al) was also included due to its effects on

178 biotic activity.

179 Topsoil P and Ca content (0-10 cm) were related to litter (P_OL and Ca_OL) and subsoil P and Ca content

180 (sub.P and sub.Ca) through single linear regressions, after log10 transforming.

181

182 3. Results and discussion

183 The surveyed humus forms (n=238) were classified as Moder (n=57), Amphi (n=92) and Mull (n=89).

184 Existing studies (Cools et al., 2014; Ponge et al, 2011; Ponge, 2013) concentrate on the Mull-Moder-Mor

185 series, Amphi forms representing minor proportions of the populations they examined. However, it is clear

186 how Amphi is a major humus form throughout Italy (Andreetta et al., 2011, 2013b; De Nicola et al., 2014;

187 Ponge et al., 2014). The issue of the conditions determining the appearance of Amphi forms is then primary

188 to the understanding of humus ecology in Italy.

189

190 *3.1 Boosted Regression Trees*

191 The relative importance of the predictors in BRT models (Table 2), and the correspondent partial

192 dependence plots for each predictor and probability of humus form occurrence (Fig. 1, 2, 3) were identified.

193 The best model for Moder included 1900 trees and showed a cross-validated ROC AUC score of 0.825 and a

194 training ROC AUC of 0.972 (55% of the variance explained). The selected model for Amphi included 1100

195 trees and showed a cross-validated ROC AUC score of 0.65 and a training ROC AUC of 0.882 (25% of the

196 variance explained). The best model for Mull included 2250 trees and showed a cross-validated ROC AUC

197 score of 0.742 and a training ROC AUC of 0.95 (40% of the variance explained). The Moder model reached

198 thus better performance than Mull and Amphi models. Grouping together macro and meso-structured

199 forms likely led to highly variable populations of these two main forms, as meso- and macro- groups were

200 reported to be differentiated in terms of soil organic carbon storage (Andreetta et al., 2011), soil organic

201 matter properties and enzyme activities (Andreetta et al., 2013b) while, on the opposite, meso-structured

202 forms, especially of Mull, show analogies with Moder forms (Andreetta et al., 2011, 2013a, 2013b).

203

204   *3.2 Climate*

205   There was a high probability to find a Moder where the mean temperature of warmest quarter (tmax)

206 was below 15°C (Table 3 and Fig 1); in contrast, Mull prevailed where tmax was higher than 15°C (Table 3

207 and Fig 3). A trend similar to Mull, though less marked, was found for Amphi forms (Table 3 and Fig 2).

208 Climate exerts a strong control on litter decomposition rates, both directly and indirectly, through effects on

209 litter chemistry (Aerts, 1997) and soil organisms (Ascher et al., 2012). It is generally agreed that higher

210 temperatures lead to increased decomposition and faunal activity, and decreased mass of organic horizons

211 (Aerts, 2006; Ponge et al., 2011). A different effect on soil organisms may be relevant in Mediterranean

212 conditions; Sadaka and Ponge (2003) and Andreetta et al. (2011) proposed that summer high temperatures

213 and drought force most faunal groups into endogeic behaviour, thus allowing for Mull forms even when

214 other conditions would lead to accumulation of OH horizons. A mirror effect, i.e. an increasing epigeic

215 behaviour with lower temperatures, was reported by Ascher et al. (2012). Climate-tree species interactions

216 should also be influential. Significant differences in occurrence of tree species were associated with MAT

217 and tmax (Table 4), species favouring Mull differentiation often being associated with higher temperatures.

218 On the other hand, mean annual precipitation (MAP) showed no significant differences between tree

219 species except for Mediterranean species (Med) for which it was significantly lower. Rainfall seasonality, as

220 expressed by pmax.min, evidenced that *P. abies* and the Mediterranean species tend to grow in sites where

221 seasonality is more marked, while for all the other species no significant differences were recorded.

222 Pmax.min was a significant variable in both Moder (Fig 1) and Amphi (Fig 2) models. Moder was clearly

223 associated with low pmax.min, while Amphi showed an opposite behaviour. Seasonality seemed to have no

224 effect on the evolution of Mull (Fig 3). Seasonal precipitation affects pedofauna composition, density and

225 activity. It is to be noted that seasonality in this dataset is not to be intended as a synonymous of

226 Mediterranean conditions, as wide areas of the Alpine chain show strong seasonality in precipitation,

227 marked by dry winter conditions.

228   Although we found evidence for climate as a driving force in humus form differentiation, the actual

229   pathways of climate influence and their direct or indirect nature are still unclear, notably with respect to the

230   relations between Mull and Amphi. It is likely that a more detailed analysis of climate and pedoclimate

231   conditions would be more effective.

232

233   *3.3 Tree species*

234   Tree diversity was the most important predictor for Moder and Mull models, with a relative importance

235   of 20.1% and 24.4%, respectively (Table 2). The effect of tree species was then further investigated; to

236   better elucidate causal chains running from tree to humus, various soil and litter properties were analyzed

237   in relation to tree species. In order to discover potential interactions producing such weights of tree species

238   as predictors, correspondences between tree species and other significant predictor variables were

239   analyzed, too.

240   A dependence between tree species and soil fauna, through litter quality, might explain the strong

241   predictive performance of the tree factor. The probability of finding Moder humus were high under

242   coniferous trees, both mixed and pure spruce, and also, though with a weaker influence, under chestnut

243   (Fig 1). Schwarz et al. (2015) found strong and consistent negative effects on earthworms, and consequently

244   on Mull formation, of European larch (*Larix decidua*) and Norway spruce (*Picea abies)*. They suggested that

245   such negative effects might be due to rather low litter palatability and to the dense canopy structure

246   reducing soil moisture and temperature. Rajapaksha et al. (2013) found that chestnut leaves were the least

247   selected, among various broadleaved trees, by typical anecic earthworms.

