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**Opposite responses of vascular and moss communities to
changes in humus form, as expressed by the Humus Index**

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Abstract

Question: Do plant species found in forests correlate with the Humus Index (based on a ranking of humus forms) and, if yes, do they exhibit different responses according to phyletic lineages?

Location: temperate atlantic climate (Paris Basin, France)

Methods: Moss and vascular (herb, fern) plant species were inventoried in two broadleaved forests, with contrasting soil conditions. Fifteen and sixteen sites were investigated, respectively, describing the variety of stand age and soil conditions which prevailed in each of these forests, with 5 plots and 20 sub-plots in a grid at each site. Mantel tests were used to estimate correlations between the Humus Index and plant species richness, taking into account spatial autocorrelation.

Results: The local (plot, sub-plot) species richness of moss communities increased with the Humus Index, i.e. when humus forms shifted from mull to moder. The reverse phenomenon was observed in vascular communities. Opposite response of these two plant groups could be explained by opposite strategies for nutrient capture which developed in the course of their evolutionary history.

Conclusions: Although not necessarily causative, the Humus Index describes fairly well changes in species richness which occur in forest vegetation, provided that phyletic lineages and geographical position are taken into consideration.

Keywords: Species richness; Forest vegetation; Angiosperms; Bryophytes; Edaphic properties.

Nomenclature: Rameau et al. (1989), Hill et al. (2006), Lambinon et al. (1999).

1 Introduction

2
3 To the light of empirical knowledge on plant-microbial-animal relationships it was
4 suggested by Ponge (2003) that the humus form, i.e. the vertical arrangement and thickness
5 of forest floor and topsoil horizons, could reflect the local species richness of terrestrial
6 communities. In short, at a given point, the more diverse plant, microbial and animal
7 communities, the more rapid the turnover of nutrients and the more productive the
8 ecosystem, with a feedback to the humus form. This is supported by theoretical work
9 (Arditi et al. 2005; Yachi & Loreau 2007) and experimental approaches (Heemsbergen et
10 al. 2004; Fargione et al. 2007), despite claims that nutrient-rich soils may favour the excess
11 development of more competitive species, thereby decreasing species richness (Huston
12 1993, but see Roem & Berendse 2000). In temperate forest stands, the Humus Index, based
13 on a ranking of humus forms in an increasing order of organic matter accumulation, was
14 shown to be well-correlated with numerous stand and soil properties, including soil acidity,
15 nutrient availability and stand age (Ponge et al. 2002; Ponge & Chevalier 2006). Its
16 relationship with other forest stand properties, such as the species richness of plant
17 communities, was not investigated so far, although reciprocal relationships between humus
18 forms and plant species are known for a long time (Olsen 1925; Ovington 1954; Ponge et
19 al. 1998).

20
21 In his abovementioned review Ponge (2003) postulated that the three main humus
22 forms mor, moder and mull successively appeared during past history of the Earth,
23 accompanying the development of more diverse and nutrient-rich terrestrial ecosystems.
24 The evolution of humus forms paralleled that of the plant kingdom, from cryptogamic to
25 phanerogamic vegetation of (i) increasing nutrient content and litter palatability, (ii)

increasing encroachment to soil for nutrient capture, and (iii) decreasing tolerance to acidity and heavy metals (Oechel & Van Cleve 1986; Grime & Hodgson 1987). According to this hypothesis, higher values of the Humus Index, shown to increase with soil acidity (Wilson et al. 2001; Ponge et al. 2002), should be associated with richer bryophytic but poorer phanerophytic communities.

We tested this hypothesis independently in two forests exhibiting contrasted humus forms, the one with nutrient-rich soils (Forêt de Brotonne, Upper Normandy), the other with nutrient-poor soils (Forêt de Saint-Palais, Berry). The Humus Index was measured at the scale of sites (16 and 15 sites, respectively, with five plots each), plots (400 m²) and sub-plots (100 m²), and was compared with moss and vascular species richness, taking into account the existence of spatial autocorrelation (Arp & Krause 1984; Riha et al. 1986; Legendre & Fortin 1989). In both forests, Humus Indices were also calculated for individual plant species, in order to characterize their ecological requirements (Falkengren-Grerup & Tyler 1993b).

