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1 **Geology and climate conditions affect more humus forms than forest**  
2 **canopies at large scale in temperate forests**

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8

9 **ABSTRACT**

10 We investigated by linear gradient analysis (RDA) the relationships between forest humus forms (9  
11 humus forms and the Humus Index) and 148 variables describing geology, climate, soil type,  
12 geography and the floristic composition of forest canopies, using 3441 plots of the EcoPlant database  
13 covering the whole French territory. Among these variables, geology (alkaline vs acidic substrate) and  
14 climate (warm/dry vs cold/rainy) were the major determinants of humus forms, scaling mull humus  
15 forms from eumull to dysmull and opposing them to mor/moder, while the contribution of tree  
16 canopies was negligible. This trend was verified by partial RDA with environment or abundance of  
17 tree species from forest canopy as co-factors. The original position of amphi was confirmed: it was the  
18 only humus form not included in the gradient of increasing biological activity ordinated according to  
19 climate and geology. Results and possible forecasts of humus forms according to global warming were  
20 discussed to the light of existing knowledge.

21 *Keywords:* EcoPlant database, humus form, Humus Index, parent rock, soil type, climate, geography,  
22 RDA

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## 23 **1. Introduction**

24           The humus form, i.e. the vertical arrangement of organic matter in topsoil horizons, is known  
25 to be influenced by biotic (litter amount and quality, soil-dwelling microbial and animal communities)  
26 and abiotic factors (climate, parent rock, soil type) according to a variety of key processes which have  
27 been reviewed by Ponge (2003). While abiotic factors such as regional climate and geology cannot be  
28 back-influenced by humus forms, at least in the short-term (but see Van Breemen, 1993; Marland et  
29 al., 2003), biotic factors are tightly linked to humus forms according to feed-back loops (Perry, 1995;  
30 Wardle and Lavelle, 1997; Ponge et al., 1999), making distal and proximal causes hard to discern and  
31 thus any predictions hardly questionable. In forests, past land use (Koerner et al., 1997; Dupouey et  
32 al., 2002) and present-day management options (Hölscher et al., 2001; Godefroid et al., 2005; Van  
33 Calster et al., 2007) are known to influence humus forms at the scale of management units. At a more  
34 local scale individual trees (Boettcher and Kalisz, 1990; Kuuluvainen et al., 1994; Peltier et al., 2001),  
35 forest vegetation (Bernier et al., 1993; Emmer, 1994; Bernier and Ponge, 1994), microtopography  
36 (Dwyer and Merriam, 1981) and animal/microbial populations (Gourbière, 1983; Wilcox et al., 2002)  
37 stem in a pronounced variation of humus forms and ground floor thickness (Arp and Krause, 1984;  
38 Riha et al., 1986; Aubert et al., 2006).

39           Soil types and humus forms do not vary at the same scale of time (Crocker and Major, 1955;  
40 Switzer et al., 1979; Turk et al., 2008), making their causal relationships highly variable in space and  
41 time, more especially in forest environments (Kuuluvainen et al., 1993; Ponge et al., 1998, 1999). It  
42 has been shown that the thickness of forest floor and the structure of organo-mineral horizons, which  
43 are under the paramount influence of ecosystem engineers such as earthworms (Hoogerkamp et al.,  
44 1983; Bernier, 1998; Wironen and Moore, 2006; but see Burghouts et al., 1998), can vary according to  
45 the age of trees (Aubert et al., 2004; Godefroid et al., 2005; Chauvat et al., 2007), plant successional  
46 processes (Leuschner et al., 1993; Emmer and Sevink, 1994; Scheu and Schulz, 1996) and undergo  
47 cycles at the scale of centuries in naturally regenerating late-successional forests (Bernier and Ponge,  
48 1994; Sagot et al., 1999; Salmon et al., 2008). Litter quality, resulting from the species composition of  
49 forest vegetation (Wolters, 1999; Loranger et al., 2002; Wardle et al., 2003) and conditions of tree

50 growth (Northup et al., 1995; Hättenschwiler et al., 2003), is known to influence and be influenced by  
51 humus forms and associated soil trophic networks (Davies et al., 1964; Nicolai, 1988; Ponge et al.,  
52 1999). At last, forest vegetation is locally selected (filtered out from regional pools of species) by  
53 forest floor and topsoil properties, combined with species interactions (Daniel and Schmidt, 1972;  
54 Goldberg, 1982; Falkengren-Grerup and Tyler, 1993) and in turn it influences the activity of soil  
55 organisms, and thus the development of humus forms, through litter and rhizosphere effects (Emmer,  
56 1994; Bradley and Fyles, 1996; Milleret et al., 2009).

57         While it is difficult to disentangle this network of multiple and often symmetrical causal  
58 relationships in the variety of situations observed in a region (Klinka et al., 1990; Kindel and Garay,  
59 2002; Galvan et al., 2008), attempts can be made to discern a limited number of strategies by which  
60 plants, microbes and animals can adapt themselves to their physical environment, and adapt it to their  
61 own requirements (Read, 1992; Northup et al., 1998; Wardle et al., 2004), stemming in the view of  
62 humus forms as ecological attractors (Beisner et al., 2003; Ponge, 2003; Graefe and Beylich, 2006). In  
63 this respect, we suggest that multivariate methods using a wide array of sites would be better able to  
64 discern a limited array of realistic patterns than comparative studies based on a limited number of  
65 selected couples. For instance, it is current tenet that conifers impoverish the topsoil and thus change  
66 locally the humus form. However, most comparative studies on existing (non-experimental) stands  
67 (Nihlgård, 1971; Gauquelin et al., 1996; Augusto et al., 2003) are flawed by the facts (not controlled  
68 by the sampling procedure) that (i) the replacement of a deciduous by a coniferous species is often  
69 (although not always) dictated by poor growth of the previous crop, due to low soil fertility or water  
70 availability, unfavourable aspect or bad management practices, (ii) the growth rate of timber species  
71 and the duration of stand rotation (much shorter for conifers, but decided by the forester) influence the  
72 balance between aboveground nutrient immobilisation and below ground nutrient recycling through  
73 litter decomposition and mineral weathering (Schlesinger, 1977; Vitousek, 1984; Ulrich, 1987).  
74 Studies on well-designed experimental plantations with homogeneous initial conditions conclude to an  
75 influence of tree species composition on humus form and litter decomposition (Ovington, 1954;  
76 Chapman et al., 1988), while studies on the same tree or litter species in a variety of soil and climate

77 conditions conclude to a strong influence of abiotic factors (Vitousek et al., 1994; Coûteaux et al.,  
78 2002; Titeux and Delvaux, 2009). But what when both biotic and non-biotic factors vary together?