248   General trends in litter Ca concentration, according to tree species (Table 5), agreed with trends in

249   humus form probability. Species groups with lowest litter Ca, i.e. "Conifers", spruce and chestnut, were the

250   most associated with Moder (Fig 1); species groups with high litter Ca, such as "Other" and "Qpub" were,

251   conversely, associated with Mull (Fig 3). Groups with intermediate litter Ca were either associated with

252   Amphi forms, as beech and Turkey oak, or not significant, as for "Med" (Fig 2). The effect of chestnut on

253   Moder formation appears weaker than could be expected from Ca litter contents (Table 5). This could result

from other litter characters, chestnut litter being frequently reported as containing significantly low lignin (Cortez et al., 1996; Sariyildiz and Anderson, 2005).

Reich et al. (2005) established that plots of tree species with Ca-rich litter had greater density, diversity and biomass of earthworms than plots of trees with Ca-poor litter. Species such as *Fraxinus excelsior*, *Acer pseudoplatanus* and *Prunus avium*, grouped in our dataset as "Other", were considered as mull-forming (Neirynck et al., 2000) and under them earthworm biomass was found to be conspicuously higher than under *Quercus robur* and *F. sylvatica* (De Schrijver et al., 2012; Neirynck et al., 2000). Relations between tree species and topsoil C/N ratio (Table 6) were similar, if at lower absolute values, to those reported by Vesterdal et al. (2008) and Cools et al. (2014). Though differences were of low statistical significance, there was a general similarity, C/N decreasing from species associated with Moder to species associated with Mull. Spruce and "Other" stood out at the two extremes, being significantly different from all others. A further significant characteristic of litter was P content (Table 5); trends in this parameter were not in direct agreement with either Ca or topsoil C/N, the most notable findings being the low P content of chestnut and "Med" litter and the very high P content of spruce. This last appears as a specific plant effect, well different from other conifers and not influenced by site factors, as there appears to be no significant differences in subsoil P for spruce (Table 8), and may explain the more favourable effect of spruce on Amphi differentiation.

Topsoil pH associated with the different tree species (Table 6) showed a clear increasing trend in the order: Pabi<Csat<Conif<Fsyl<Med≈Qcer<Qpub≈Other. Trees likely influence soil habitat by modifying soil pH (Augusto et al., 2002; Mueller et al., 2012), but differences in topsoil pH are also due to differences in parent material. Topsoil and subsoil pH (Table 9) were found to be well correlated for both the whole dataset and for each humus form. The pH differences between subsoil and topsoil, for sites with subsoil pH higher than 6.9, evidenced a mean decrease in pH at least of 0.5 unit for all species and groups, with significant differences (Table 7). This suggests that topsoil pH, a most important soil factor driving towards Moder instead of Amphi and Mull, was also related to tree species. The strongest acidification impact

279 appeared for *P. abies*, in agreement with Augusto et al. (2002), followed by *C. sativa* and *F. sylvatica*, while

280 *Q. pubescens* and "Other" had the lowest acidification impact.

281 Although comparison between species evidenced clear specific plant effects, tree/site interactions must

282 also be considered. Conifers and chestnut tend to be found on sites with low subsoil Ca (Table 8); low Ca

283 content of litter (Table 5) may then be at least partly ascribed to low-Ca soils. There is also a trend towards

284 sites with low subsoil pH, but this is not very strong for mixed conifers. On the other hand, "Other" thrive

285 on subsoil with high Ca and P, associated with similar litter properties.

286 Interactions with subsoil and climate parameters also help to elucidate specific pathways that lead to

287 Amphi formations under species such as beech. Beech, although having high acidification impact (Table 7)

288 and intermediate values of litter Ca, shows high litter P content and clearly concentrates on sites with

289 neutral subsoil and high subsoil P (Table 8). Thus, beech combines with site effects in favoring Amphi over

290 Moder formation.

291 The tree species effect which were more difficult to explain concerned some oaks. The association with

292 humus forms of Turkey oak, rather favorable to Amphi and Moder, and of the downy oak-dominated

293 "Qpub" group, clearly favorable to Mull, are strong. Analysis of both litter quality and site interactions failed

294 to point out significant differences. Cools et al. (2014) also evidenced very similar leaf and litter C/N ratios,

295 in agreement with similar topsoil C/N in our result (Table 6). Certain parameters showed high variability, as

296 acidifying power for Turkey oak or litter Ca content for the "Qpub" group, and strong statistical tails may

297 influence BRT results in absence of overall significant differences. Data on the organic litter fraction of these

298 species are exceedingly hard to found. Difference in tannin content was shown to influence humus form

299 differentiation under two different *Quercus* species (Bonifacio et al., 2015). Hints to high polyphenol and

300 tannin content in *Q. cerris* leaves (Al-Masri and Mardini, 2013) and to much higher tannin content in *Q.*

301 *cerris* than in *Q. pubescens* acorns (Ancillotto et al., 2015) were previously found, representing an

302 interesting suggestion for further investigation.

303

304 *3.4 EfVol*

305   In the BRT analysis, EfVol was the most significant driver of Amphi/Mull differentiation (Fig 2 and 3).

306   Significant differences between Amphi and Mull were detected (Table 3). Amphi forms tend to be found

307   when soil volume for fauna, especially burrowing earthworms, is constrained by either reduced depth or

308   high content of rock fragments. Several studies support the hypothesis that carbon incorporation in mineral

309   soil by annelids is conditioned by effective soil volume for burrowing. Lee (1985) suggested rock fragment

310   abrasiveness as the limiting factor for faunal activity. Ponge et al. (2014), found a positive correlation

311   between thickness of organic layers and rock fragment content in the A horizon of Italian Amphi humus.

312   Loranger-Merciris et al. (2007) and Xu et al. (2013) pointed to deep and stone-free soils offering better

313   conditions for earthworms to endure summer drought, a likely explanation for the frequency of Amphi

314   forms in Mediterranean conditions.