Study sites

The Forêt de Saint-Palais (1907 ha) is a lowland deciduous state forest with sessile oak *Quercus petraea* (Liebl.) as a dominant tree, located North-West of Bourges, Pays Fort, Berry. The altitude varies from 205 to 315 m, with a slope varying from 2 to 4%. The climate is temperate atlantic under continental influence, with an annual rainfall of 940 mm and a mean temperature of 10.8°C. The geological substrate is clay with flints of Upper Cretaceous origin. There is a wide variety of soils of varying acidity and waterlogging

conditions, but cambisols and luvisols sensu World Reference Base (Bridges et al. 1998) are mostly represented.

The Forêt de Brotonne (6754 ha) is a very old, mostly deciduous state forest with common beech (*Fagus sylvatica* L.) as a dominant tree, located in an abandoned meander of the River Seine, West of Rouen, Upper Normandy. The climate is temperate oceanic, with an annual rainfall of 752 mm and a mean temperature of 10.7°C. The geological substrate is Upper Cretaceous chalk, with superficial deposits of varying origin, flints and loess in the southern part, and alluvial deposits in the northern part. Except hill ridges and valleys with cambisols, most of the surface is covered with acidic soils, ranging from luvisols to podzols. Sulphur deposition is prominent in this forest (Ulrich et al. 2002), and was even more pronounced in the past, given its location 45 km downwind of oil refineries (le Havre).

Sixteen and fifteen sites have been selected in Brotonne and Saint-Palais forests, respectively, embracing a balanced pannel of developmental stages prevailing in atlantic acidophilous beech forest stands (Table 1). Both forests were managed similarly, i.e. stands were made of full-grown trees of near similar age. Stands 100-yr-old and more were converted from old coppices-with-standards, while younger stands were grown after clear-cut. From a phytosociological point of view all studied beech-oak stands belong to *Ilici aquifolii-Fagetum sylvaticae* (Durin et al. 1967).

Methods

At each site five plots 20 x 20 m, each subdivided into four 10 x 10 m sub-plots (Fig. 1) were surveyed for ground vascular (herbs, ferns) and moss vegetation, identified at the species level and quantified according to the Braun-Blanquet method. Vascular plants and mosses living in aboveground micro-habitats (trunk bases, boulders, dead branches and trunks) were not recorded. Only species richness at three scales of census (100 m², 400 m², 2,000 m²) will be accounted for in the present study.

The humus form was described in each sub-plot according to criteria established by Brêthes et al. (1995) for the classification of forest humus forms. The Humus Index was calculated by scaling humus forms from less acidic to more acidic types, according to Ponge et al. (2002) and Ponge & Chevalier (2006):

- 1 Eumull (crumby A horizon, OL horizon absent, OF horizon absent, OH horizon absent)
- 2 Mesomull (crumby A horizon, OL horizon present, OF horizon absent, OH horizon absent)
- 3 Oligomull (crumby A horizon, OL horizon present, OF horizon 0.5 cm thick, OH horizon absent)
- 4 Dysmull (crumby A horizon, OL horizon present, OF horizon 1 cm or more thick, OH horizon absent)
- 5 Hemimoder (compact A horizon, OL horizon present, OF horizon present, OH horizon absent)
- 6 Eumoder (compact A horizon, OL horizon present, OF horizon present, OH horizon 0.5 cm or 1 cm thick)

7 Dysmoder (compact A horizon, OL horizon present, OF horizon present, OH horizon more than 1 cm thick)

This index, which is correlated with a wide range of soil and stand properties, as mentioned above, allows a numerical treatment of otherwise purely morphological data.

The two forests investigated were treated separately, in order to account for geographical distance and associated shifts in the ecological requirements of forest plant species (Diekmann & Lawesson 1999, but see Prinzing et al. 2002). In each forest the spatial variation of humus forms was analysed by comparing the variance of the Humus Index at three scales, that of the site, that of the plot and that of the sub-plot, using the Fisher-Snedecor F ratio (Sokal & Rohlf 1995) for testing for significant variation across scales. When the variation of a parameter is scale-dependent, correlation studies must use special tests accounting for non-independence of data, such as Mantel tests (Legendre & Fortin 1989). Such tests were performed, using distance matrices between samples. The distance between two samples was estimated by the algebraic difference between corresponding values of Humus Index or species richness of moss or vascular vegetation. Simple and partial product-moment correlation coefficients were calculated between distance matrices according to the Monte-Carlo method, using 5,000 random cross-permutations of rows and columns for the construction of empirical probability tables (Sokal & Rohlf 1995). Statistical treatment of the data was performed using XLSTAT® statistical software (Addinsoft).