79 We aimed here at investigating the respective influence of abiotic conditions and tree forest  
80 species on the spatial variability of humus forms at the scale of the French continental territory. The  
81 use of a large array of forest sites of varying tree composition (including coniferous and deciduous  
82 species), soil type, climate, and parent material may help to reveal distal factors acting on humus  
83 forms, making realistic predictions possible despite of the ground noise to be expected from the  
84 variety of ecological conditions thus analysed in the same data matrix (Bednorz et al., 2000). We used  
85 3441 plots from the phytoecological database EcoPlant (Gégout et al., 2005), covering the whole  
86 forested French territory, to investigate relationships between humus forms and environmental  
87 conditions. Plots were characterized by:

- 88 • Humus form
- 89 • Composition of the forest canopy
- 90 • Soil type
- 91 • Geological substrate
- 92 • Climate (rainfall and temperature indices)
- 93 • Geography (latitude and longitude, phytoecological region)

94 Data about soil chemical and physical analyses were discarded, being too fragmentary in the database  
95 and thought redundant with soil type and geological substrate (Chaplot et al., 2003). In order to better  
96 relate variations of humus forms to environmental factors, we used a Humus Index as a mean to  
97 transform the qualitative assessment of humus forms, based on a typology of morphological diagnostic  
98 characters (Green et al., 1993; Brêthes et al., 1995), into a numerical scale easier to be treated  
99 statistically (Ponge et al., 2002; Ponge and Chevalier, 2006; Lalanne et al., 2008). We used total (Van  
100 den Wollenberg, 1977; Kenkel, 2006) and partial redundancy analysis (Borcard et al., 1992; Ter Braak  
101 and Wiertz, 1994) to measure the respective contribution to humus form variation of tree canopy  
102 composition vs environmental data. Our hypothesis was that the correlation between aboveground

103 vegetation and topsoil properties, which has been often described at local scales (Emmer, 1994; Ponge  
104 et al., 1997; Kounda-Kiki et al., 2006) does not hold at a more regional or even continental scale,  
105 where the influence of long-lasting distal factors such as geology and climate prevail over that of  
106 short-duration proximal factors such as forest stand composition (Augusto et al., 2003; Sadaka and  
107 Ponge, 2003; Zhang et al., 2008), while both factors combine in a nested manner (Coûteaux et al.,  
108 1995; Bernier, 1996; Aerts, 1997). Consequences of present-day anthropogenic global changes  
109 (Walther et al., 2005; Vetter et al., 2005; Rosenzweig et al., 2008) for protracted trends in the  
110 evolution of humus forms will be discussed to the light of present results and existing knowledge.

111

## 112 **2. Material and methods**

### 113 *2.1. Data matrix*

114 The complete data matrix crossed 3441 rows (sites) and 148 columns (variables). Sites were  
115 adult forest stands distributed over the whole French continental territory, with a sampling density  
116 roughly representing the distribution of forested areas (Fig. 1). No attempt was made to compensate  
117 for the over- or under-representation of some regions, given that plots were near always located  
118 several kilometres apart, thereby alleviating the risk of autocorrelation for humus profiles (Aubert et  
119 al., 2006).

120 Humus forms were classified in nine types according to the French classification system  
121 (Brêthes et al., 1995; Jabiol et al., 2007), which allowed the calculation of the Humus Index or HI  
122 (Ponge et al., 2002) according to the following scale of decreasing incorporation of organic matter to  
123 the mineral soil, ranging from 1 to 8:

- 124 1. Eumull (crumby A horizon, OL horizon absent, OF horizon absent, OH horizon absent)
- 125 2. Mesomull (crumby A horizon, OL horizon present, OF horizon absent, OH horizon absent)
- 126 3. Oligomull (crumby A horizon, OL horizon present, OF horizon < 1 cm, OH horizon absent)
- 127 4. Dysmull (crumby A horizon, OL horizon present, OF horizon  $\geq$  1 cm, OH horizon absent)

- 128 5. Amphimull (crumby A horizon, OL horizon present, OF horizon present, OH horizon present)  
129 and Hemimoder (compact A horizon, OL horizon present, OF horizon present, OH horizon  
130 absent): these humus forms are quite different in their diagnostic A horizon but both exhibit  
131 intermediate characters between dysmull and eumoder, hence same HI value)
- 132 6. Eumoder (compact A horizon, OL horizon present, OF horizon present, OH horizon  $\leq 1$  cm)
- 133 7. Dysmoder (compact A horizon, OL horizon present, OF horizon present, OH horizon  $> 1$  cm)
- 134 8. Mor (no A horizon, OL horizon present, OF horizon present but with few animal faeces)

135 In the following text amphimull will be referred to amphi according to Graefe and Beylich (2006),  
136 Graefe (2007), Galvan et al. (2008) and Zanella et al. (2009). Humus forms were coded as dummy  
137 variables (taking the value 1 or 0 according to presence or absence in a given site of the corresponding  
138 humus form). Clearly, the assignment of humus forms to the system of 9 humus forms used for the  
139 calculation of HI, was sometimes imperfect. Depending on the time at which data were collected,  
140 some older classification systems were used by field collectors. In a few instances, the distinction  
141 between hemimoder, dysmull and amphimull, which is based on the presence/absence of an OH  
142 horizon and on the structure of the A horizon (Brêthes et al., 1995), could not be done because these  
143 forms were confused under the old-fashioned name mull-moder. In these cases, they were arbitrarily  
144 assigned to dysmull. In most cases field collectors have been trained to the recognition of diagnostic  
145 biological processes (fragmentation of litter, deposition of animal faeces, mixing of mineral with  
146 organic matter) by using the field identification booklet by Jabiol et al. (2007).

147 The composition of forest canopies was described by 88 variables (Appendix) measuring the  
148 percent cover of tree species according to a scale from 0 to 6. The environment (geography, climate,  
149 geology, soil type) was described by 36 variables (Table 1) to which were added 11 geographical  
150 regions, thus totalling 47 variables, 38 of them being dummy variables. Table 1 summarizes the main  
151 characteristics of the 11 regions covering the whole continental French territory.

152 A soil profile was dug under a clump of adult trees with a near complete canopy cover ( $\geq$   
153 80%) at more than 2 m from the nearest trunk. Soil types were classified according to the last version

154 of the French Référentiel Pédologique (AFES, 2009) and main correspondences with WRB  
155 classification (IUSS, 2006) are given in Table 1.