315

316   *3.5 Subsoil pH and Ca content*

317   Among variables describing soil buffering and mineral nutrient availability, subsoil pH and extractable Ca

318   revealed the strongest predictive ability (Table 2), especially with respect to Moder (Fig 1) and Mull forms

319   (Fig 3). Known relations for these two forms were generally confirmed; Moder probability was much

320   enhanced by low subsoil pH and Ca, while Mull occurrence was positively affected by high subsoil Ca

321   content and subsoil pH between 6.5 and 7.5. It then appears that such conditions, and the resulting humus

322   forms, are heavily influenced by parent material. A clear association existed between subsoil and topsoil

323   conditions, statistical differences being strong, significant and consistent for both subsoil and topsoil

324   parameters (Table 9 and 10). There are several reports that Ca content is directly influential on faunal

325   diversity and activity, beyond the effect of pH. According to Ponge (2013) macro-invertebrates have higher

326   Ca demand than other fauna, while Ponge et al. (2014) state that Ca availability is a major factor of

327   earthworm activity, pH rather playing the proxy in this context, and that its influence is more marked on

328   anecic species. Ponge et al. (1999) found that small differences in parent material, acting on Ca availability,

329   promoted humus form differentiation under an otherwise homogeneous forest stand.

330   A further topsoil condition associated with Moder humus was found to be topsoil exchangeable Al (Table

331   3). The pH range favoring Moder was clearly superimposed with the field of presence of soluble Al^{3+} (cf.

332   Ponge et al., 2014); studies on Al effect on soil fauna agree that it is toxic for earthworms (Bilalis et al.,

333   2013; van Gestel and Hoogerwerfa, 2001; Tejada et al., 2010; Zhang et al., 2013). Exchangeable Al then

334   appears as a significant proximal cause for Moder formation; Ponge et al. (2002) found a positive

335   correlation between aluminum content and humus index (from Eumull to Dysmoder).

336   Concerning Amphi forms, these parameters were clearly of less impact. Population statistics (Table 3 and

337   Fig 2) suggest that the typical field of occurrence of Amphi forms, concerning nutrients, tends to overlap

338   with that of Mull forms, soil effective volume being more influent on the differentiation of these two form

339   groups.

340

341   *3.6 Subsoil P*

342   Subsoil P was among the most important predictors for all humus forms (Table 2). Both subsoil and

343   topsoil P content in Moder were significantly lower ($p<0.001$) than in Amphi and Mull (Table 3), while little

344   difference appeared between the last two forms. Phosphorus is present in both organic and inorganic forms

345   (Frossard et al., 2000; Condron and Newman, 2011), and its dynamics are controlled by multiple chemical

346   and biological processes. Topsoil phosphorus content was better correlated with P content in the subsoil

347   than with P content of litter (Table 10). The trend holds very well for Amphi and Mull. In Moder forms,

348   correlations were much poorer, but followed the same trend. In Amphi and Mull sites, topsoil P content was

349   then likely mostly related to soil parent material and geochemical evolution, a result consistent with the

350   study of Marichal et al. (2011) that found no relationship between litter and soil stoichiometry (C:N:P). In

351   Moder, greater complexity was injected by the frequency of podsolization. Formation of Al^{3+} and Fe^{3+}

352   chelates can reduce the availability of Al^{3+} and Fe^{3+} for P fixation, increasing P solubility (Šantrůčková et al.,

353   2004), while P ions can be immobilized as Fe- and Al- phosphates when Al^{3+} and Fe^{3+} are present in high

354   concentration (Hinsinger, 2001). The first process is more likely in topsoil and the second in soil B horizons,

355   this can foster some P transportation.

356   These findings suggest that P might represent a limiting factor for faunal activities. Biological

357   stoichiometry suggests that high biomass P content and low C: P ratio reflect increased allocation to P-rich

358   ribosomal RNA, which in turn enables increased protein synthesis and growth rates, of both individuals and

359   populations (Elser et al., 2000, 2003; Mulder and Elser, 2009). P limitation was reported for many soil

360   invertebrates (Mulder and Elser, 2009; Bishop et al., 2010; Huang et al., 2012; Lemoine et al., 2014),

361   evidencing that P-limitation is potentially as strong as N-limitation (Lemoine et al., 2014; Vonk and Mulder,

362   2013) and that N availability for arthropods is P-limited (Bishop et al., 2010). Mulder and Elser (2009),

363   suggested that microfauna (e.g., nematodes) copes better with P-scarcity than mesofauna (micro-

364   arthropods), as stoichiometric theory predicts that fauna with higher P demand suffers a competitive

365   disadvantage in low-P soils, due to poorer resource quality. Marichal et al. (2011) found that earthworms

366   show strict tissue homeostasis, i.e., they maintain their stoichiometry independently from food resources.

367   This would lead to limitation of earthworm activity by the most deficient nutrient, an hypothesis that was

368   also supported by a positive correlation between earthworm density and soil P content. Moder forms are

369   dominated by micro-invertebrates (Schaefer and Schauermann, 1990; Scheu and Falca, 2000), which are

370   likely better able to cope with constrained nutrition.

371

372   *3.7 Moder, Amphi and Mull models*

373   Moder (Fig. 1 and Table 3) evolved in sites with low temperature, associated to tree species with Ca-poor

374   detritus and high acidification impact. Acidic condition were often associated with high level of Al^{3+}, with

375   toxicity effect on pedofauna and seemed to contribute to a decreased P content in topsoil, further reducing

376   meso and macro fauna activities. Thus, Moder forms should be associated to a plant-pedofauna-soil

377   feedback where a nutrient poor environment, due to poor inputs from litter decomposition and parent

378   material weathering is the habitat for a low and localized biological activity that, in combination with low

379   temperature, slows down nutrient release and allows for organic horizons' accumulation.

380   Amphi (Fig 2) and Mull (Fig 3) evolved in similar, nutrient rich, systems with favorable conditions for

381   pedofauna activity. The optimal ranges of soil acidity and fertility of Amphi and Mull are not fully

382 overlapping, Amphi being better predicted by higher P and Ca contents, Mull by near neutral pH values and

383 very low Exc_Al. Altogether, these data suggest that Amphi and Mull mostly tend to appear in the range of

384 well buffered and fertile soils, differentiation being often driven by soil physical conditions. This last

385 hypothesis is also supported by the weight of rainfall seasonality in the Amphi model, high pmax.min being

386 physically synergic with low Efvol in creating unfavorable, dry, seasonal conditions for faunal activity. A non-

387 monotonic trend is visible in climate effects; Amphi is clearly associated with high rainfall seasonality but

388 definitely not with high summer temperature (Tmax). Population statistics show that no significant

389 differences between the three humus forms can be ascertained for pmax.min, while Mull populations are

390 clearly differentiated for Tmax. This complex relation can be explained by a vanishing of the Amphi-favoring

391 effect of soil dryness when high summer temperatures force all faunal populations to endogeic behavior

392 (Andreetta et al., 2011, 2013a).

393

394 *3.8 Inconsistent and peculiar conditions*

395 Various peculiar conditions occurred within the database, which help to explain the somewhat limited

396 performance of the BRT models. First comes the issue of certain calcareous soils, showing either Moder or

397 Amphi humus, irrespectively of them being in Mediterranean environments. To our best knowledge,

398 association of high pH with Moder forms has never yet been reported, even on highly calcareous mountain

399 soils. High pH-topsoils with Moder or Amphi humus were found in Central Italy soils, developed on non-

400 coherent marine sands and clays, while in the many sites on hard calcareous rock, with high subsoil pH,

401 topsoil pH very rarely exceeded 8, irrespectively of total carbonate content. The difference can be explained

402 by finely divided lime, commonly present on non-coherent parent materials but not on hard limestone.

403 Finely divided lime is then likely a factor having strong negative influence on faunal activity. Studies of

404 agroecosystems suggest that high pH can affect pedofauna activity as much as low pH. Tripati and Bhardway

405 (2004) found that maximum biomass for *Eisenia fetida* and *Lampito mauritii* was reached at pH 6.5 and 7.5,

406 respectively, then decreasing at higher values. In neutral to alkaline soils, fertilization and amendments

407 decreasing soil pH were found to increase faunal biomass (McCormack et al., 2013; Wang et al., 2015;), the

408 opposite effect holding for practices increasing soil pH (Liesch et al., 2010; Wang et al., 2015). In forest soils,

409 such stressful effects may drive a shift of soil fauna to the organic layers which very rarely, if ever, reach pH

410 values ≥8. This poorly known effect would justify more investigations.

411   A similar case concerns Andosols; in these soils, Amphi humus is clearly dominant, as can be expected by

412 causal hypotheses. Andosols tend to be too acid and Al-rich for Mull development, but their properties of

413 organic matter stabilization and eluviation suppression (Cecchini et al., 2002) make highly unlikely the

414 absence of a substantial A horizon.

415   A final group of inconsistencies concerns Mull forms developing in very acid conditions, not uncommon

416 in mountain regions and even found in Al-rich soils; this condition is closely associated to the development

417 of Umbrisols, and the small number of samples in this database does not allow further investigation. It

418 appears likely that the composition of pedofauna in both Andosols and Umbrisols may be quite different

419 from established knowledge, and that it would well warrant further investigation.

420

421   4.   Conclusions

422   The statistically based analysis of the recurrence of humus forms in Italian forests pointed out the

423 relative roles played by various environmental factors as drivers of humus form differentiation; at least in

424 part, the processes through which such factors influence humus development were also clarified.

425   The role of soil nutritional status, as conditioned by parent material properties, was found to be

426 fundamental; the major role played by calcium was further evidenced, together with the hitherto

427 understated importance of phosphorus. Soil nutritional status appears to influence pedofauna composition

428 and activity both directly and through litter quality.

429   It can be stated, from our results, that Italian forest species are geographically distributed with a major

430 influence of soil and climate conditions. This partly explains the weight of tree species as a factor in humus

431 differentiation; nonetheless, various specific plant effects were evidenced. Specific characters of soil-plant-

432 litter nutrient flows, acting on litter quality, were evidenced for such major species as Norway spruce,

433 European beech and Turkey oak. These specific characters represent a direct effect of tree species on

434 humus form development. Given the weight of these species in the sample population, it is likely that

435 similar effects could be evidenced for other species, if suitably large samples could be studied. Our results

436 evidence how vegetation and humus form can, when considered together, supply highly detailed insights on

437 the status and evolving trend of a forest ecosystem, especially about availability and management strategies

438 for nutrients. For the practical application of soil nature prediction, it clearly appears that joint analysis of

439 vegetation and humus is a potentially powerful means of disentangling soil geography, at all scales.

440 The distinctive variability of Italian climate conditions allowed to better evidence climate effects on

441 humus formation that were either recently proposed or not yet studied in detail. It was thus confirmed that

442 conditions leading to seasonal soil dryness, due either to rainfall pattern or to limited soil water storage,

443 have a primary role in inducing Amphi formation in soils with fair to good nutrient status. On the other

444 hand, our data suggest that, in sites with really high average temperature, the Mull form is dominant. Other

445 peculiar humus-forming conditions were evidenced in Andosols and in soil containing finely divided lime,

446 and this ensemble of results suggest that Mediterranean forest soils are habitats for unique assemblages of

447 pedofauna and microflora.

448 As reported by previous studies, environment-humus modelling produces significant results in terms of

449 process understanding, but overall predictive performance is not necessarily very high. In our opinion, our

450 results further evidence that this is due to humus being somewhat sensitive and fast-responding. Changes

451 in nutrient flow and soil conditions driven by such lower-order factors as forest growth cycle, forest

452 management, specific soil chemical and physical characters, can overprint the larger-scale environment

453 "signature" on humus form. If this reduces the accuracy of region-wide pictures, it does evidence the

454 potential of humus as an indicator of specific ecosystem conditions and as a tool to assess the effects of

455 lesser and man-induced perturbations. This appears to be quite an interesting perspective, also given the

456 strong relationship between humus forms and soil carbon storage already evidenced by various studies.