156

## 157 2.2. Data analysis

158 Data were analysed by RDA (Redundancy Analysis). A total RDA was performed, using both  
159 environmental and floristic variables as independent variables ( $n = 171$ ) and variables describing  
160 humus forms (9 dummy variables) and the Humus Index (discrete variable) as dependent variables.  
161 All variables were centred and reduced (mean = 0, variance = 1) prior to analysis. Partial RDAs were  
162 performed using either floristic or environmental variables as co-variables in order to estimate their  
163 respective influence on humus forms (and their interaction) and to decompose the total variance  
164 according to Borcard et al. (1992). Some particular trends depicted by RDA were verified by classical  
165 statistics such as t- and  $\chi^2$ -tests and simple linear regression. All statistical treatments were performed  
166 with XLSTAT<sup>®</sup> (Addinsoft, Paris, France) under EXCEL 7<sup>®</sup> (Microsoft Corporation, Redmond, WA).

167

## 168 3. Results

169 The first three axes of RDA (F1, F2 and F3) extracted 83% of the explained variance (60% for  
170 F1, 15% for F2 and 8% for F3). The variance explained by floristic and environmental data  
171 represented 21% of the total variance, but permutation tests (500 permutations of rows and columns)  
172 showed that the explanatory value of independent variables was highly significant ( $p < 0.0001$ ). The  
173 projection of humus variables in the plane of the first and third canonical axes (Fig. 2) showed that  
174 humus forms were distributed along F1 from most active (mull) to less active (moder, mor) forms.  
175 Humus forms belonging to the mull group (eumull, mesomull, oligomull, dysmull) were discriminated  
176 in the order of increasing accumulated organic matter while those of the moder-mor group (eumoder,  
177 dysmoder, mor) were imperfectly discriminated, pointing to other factors than geology, pedology,  
178 climate and woody flora that might influence them. Hemimoder was not fully discriminated from



179 dysmull along F1, both humus forms occupying an intermediate position. The position far from the  
180 origin of the Humus Index indicated a good correlation of this numerical variable with the first  
181 canonical axis, which was verified by regression analysis (Fig. 3): the Humus Index explained by itself  
182 57% of the variance of F1. Amphi, which occupied an intermediate position along F1, like hemimoder  
183 and dysmull, was fully discriminated by the third canonical axis, pointing to a distinct factor  
184 explaining this humus form. The second canonical axis did not correspond to any interpretable factor,  
185 the parabolic arrangement of sites in the F1-F2 plane (not shown) suggesting a horseshoe (Guttman)  
186 effect.

187         The projection of independent variables in the F1-F3 plane (Fig. 4) showed that points  
188 corresponding to tree species were projected near the origin while most environmental variables were  
189 projected far from the origin, more especially along F1. Tree canopies had a feeble explanatory value  
190 for humus forms, compared with environmental variables, to the exception of *Abies alba* Mill. for  
191 amphi. Most prominent relationships with the humus form were displayed by geology: 'alkaline' and  
192 'acid' geological substrates were projected far from the origin on opposite sides of F1 (on 'mull' and  
193 'mor-moder' sides, respectively), while the 'neutral' substrate was projected in an intermediate  
194 position, i.e. not far from the origin. Soil types scaled accordingly along F1, from calcisols  
195 (hypereutric cambisols) and calcosols (calcaric cambisols) on the 'mull' side to alocrisols  
196 (hyperdystric cambisols) and podzosols (podzols) on the 'mor-moder' side. This might suggest a  
197 gradient of soil acidity and nutrient availability along F1, but climatic and geographical variables  
198 scaled also along the same canonical axis, in particular 'July temperature' and 'Northern continental  
199 plains', suggesting that mull (in particular eumull) was associated with milder climate, too, without  
200 any discrimination between the respective influences of geology and temperature. This was verified by  
201 studying the distribution of humus forms and of the Humus Index according to geological substrates  
202 (Fig. 5a) and temperatures of the warmest month (Fig. 5b). The distribution of humus forms, and  
203 accordingly the value of the Humus Index (H.I.), changed significantly between 'alkaline' and  
204 'neutral' substrates (H.I. = 2.3 and 4.1, respectively), while they did not differ between 'neutral' and  
205 'acid' substrates (H.I. = 4.1 and 4.3, respectively), which were thus equivalent for the distribution of

206 humus forms but not for other environmental variables, as suggested by F1 scores of environmental  
207 variables (Fig. 4).

208 Among climate variables, July temperature, and to a lesser extent mean annual temperature,  
209 were projected on the 'mull' side while annual rainfall and Thornthwaite Aridity Index (which  
210 increases with rainfall) were projected on the 'mor-moder' side of F1, indicating a combined influence  
211 of temperature and precipitation on humus forms, temperature having a prevailing influence as  
212 indicated by respective F1 scores. The influence of climate was verified by comparing the distribution  
213 of humus forms and the value of the Humus Index in three groups differing by July temperature  
214 ( $>19^{\circ}\text{C}$ ,  $15\text{-}19^{\circ}\text{C}$  and  $<15^{\circ}\text{C}$ ): all differences were significant, indicating that there is a continuous  
215 gradient of decreasing presence of mull and increasing presence of mor and moder and a higher  
216 Humus Index when the environment becomes colder (Fig. 5b).

217 The poor influence of tree canopy on humus forms (at the scale of the whole French territory)  
218 was verified by classifying the sites in deciduous and coniferous forests (Fig. 5c): differences in the  
219 distribution of humus forms between these two groups of contrasted canopy composition were only  
220 marginally significant ( $P = 0.05$ ) and their Humus Index did not differ. Mixed forests were not taken  
221 into account, being too weakly represented in the EcoPlant database (5%).

222 The third canonical axis F3 showed that 'amphi' was mostly associated with high mountain  
223 environments of the Alps and Pyrenees and to a lesser extent to Mediterranean and Aquitaine basins,  
224 and with poorly developed soils such as organosols (folic umbrisols), dolomitisols (dolomitic  
225 cambisols), peyrosols (episkeletic soils), lithosols (leptosols) and arenosols (in decreasing order of  
226 association with amphi according to F3 scores). The position of the variable 'altitude' on both positive  
227 sides of F1 and F3 (Fig. 4) indicated that higher elevation favours either 'amphi' or 'mor-moder'  
228 according to the geological substrate being 'alkaline' or 'acid', respectively (as shown by the  
229 respective projection of these two variables on F3). The projection of the variable 'latitude' on the  
230 negative side of F3 (i.e. opposed to 'amphi') can be explained by the southern localisation of high  
231 altitude and Mediterranean sites across the French territory. The respective position of 'amphi' and

232 'hemimoder' along F3 also showed that they differed according to ecological factors, although being  
233 given the same Humus Index value (5).