457

458

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1. Moder
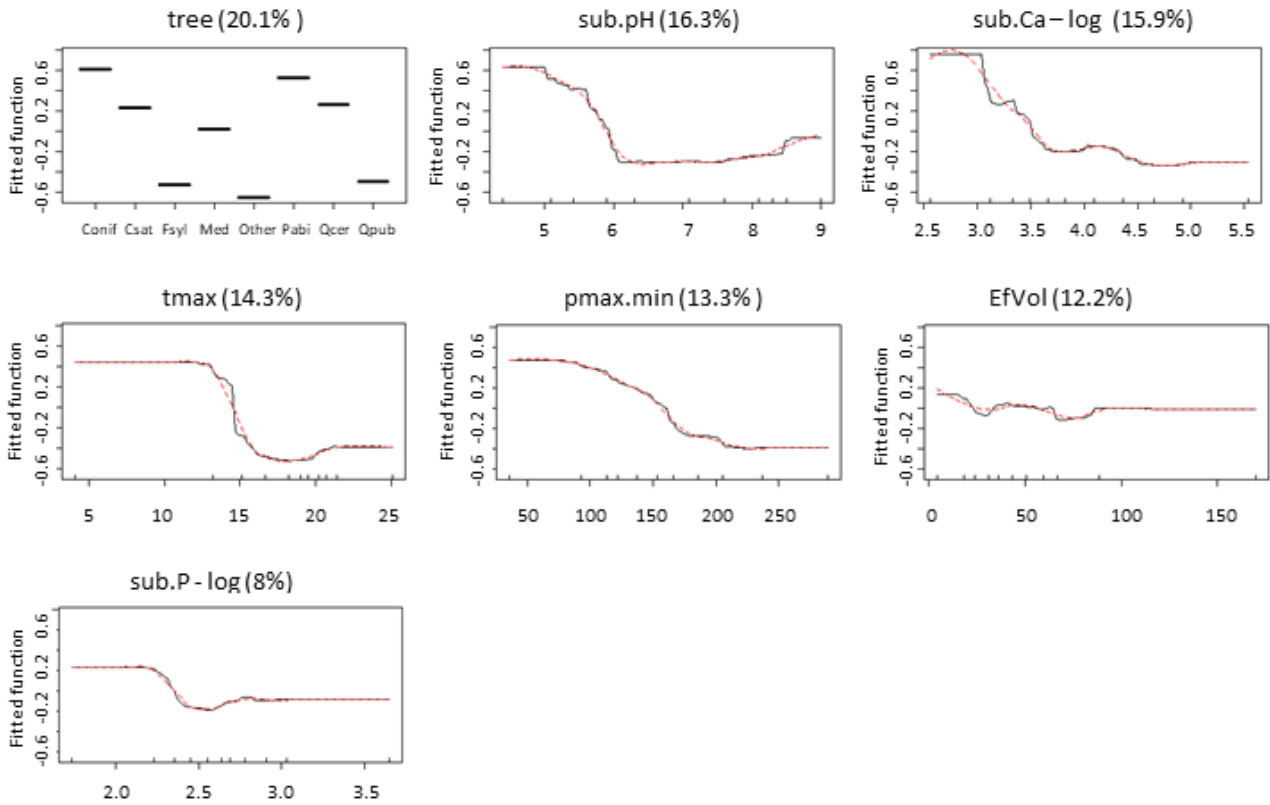
Fig 1. Partial dependence plots from Moder BRT model for environmental factors: tree: tree species; pmax.min: the range between the precipitation of the wettest quarter and the precipitation of the dryer quarter; tmax: mean temperature of warmest quarter; EfVol: effective soil volume; Ca.sub (log): subsoil Calcium content (log-transformed); P.sub (log): subsoil phosphorus content (log-transformed); pH.sub: subsoil pH.

2. Amphi

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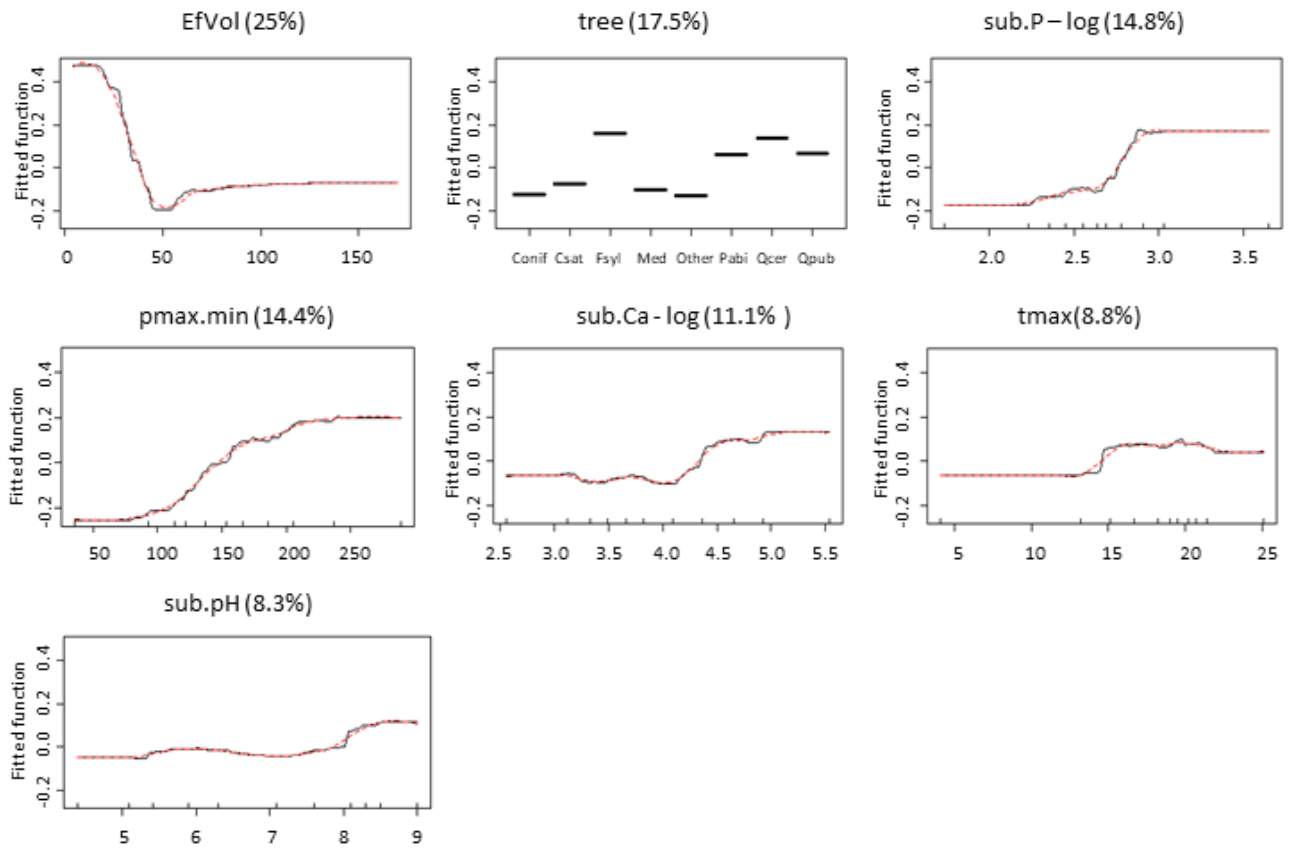
Fig 2. Partial dependence plots from Amphi BRT model for environmental factors: tree: tree species; pmax.min: the range between the precipitation of the wettest quarter and the precipitation of the dryer quarter; tmax: mean temperature of warmest quarter; EfVol: effective soil volume; Ca.sub (log): subsoil Calcium content (log-transformed); P.sub (log): subsoil phosphorus content (log-transformed); pH.sub: subsoil pH.

3. Mull
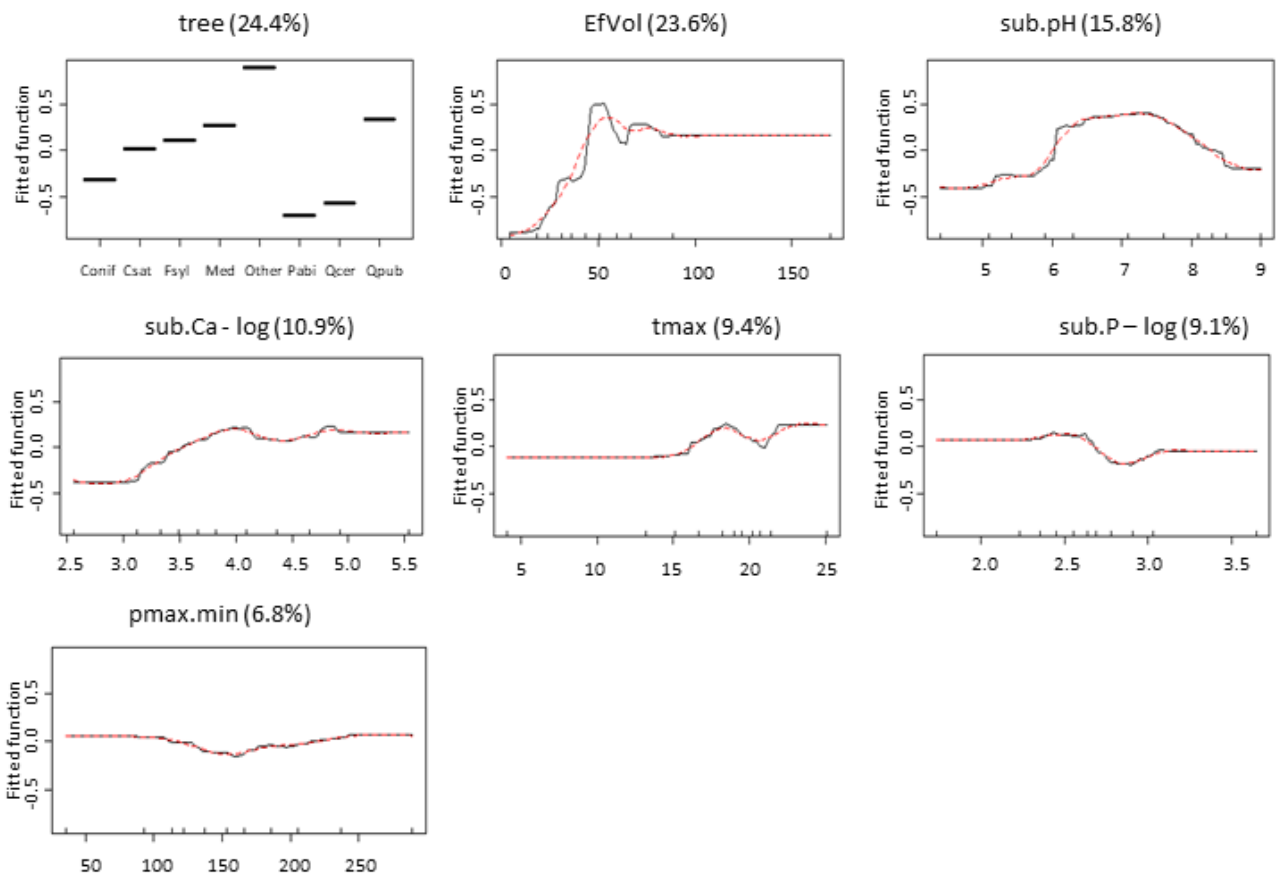
718 Fig 3. Partial dependence plots from Mull BRT model for environmental factors: tree: tree species;

719 pmax.min: the range between the precipitation of the wettest quarter and the precipitation of the dryer

720 quarter; tmax: mean temperature of warmest quarter; EfVol: effective soil volume; Ca.sub (log): subsoil

721 Calcium content (log-transformed); P.sub (log): subsoil phosphorus content (log-transformed); pH.sub:

722 subsoil pH.

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Table 1

Frequency table of tree species and humus forms.