234 Partial RDA showed that tree species composition and abiotic variables did not contribute to  
235 the same extent to the distribution of humus forms. When the composition of tree canopy was kept  
236 constant, environmental variables explained a significant part (19%) of humus form variation (Monte-  
237 Carlo permutation test, Pseudo-F = 0.23,  $P < 0.0001$ ), while when only tree species variables were  
238 allowed to vary, a much lower (3%) and insignificant part of humus form variation was explained  
239 (Pseudo-F = 0.03,  $P = 1$ ). The interaction between environment and tree species composition was  
240 negligible (0.2%). Residual (unexplained) variation amounted to 79%.

241

#### 242 **4. Discussion**

243 We showed that at the scale of the French continental territory (1000 km from West to East  
244 and 1000 km from North to South, elevation from 1 to 2500 m) the distribution of humus forms and  
245 the value of the Humus Index were but poorly explained by the composition of the forest canopy, but  
246 were affected by geology, climate and associated soil types. This contradicts current tenets about the  
247 detrimental influence of coniferous litter on soil biological activity, which has been always  
248 demonstrated at a scale at which geology and climate could not vary and interfere with it. Our results  
249 point to a decisive influence of large-scale factors such as parent rock, temperature and to a lesser  
250 extent rainfall. We are more cautious about the influence of soil conditions on humus forms, shown by  
251 the distribution of soil types along the first canonical axis of RDA, given that the development of the  
252 soil profile is strongly influenced by soil biology (Bullinger-Weber et al., 2007; Frey et al., 2010),  
253 pointing to symmetric influences during the common development of humus forms and soils (Van  
254 Breemen, 1993; Ponge, 2003).

255 The influence of parent rocks on the development of humus forms may be at least partly  
256 explained by biogeochemical cycles: the nature of the subsoil influences (1) the quality of litter, in  
257 particular its mineral content (Ponge et al., 1997, 1999), and (2) the access of soil-dwelling animals to

258 nutrients through their direct use of mineral matter (Bernier, 1998). Earthworms, when digging the  
259 soil, ingest mineral particles and may contribute to mineral weathering (Carpenter et al., 2007), quite  
260 to the same extent as plant roots and their symbionts (Van Breemen et al., 2000). In the sandy context  
261 of the Fontainebleau forest, it has been shown that the presence of a limestone table, at a depth not  
262 exceeding that available to beech roots, allowed the maintenance of an active mull-forming earthworm  
263 population through a litter enriched in calcium (Ponge et al., 1999). Other studies showed that  
264 earthworms were able to modify mineral assemblages, thereby increasing the available nutrient pool of  
265 the topsoil (Rangel et al., 1999).

266         The influence of climate (mull associated with more heat) can be understood through the  
267 stimulatory influence of temperature on most chemical processes, in particular those involved in  
268 organic matter decomposition (Aerts, 1997) and mineral weathering (Turner et al., 2010; Williams et  
269 al., 2010). In addition to benefits of heat for their own activity of cold-blooded animals (Briones et al.,  
270 2010), mull-forming invertebrates may benefit from the more rapid recycling of elements authorized  
271 by an increase in temperature (Zhang et al., 2008), at least in the absence of any limitation by drought  
272 (Cortez, 1998) which is often marginal in OF and OH horizons. The association of mor and moder  
273 with heavy rainfall can be explained by (1) the intensity of leaching, which favours nutrient losses and  
274 thus topsoil impoverishment (Turner et al., 2010), and (2) the association of heavy rainfall with  
275 altitude and low temperatures (Roe, 2005).

276         The poor influence of tree species on humus forms, compared to that of geology and climate,  
277 can be explained by the influence of parent material and climate on litter quality. For a given tree  
278 species, the composition of leaf or needle foliage may vary according to substrate (Nicolai, 1988;  
279 Hättenschwiler et al., 2003) and to a lesser extent according to climate (Aerts, 1997), making  
280 palatability and nutritional quality of tree litter more dependent on the environmental context than on  
281 the taxonomic level. Bernier (1998) showed that the anecic earthworm *Lumbricus terrestris* L.  
282 consumed spruce needles from a coniferous selection forest (not planted) and mixed them with the  
283 mineral soil, stemming in the building of mull humus. Such results point on possible confusion of  
284 negative coniferous effects with the detrimental influence of (1) plantation forests (whether deciduous

285 or not) to which local animal and microbial communities needs time to become, if any, adapted  
286 (Hansen, 1999), and (2) associated ground vegetation (Wolters, 1999). In the present database most  
287 measurement plots were installed in indigenous forest stands, avoiding young plantations. However, it  
288 must be noticed that we found a marginally significant negative correlation between the Humus Index  
289 and the species richness of the tree canopy ( $r = -0.035$ ,  $P = 0.041$ ), which could be explained by either  
290 or both (1) the favourable effect of tree mixture on litter decomposition and (Chapman et al., 1988;  
291 Aubert et al., 2006; but see Wardle et al., 2003), and (2) distal effects of environmental factors on both  
292 humus forms and plant diversity (Ponge, 2003; Wardle et al., 2004). A much better negative  
293 correlation (the higher the Humus Index the lower the species richness) was observed with ground  
294 flora but this relationship held true at the local scale only (Lalanne et al., 2010).

295         The fact that moder (eumoder and dysmoder) and mor could not be discriminated by the first  
296 canonical axis of RDA points to the existence of other possible environmental influences, not taken  
297 into account in our data matrix, such as soil chemistry, known to discriminate moder and mor in  
298 addition to morphological and biological characters (Wilson et al., 2001). In addition, it must be  
299 pointed out that in the French context the mor humus form is rare and never typical.

300         The particular case of amphi is worth to notice. This humus form, which has been previously  
301 confused with dysmull, hemimoder or moder (Brêthes et al., 1995), is associated with highly seasonal  
302 mull-forming activity in an otherwise favourable geological context (Tagger et al., 2008; Galvan et al.,  
303 2008): the shorter the season during which invertebrate (and microbial) activity is possible, the thicker  
304 will be the organic horizon (of moder type) overlying a crumby A horizon (of mull type). This may  
305 happen both at higher elevation and in Mediterranean landscapes when the richness of the substrate  
306 (limestone, dolomitic rocks) allows the activity of subterranean animals during less favourable  
307 seasons. Although still badly understood and imperfectly described, amphi does not seem in line with  
308 the temperature/acidity gradient corresponding to the contrast between mull and mor.