	Conif (n=32)	Csat (n=27)	Fsyl (n=49)	Med (n=25)	Other (n=20)	Pabi (n=27)	Qcer (n=25)	Qpub (n=33)
Moder (n=57)	14 (0.24)	10 (0.18)	6 (0.11)	4 (0.07)	0 (0.00)	13 (0.23)	7 (0.12)	3 (0.05)
Amphi (n=92)	10 (0.11)	7 (0.08)	24 (0.26)	8 (0.08)	6 (0.07)	12 (0.13)	11 (0.12)	14 (0.15)
Mull (n=89)	8 (0.09)	10 (0.11)	19 (0.21)	13 (0.15)	14 (0.16)	2 (0.02)	7 (0.08)	16 (0.18)

743　**Table 2**

744　Relative influence (RI%) of the factors on Moder, Amphi and Mull occurrence following a boosted regression tree analysis. Site factors: tree: tree species;

745　pmax.min: the range between the precipitation of the wettest quarter and the precipitation of the dryer quarter; tmax: mean temperature of warmest quarter;

746　EfVol: effective soil volume; sub.Ca: subsoil calcium content; sub.P: subsoil phosphorus content; sub.pH: pH of the subsoil.

Moder		Amphi		Mull	
Factor	RI (%)	Factor	RI (%)	Factor	RI (%)
tree	20.1	EfVol	25.0	tree	24.4
sub.pH	16.3	tree	17.5	EfVol	23.6
sub.Ca (log)	15.9	sub.P (log)	14.8	sub.pH	15.8
tmax	14.3	pmax.min	14.4	sub.Ca (log)	10.9
pmax.min	13.3	sub.Ca (log)	11.1	tmax	9.4
EfVol	12.2	tmax	8.8	sub.P (log)	9.1
sub.P (log)	8.0	sub.pH	8.3	pmax.min	6.8

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758 Summary statistics: mean, standard deviation (sd), minimum (min) and maximum (max) value for each predictor among humus forms. Efvol: effective soil
759 volume; Pmax.min: the range between the precipitation of the wettest quarter and the precipitation of the dryer quarter; Tmax: mean temperature of warmest
760 quarter; P.sub: subsoil phosphorus content; Ca.sub: subsoil calcium content. Soil factors: topsoil (0-10 cm) C/N; topsoil pH; Exc_Al: top soil exchangeable
761 Aluminium; Ext_Ca: topsoil calcium content; P: topsoil phosphorus content; Ca_OL: litter Ca content.

	Moder				Amphi				Mull			
	mean	sd	min	max	mean	sd	min	max	mean	sd	min	max
Efvol (cm)	44.2 a	23.3	7.5	110.0	46.6 a	36.0	4.5	170.0	57.8 b	31.8	14.0	150.0
Tmax (C°)	16.5 a	4.1	7.2	22.4	17.9 a	3.4	4.1	23.8	19.0 b	2.6	10.8	25.1
Pmax.min (mm)	149 a	51	42	247	168 a	51	75	289	155 a	58	36	289
pH.sub	6.2 a	1.4	4.4	8.7	7.1 b	1.3	4.6	8.9	7.2 b	1.15	5	9
P.sub (mg/Kg)	421 a	275	65	1256	633 b	564	55	4449	560 b	525	97	3363
Ca.sub (mg/Kg)	17274 a	50142	825	344539	34010 b	49435	366	266419	29320 b	47762	802	329178
pH	5.6 a	1.4	3.9	8.6	6.5 b	1.2	4.4	8.6	6.6 b	1.1	4.1	8.6
Ext_Ca (mg/Kg)	16308 a	54427	939	395041	26257 b	38017	635	202010	25263 b	40602	1088	269779
P (mg/Kg)	450 a	250	109	1196	765 b	559	67	3591	698 b	489	126	2675
Exc_Al (cmol+/Kg)	4.5 a	4.7	0.01	18.1	1.3 b	2.4	0.01	11.9	0.9 b	2.0	0.01	9.8
Ca_OL (mg/Kg)	15534 a	8176	1973	44475	23155 b	11367	3805	68694	22134 b	11620	1082	62126

762 Low-case letters indicate significant differences ($p<0.05$) between humus forms with Kruskal-Wallis test.

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Table 4

Summary statistics: mean, standard deviation (sd), minimum (min) and maximum (max) value for climate parameters (MAP: mean annual precipitation; pma.min: range between the precipitation of the wettest quarter and the precipitation of the dryer quarter; tmax: mean temperature of warmest quarter; MAT= mean annual temperatures) among tree species. Conif: coniferous; Csat: *C. sativa*; Fsyl: *F. sylvatica*; Med: Mediterranean species; Other: broadleaves other than those represent as single group; Pabi: *P. abies*; Qcer: *Q. cerris*; Qpub: *Q. pubescens*.

	MAP (mm)				pmax.min (mm)				tmax (C°)				MAT (C°)			
	mean	sd	min	max	mean	sd	min	max	mean	sd	min	max	mean	sd	min	max
Conif	939 b	185	512	1332	161 bc	70	36	286	14.8 b	4.3	4.1	21.3	7.2 b	3.6	-1.2	12.2
Csat	929 b	139	746	1267	155 ab	45	71	277	19.6 c	1.2	16.4	21.7	11.1 c	1.6	7.5	14.2
Fsyl	909 b	161	607	1296	148 a	49	72	288	17.0 b	1.9	13.9	21	8.4 b	1.9	4.9	12.7
Med	725 a	152	454	1019	188 cd	49	77	280	21.2 e	1.7	17.7	25.1	13.5 d	1.7	10.7	17.5
Other	869 b	186	483	1327	137 a	61	51	289	19.1 cd	2.6	10.8	22.9	11.0 c	2.0	6.9	15.0
Pabi	890 b	137	738	1276	201 d	30	125	247	13.4 a	2.3	8.1	17.5	5.5 a	1.8	2.8	9.5
Qcer	805 b	102	596	953	138 a	44	75	266	20.5 de	1.2	17.7	22.6	12.2 b	1.5	9.3	14.8
Qpub	822 b	111	512	1094	148 ab	52	71	289	20.1 ce	1.9	18.3	22.8	11.9 b	1.8	7.4	15.4

Low-case letters indicate significant differences (*p*<0.05) between tree species using Kruskal-Wallis test.

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Table 5

Summary statistics: mean, standard deviation (sd), minimum (min) and maximum (max) value for topsoil and subsoil pH values among tree species. Conif: coniferous; Csat: *C. sativa*; Fsyl: *F. sylvatica*; Med: Mediterranean species; Other: broadleaves that are not grouped in other classes; Pabi*: P.abies*; Qcer: *Q.cerris*; Qpub: *Q. pubescens*.