309         A large part of the variation of humus forms was not explained by the abovementioned  
310 factors. The bulk of unexplained variation (79%) could be ascribed to local factors, the influence of

311 which has been demonstrated in particular cases (detailed in the Introduction), such as ground  
312 vegetation, previous land use, management options, canopy density, and the mosaic patchwork of  
313 animal and microbial populations. Nonetheless, the fact that geology and climate may explain by  
314 themselves a fifth of the total variation of this highly fluctuating compartment of the forest ecosystem  
315 may help to discern possible trends in the actual context of global warming. Linear regression analysis  
316 ( $F = 182, P < 0.0001$ ) showed that the Humus Index (H.I.) was related to July temperature (J) according  
317 to the following equation:

$$318 \text{ H.I.} = 9 - 0.3 J$$

319 According to this linear relationship any increase of 1°C would correspond to a decrease of the Humus  
320 Index averaging 0.3 units. This is highly speculative, given what we know about the counteracting  
321 influences of litter recalcitrance due to fertilisation with CO<sub>2</sub> (Cotrufo and Ineson, 1996; but see  
322 Coûteaux et al., 1999) and anthropogenic acidification and eutrophication (Thimonier et al., 1994).  
323 Nonetheless, in the present state of our knowledge, we can hypothesize in accordance with Graefe  
324 (2007) that the combined influence of increased litter recalcitrance and acidification (favouring the  
325 accumulation of litter) and warming trends and eutrophication (favouring the activity of soil  
326 organisms) will extend the domain of amphi, a humus form not fitted with the mull-mor gradient of  
327 decreasing litter quality and biological activity associated with climate/trophic constraints (Ponge,  
328 2003).

329

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334

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- 605

606

607 **Figure captions**

608

609 **Figure 1.** Distribution of the 3441 forest plots selected within the EcoPlant database over the French  
610 continental territory.

611

612 **Figure 2.** Total Redundancy Analysis (RDA): projection of dependent variables (9 humus forms as  
613 dummy variables and the Humus Index as discrete variable) in the F1-F3 plane of canonical  
614 axes

615

616 **Figure 3.** Diagram showing the linear relationship between the Humus Index and the first canonical  
617 axis (F1) of total RDA.

618

619 **Figure 4.** Total Redundancy Analysis (RDA): projection of independent variables (148 variables  
620 describing geology, climate, soil type, geography and woody flora) in the F1-F3 plane.  
621 Environmental variables are described in Table 1. Tree species (listed in the Appendix) were  
622 represented as black dots, given their position not far enough from the origin. A more detailed  
623 view of this zone, showing plant codes (see Appendix), was inserted for the sake of clarity.

624

625 **Figure 5.** Distribution of humus forms and average values of the Humus Index according to geology  
626 (a), mean July temperature (b) and forest types (c).

627

**Table 1.** Average values of quantitative variables (geography, climate) and percent occurrence of dummy variables (geology, pedology) used in Redundance Analysis (RDA) in each geographical region covered by the study.

Geographical regions were also included as dummy variables (refer to text for further details)