	Topsoil pH				Subsoil pH				Topsoil C/N			
	mean	sd	min	max	mean	sd	min	max	mean	sd	min	max
Conif	6.2 b	1.3	4.0	8.2	6.7 abc	1.4	4.4	8.6	13.6 bc	3.46	7.5	21.7
Csat	5.3 a	0.9	3.9	7.7	5.8 a	1.0	4.6	7.9	13.4 b	2.92	9.6	22.1
Fsyl	6.1 b	1.3	4.3	8.0	6.9 bcd	1.2	4.8	8.7	13.1 b	2.4	5.7	18.8
Med	6.9 c	0.9	5.1	8.6	7.2 cd	1.2	5.1	9.0	13.0 abc	3.6	5.8	21.6
Other	7.0 ce	1.2	4.8	8.2	7.5 de	1.2	5.2	8.6	11.0 a	2.4	7.3	15.9
Pabi	5.2 a	1.1	4.0	7.9	6.2 ab	1.4	4.8	8.6	14.5 d	3.06	9.9	20
Qcer	6.7 bc	1.2	5.0	8.6	7.3 de	1.2	5.3	8.7	12.0 c	2.1	5.2	15.8
Qpub	7.3 e	1.2	4.4	8.6	7.7 e	1.3	5.2	8.9	11.8 ac	2.3	4.8	15.9

Low-case letters indicate significant differences ($p<0.05$) between tree species using Kruskal-Wallis test.

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787 Table 6

788 Summary statistics: mean, standard deviation (sd), minimum (min) and maximum (max) value for pH.range,

789 pH difference between sub soil and topsoil for sites with pH value higher than 6.9, among tree species.

790 Conif: coniferous; Csat: *C. sativa*; Fsyl: *F. sylvatica*; Med: Mediterranean species; Other: broadleaves that are

791 not grouped in other classes; Pabi: *P.abies*; Qcer: *Q.cerris*; Qpub: *Q. pubescens*.

	pH range			
	mean	sd	min	max
Conif	0.7 c	0.5	0.2	1.9
Csat	1.2 cd	1.0	0.2	2.9
Fsyl	1.1 c	0.9	0.1	4.4
Med	0.6 b	0.2	0.4	1.0
Other	0.6 b	0.4	-0.2	1.5
Pabi	1.5 d	0.8	0.5	3.0
Qcer	0.8 abc	0.9	0.1	3.6
Qpub	0.4 a	0.5	-0.3	1.9

792 Low-case letters indicate significant differences ($p<0.05$) between tree species using Kruskal-Wallis test.

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794 Table 7

795 Ca (Ca_OL) and P (P_OL) content in the OL layer among different tree species.

	Ca_OL (mg/Kg)				P_OL (mg/Kg)			
	mean	sd	min	max	mean	sd	min	max
Conif	16173 ab	7800	4908	44475	803 ab	289	319	1496
Csat	15611 a	7352	1973	32830	740 a	340	165	1558
Fsyl	20395 bc	10408	3011	68694	915 bc	338	326	1947
Med	22367 b	10700	8868	42980	727 ab	283	277	1583
Other	31097 d	12634	11755	62126	1062 cd	324	551	1742
Pabi	15948 ab	6495	6400	36518	1031 d	256	537	1693
Qcer	22886 cd	11015	4309	50009	906 bc	312	350	1449
Qpub	26375 cd	13842	1082	54573	765 ab	247	255	1498

796 Low-case letters indicate significant differences ($p<0.05$) between tree species with Kruskal-Wallis test

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803 Table 8

804 Subsoil Ca (sub.Ca) and P content (sub.P) among different tree species.

	sub.Ca (mg/Kg)				sub.P (mg/Kg)			
	mean	sd	min	max	mean	sd	min	max
Conif	35825 ab	67263	956	344539	450 b	273	65	1256
Csat	5161 a	5737	825	21712	390 a	357	55	1546
Fsyl	24911 c	39425	366	186772	701 bc	606	132	3364
Med	23632 bc	36760	1074	144237	495 ab	501	96	2457
Other	48143 d	73630	2041	329178	917 c	951	225	4449
Pabi	13815 ab	22936	959	82999	465 abc	280	73	1039
Qcer	30123 cd	39340	541	159075	516 bc	280	127	1117
Qpub	46258 cd	63550	802	266419	504 bc	328	119	1620

805 Low-case letters indicate significant differences ($p<0.05$) between tree species with Kruskal-Wallis test

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817 **Table 9**

818 Single linear regression models for pH of the mineral topsoil (0-10 cm) as dependent on pH of the subsoil

819 (sub.pH), for the entire dataset (tot) and for each humus form (Moder, Amphi and Mull)

	R^2	Intercept	p
tot	0.77	0.42	<0.001
Moder	0.78	0.16	<0.001
Amphi	0.86	0.52	<0.001
Mull	0.62	1.00	<0.001

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Table 10

Single linear regression models for the P and Ca content in the mineral topsoil (0-10 cm) as dependent on P and Ca in the litter (P_OL) and P and Ca content in the subsoil (sub.P and sub.Ca), for the entire dataset (tot) and for each humus form (Moder, Amphi and Mull)

		R^2	Intercept	p
tot	P_OL	0.27	0.30	<0.001
	sub.P	0.70	0.74	<0.001
Moder	P_OL	0.15	1.13	<0.01
	sub.P	0.45	1.26	<0.001
Amphi	P_OL	0.30	-0.09	<0.001
	sub.P	0.73	0.78	<0.001
Mull	P_OL	0.31	0.26	<0.001
	sub.P	0.80	0.60	<0.001
tot	Ca_OL	0.43	-2.34	<0.001
	sub.Ca	0.81	0.88	<0.001
Moder	Ca_OL	0.36	-1.71	<0.001
	sub.Ca	0.79	0.80	<0.001
Amphi	Ca_OL	0.51	-4.04	<0.001
	sub.Ca	0.84	0.96	<0.001
Mull	Ca_OL	0.32	-0.79	<0.001
	sub.Ca	0.76	0.96	<0.001

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