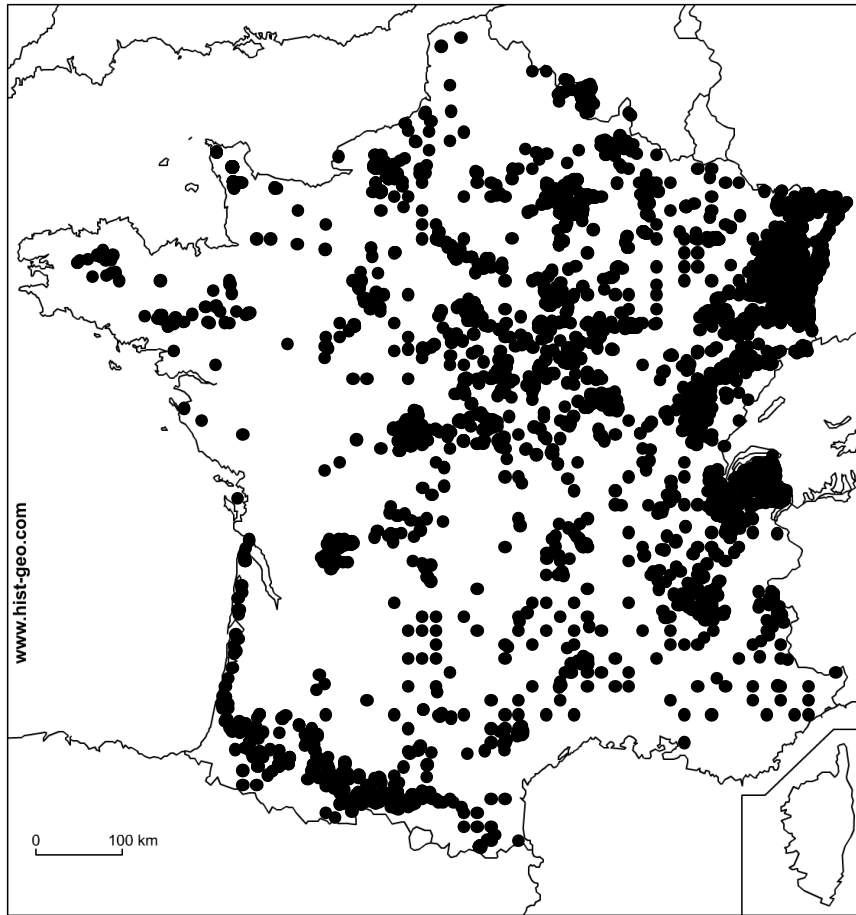
Variable name	Meaning	Brittany (n = 99)	Northern continental plains (n = 654)	Vosges (n = 472)	Jura (n = 171)	Paris basin (n = 971)	Massif Central (n = 229)	Alps (n = 417)	Pyrenees (n = 151)	Rhone valley (n = 18)	Aquitaine basin (n = 247)	Mediterranean basin (n = 15)
<b>Geography:</b>												
Longitude	Lambert II extended X coordinates (m)	281307	900896	952636	893364	614624	673735	906434	494659	821386	414911	783533
Latitude	Lambert II extended Y coordinates (m)	2397578	2356856	2377920	2227127	2359891	2044778	2067732	1771497	2053854	1907341	1876533
<b>Climate:</b>												
Mean temperature	Mean annual temperature	11°C	10°C	8°C	9°C	10°C	9°C	7°C	10°C	11°C	12°C	13°C
January temperature	Mean January temperature	5°C	1°C	-0.2°C	0.4°C	3°C	1.5°C	-1.3°C	4°C	2.4°C	6°C	5°C
July temperature	Mean July temperature	17°C	19°C	17°C	18°C	18°C	17°C	16°C	18°C	21°C	20°C	22°C
Altitude	Elevation (m)	96	252	617	596	161	743	1277	834	290	157	280
Rainfall	Mean annual rainfall (mm)	894	854	1279	1307	744	1202	1386	1101	938	969	855
Water balance	Rainfall-potential evaporation (May to September) Thornthwaite index	-175	-124	28	69	-183	-30	122	-39	-119	-154	-251
Aridity index	Rainfall:temperature Martonne index	43	43	71	70	37	65	84	55	44	43	38
<b>Parent rock:</b>												
Acid	Acid silicate rocks	52%	41%	91%	9%	66%	74%	30%	57%	39%	73%	13%
Neutral	Weakly acidic silicate rocks	46%	0%	6%	0%	2%	19%	5%	8%	0%	0%	0%
Alkaline	Calcareous rocks	2%	59%	3%	91%	31%	4%	65%	35%	61%	26%	87%
<b>Soil type (WRB):</b>												
<b>Soil type (AFES):</b>												
Alocrisol	Cambisol (Hyperdystric)	37%	7%	27%	4%	8%	31%	14%	12%	0%	12%	0%
Andosol	Andosol	0%	0.0%	0%	0%	0%	0.4%	0%	0%	0%	0%	0%
Arenosol	Arenosol	1%	1%	0%	0%	0.1%	0%	0%	0%	0%	6%	0%
Brunisol	Cambisol	19%	21%	36%	25%	17%	31%	23%	31%	17%	21%	7%
Calcisol	Cambisol (Hyperautric)	0%	8%	1%	17%	8%	1%	12%	15%	11%	13%	27%
Calcisol	Cambisol (Calcaric)	0%	10%	0.4%	14%	6%	0.4%	10%	3%	6%	6%	13%
Colluviosol	RSG (Colluvic)	1%	3%	2%	7%	2%	3%	6%	0%	28%	0.4%	0%
Dolomitisol	Cambisol (Dolomitic)	0%	0%	0%	0%	0%	0%	0%	1%	0%	0%	7%
Fluvisol	Fluvisol	0%	15%	1%	0%	1%	1%	2%	1%	17%	3%	0%
Histosol	Histosol	0%	0.2%	0%	0%	0.1%	0%	0%	0%	0%	0%	0%
Lithosol	Leptosol	0%	0.3%	1%	0%	0.1%	2%	3%	3%	0%	0%	13%
Luvisol	Luvisol	2%	6%	0.2%	4%	14%	3%	2%	6%	11%	6%	0%
Neoluvisol	Cambisol (Luvic)	9%	9%	3%	9%	11%	2%	3%	12%	6%	9%	0%
Organosol	Umbrisol (Folic)	0%	0.3%	0.2%	6%	0%	1%	6%	4%	0%	0%	0%
Pelosol	Regosol (Clavic)	0%	3%	0%	1%	2%	0%	0%	0%	0%	0%	0%
Peyrosol	suffix qualifier Episkeletic	0%	0.3%	3%	1%	1%	0%	1%	5%	0.0%	0.4%	0%
Planosol	Planosol	0%	1%	0%	0%	6%	0%	0%	0%	0%	0.4%	0%
Podzsol	Podzol	17%	3%	22%	1%	14%	16%	7%	5%	0%	11%	0%
Rankosol	Leptosol	5%	0.3%	3%	0%	0.2%	6%	2%	2%	0%	0%	7%
Redoxisol	Stagnosol	7%	3%	0.4%	0%	5%	1%	1%	0%	0%	4%	0%
Reductisol	Gleysol	1%	3%	1%	1%	1%	0.4%	1%	0%	0%	4%	0%
Regosol	Regosol	0%	0.3%	0%	0%	0%	0%	0.2%	0%	0%	1%	7%
Rendisol	Leptosol (Rendzic)	0%	1%	0.2%	6%	1%	0.4%	3%	1%	6%	2%	0%
Rendosol	Leptosol (Rendzic)	0%	5%	0.2%	6%	3%	0%	5%	1%	0%	2%	20%

**Appendix.** Codes and names of woody plant species used for RDA analysis

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Aal	<i>Abies alba</i>
Agr	<i>Abies grandis</i>
Aca	<i>Acer campestre</i>
Amo	<i>Acer monspessulanum</i>
Ama	<i>Acer monspessulanum subsp. martinii</i>
Ane	<i>Acer negundo</i>
Aop	<i>Acer opalus</i>
Apl	<i>Acer platanoides</i>
Aps	<i>Acer pseudoplatanus</i>
Ahi	<i>Aesculus hippocastanum</i>
Aco	<i>Alnus cordata</i>
Agl	<i>Alnus glutinosa</i>
Ain	<i>Alnus incana</i>
Bpe	<i>Betula pendula</i>
Bsp	<i>Betula sp.</i>
Cbe	<i>Carpinus betulus</i>
Csa	<i>Castanea sativa</i>
Cat	<i>Cedrus atlantica</i>
Cse	<i>Cupressus sempervirens</i>
Fsy	<i>Fagus sylvatica</i>
Fan	<i>Fraxinus angustifolia</i>
Fox	<i>Fraxinus angustifolia subsp. oxycarpa</i>
Fex	<i>Fraxinus excelsior</i>
For	<i>Fraxinus ornus</i>
Iaq	<i>Ilex aquifolium</i>
Jni	<i>Juglans nigra</i>
Jre	<i>Juglans regia</i>
Lde	<i>Larix decidua</i>
Ltu	<i>Liriodendron tulipifera</i>
Msy	<i>Malus sylvestris</i>
Oca	<i>Ostrya carpinifolia</i>
Pab	<i>Picea abies</i>
Psi	<i>Picea sitchensis</i>
Pce	<i>Pinus cembra</i>
Pha	<i>Pinus halepensis</i>
Pni	<i>Pinus nigra</i>
Pla	<i>Pinus nigra subsp. laricio</i>
Pns	<i>Pinus nigra subsp. nigra</i>
Ppi	<i>Pinus pinaster</i>
Ppa	<i>Pinus pinea</i>
Pst	<i>Pinus strobus</i>
Psy	<i>Pinus sylvestris</i>
Pun	<i>Pinus uncinata</i>
Pac	<i>Platanus acerifolia</i>
Psp	<i>Platanus sp.</i>
Pal	<i>Populus alba</i>
Pca	<i>Populus canescens</i>
Pna	<i>Populus nigra</i>
Pos	<i>Populus sp.</i>
Ptr	<i>Populus tremula</i>
Pxc	<i>Populus x-canadensis</i>
Pav	<i>Prunus avium</i>
Prs	<i>Prunus sp.</i>
Pme	<i>Pseudotsuga menziesii</i>
Pco	<i>Pyrus communis</i>
Ppy	<i>Pyrus pyraeaster</i>
Pys	<i>Pyrus sp.</i>
Qce	<i>Quercus cerris</i>
Qhu	<i>Quercus humilis</i>
Qil	<i>Quercus ilex</i>
Qpe	<i>Quercus petraea</i>
Qpy	<i>Quercus pyrenaica</i>
Qro	<i>Quercus robur</i>
Qru	<i>Quercus rubra</i>
Qsp	<i>Quercus sp.</i>
Qsu	<i>Quercus suber</i>
Qca	<i>Quercus x-calvescens</i>
Rps	<i>Robinia pseudoacacia</i>
Sal	<i>Salix alba</i>
Sca	<i>Salix caprea</i>
Ssp	<i>Salix sp.</i>
Sar	<i>Sorbus aria</i>
Sau	<i>Sorbus aucuparia</i>
Sdo	<i>Sorbus domestica</i>
Sla	<i>Sorbus latifolia</i>
Smo	<i>Sorbus mougeotii</i>
Ssp	<i>Sorbus sp.</i>
Sto	<i>Sorbus torminalis</i>
Sin	<i>Sorbus x-intermedia</i>
Tba	<i>Taxus baccata</i>
Tpl	<i>Thuja plicata</i>
Tco	<i>Tilia cordata</i>
Tpl	<i>Tilia platyphyllos</i>
Tvu	<i>Tilia x-vulgaris</i>
Ugl	<i>Ulmus glabra</i>
Ula	<i>Ulmus laevis</i>
Umi	<i>Ulmus minor</i>
Usp	<i>Ulmus sp.</i>

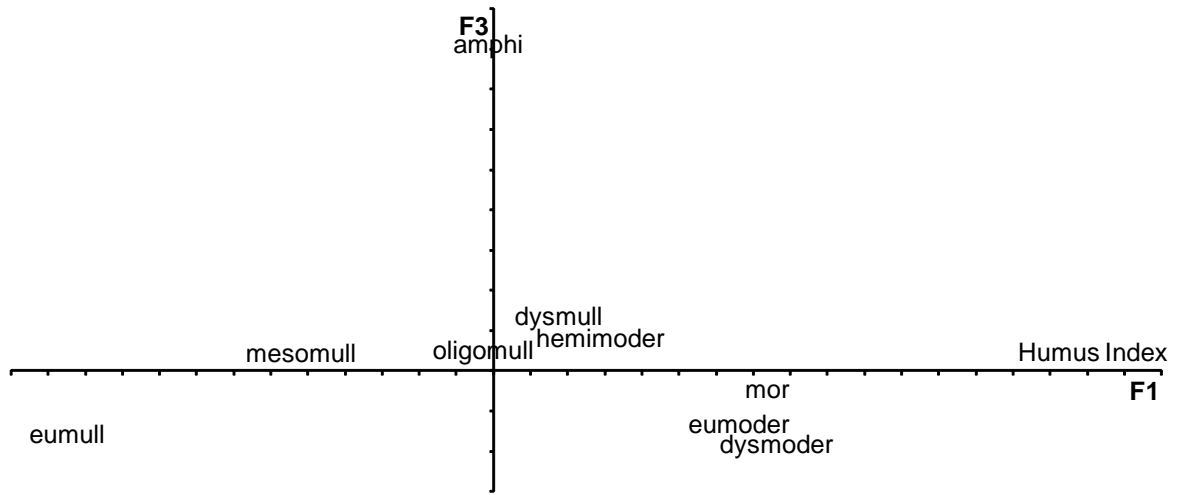
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632 Fig. 1

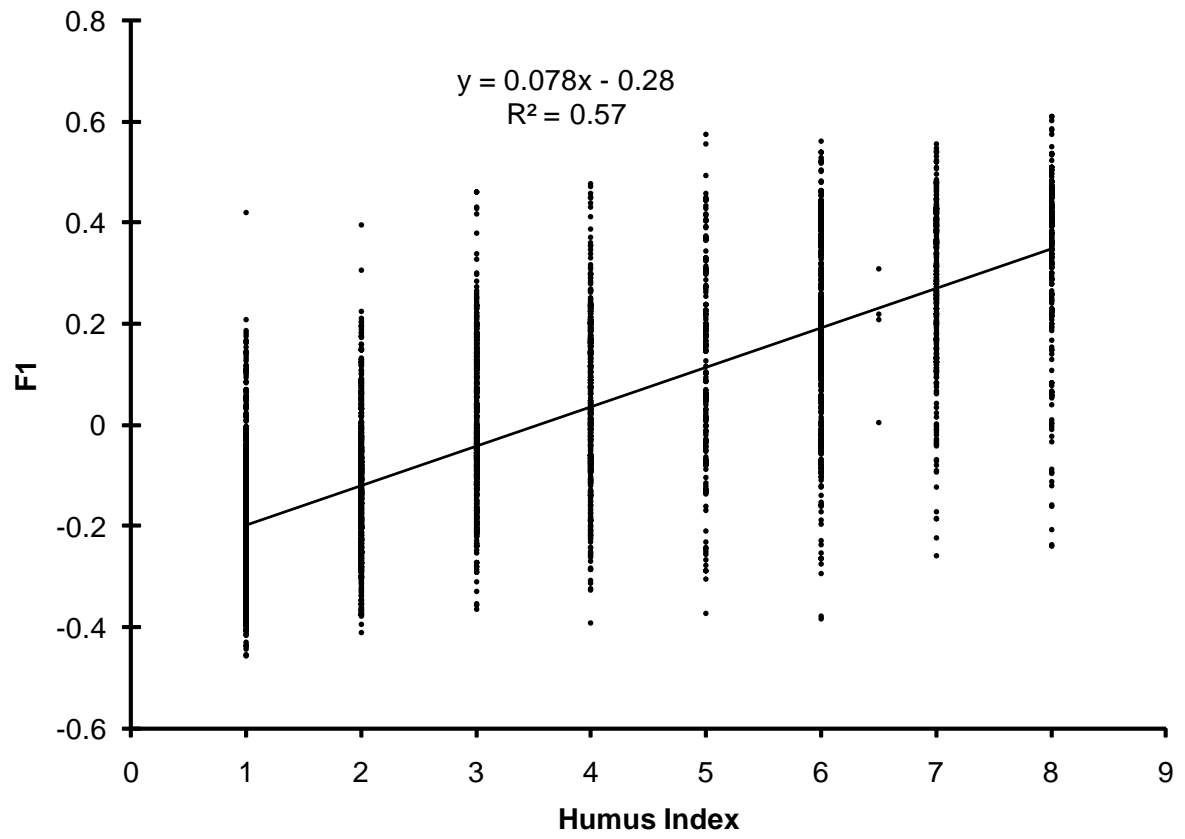
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634

635 Fig. 2

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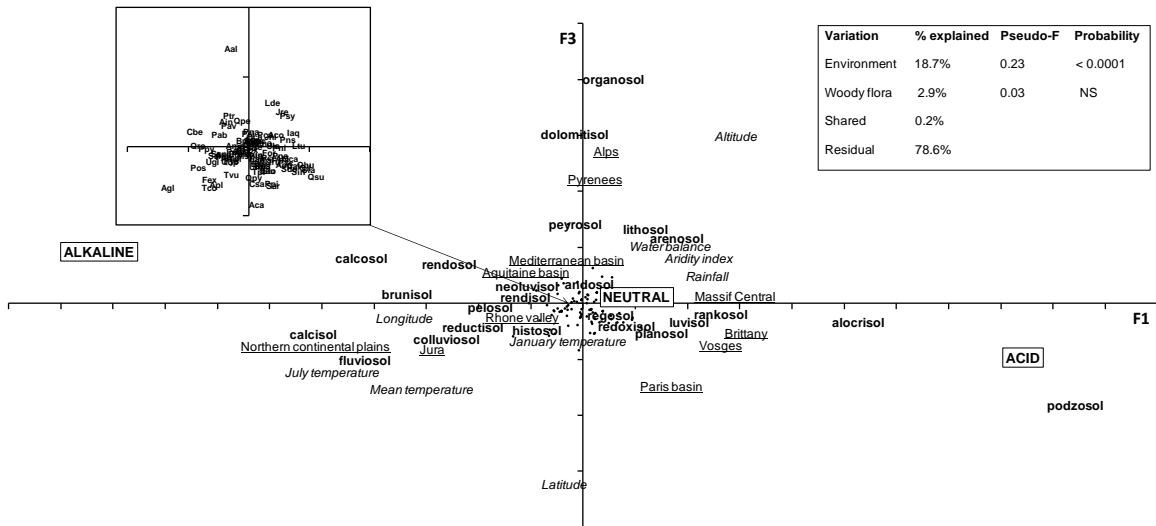


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638 Fig. 3

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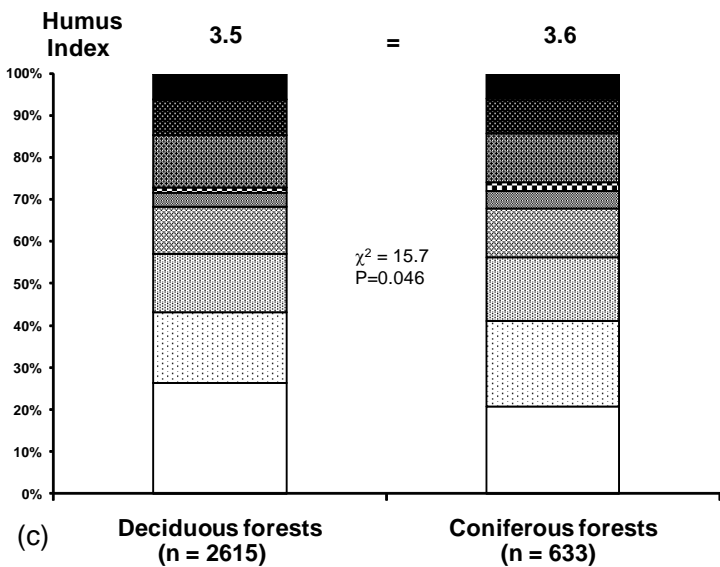
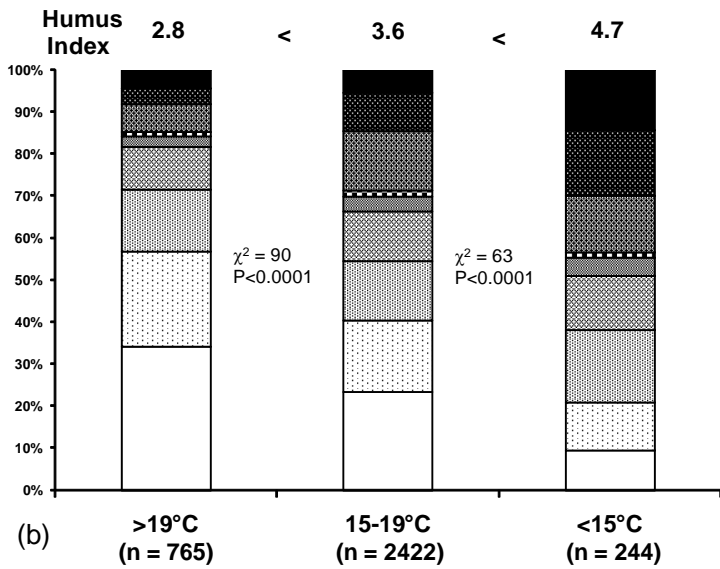
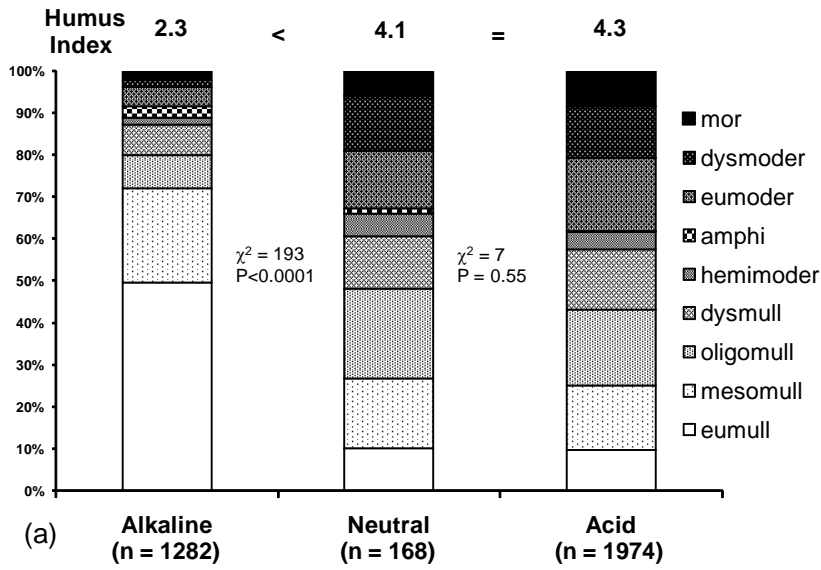




640

641 Fig. 4

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643

644 Fig. 5