In the two forests investigated, mean Humus Indices were calculated for moss and vascular plant species which were present in at least three samples (sub-plots). For that

purpose the Humus Index was averaged among samples where each species was found. This just allowed mean ecological requirements of species to be compared within the same local context, without any aim at establishing their absolute requirements.

Results

When calculated at the scale of the sub-plot (original values) the Humus Index (H.I.) did not display the same mean and variation in Saint-Palais and Brotonne forests (Fig. 2, Table 2). Saint-Palais exhibited a bimodal distribution of H.I. values, with a peak at 3 (Oligomull) and another peak at 5 (Hemimoder). In Brotonne H.I. values averaged and peaked at 6 (Eumoder), their distribution being negatively skewed, with a weak contribution of mull humus forms ($H.I. < 5$) and a number of sub-plots at the upper value of 7 (Dysmoder). All humus forms, from Mesomull (H.I. 2) to Dysmoder (H.I. 7), were represented in Saint-Palais, while Mesomull was absent from the census done in Brotonne.

The variation of the Humus Index did not vary from the scale of the sub-plot to that of the plot, plot/subplot F values being low and not significant (Table 2). However, although not significant at 0.05 level ($P = 0.06$), the passage from the scale of the plot to that of the site displayed F values far higher than when passing from the sub-plot to the plot scale. As a consequence, we considered that values of the Humus Index were spatially dependent, two distinct sites exhibiting a higher variation of their mean H.I. than plots sampled within the same site. However, it remains true that H.I. did not vary more at 50 m distance (between plots) than at 10 m distance (between sub-plots).

The Saint-Palais forest showed a wide variation of the mean Humus Index for vascular species (Table 3). The lowest value of the Humus Index (2.5) was exhibited by *Vinca minor*, while the highest value (5.5) was exhibited by *Convallaria majalis*. Some species exhibited a wide variation in their H.I. values, as shown by their standar errors, such as *Dryopteris filix-mas*, *Hypericum perforatum* and *Luzula campestris*. In the Brotonne forest, a slightly lower number of vascular species were censused (26 frequent species against 29 in Saint-Palais), spread on a narrow range of H.I. values, the lowest being 5.6 for *Holcus mollis* and the highest 6.5 for *Holcus lanatus*. Here, too, *H. perforatum* exhibited a wide variation in its H.I. values. Saint-Palais exhibited a much higher number of frequent moss species than Brotonne (12 against 6), with *Fissidens taxifolius* and *Leucobryum glaucum* at the lowest and highest H.I. values, respectively.

When censused at the sub-plot scale, the number of vascular species decreased when the Humus Index increased, contrary to moss species (Fig. 3). The same trend was depicted by both forests, although some differences were observed. The number of moss species per sub-plot was higher in Saint-Palais than in Brotonne, and the decrease in the number of vascular species was less abrupt in Brotonne than in Saint-Palais. In Saint-Palais the number of moss species exceeded that of vascular species at H.I. 7 (Dysmoder), while it remained always far lower than that of vascular species in Brotonne.

We tested the correlation between the Humus Index and the species richness of vascular and moss communities by the Mantel test. For technical reasons, sub-plot values could not be used, because of their high number (300 in Saint-Palais, 320 in Brotonne). Rather, we used plot values, i.e. the mean of four H.I. values and the total number of vascular and moss species censused in 400 m², which gave 75 and 80 values in Saint-Palais

and Brotonne, respectively. Simple Mantel tests showed that at the plot level the Humus Index was positively correlated with the number of vascular species, and negatively with the number of moss species, whatever the forest (Table 2). As expected, moss and vascular species were negatively correlated (Mantel test, $P < 0.0001$) but no correlation between both plant groups was displayed when the Humus Index was used as a covariate (partial Mantel test, $P = 0.27$). When moss species richness was used as a covariate, the correlation between H.I. and vascular species richness remained negative and significant (Mantel test, $P < 0.0001$). When vascular species richness was used as a covariate, the correlation between H.I. and moss species richness remained positive and significant (Mantel test, $P = 0.0002$). According to Legendre & Fortin (1989) this indicates that positive and negative interactions exist between the Humus Index and moss and vascular communities, respectively, without any additional interaction between both plant groups.

Discussion

Both forests exhibited at the local level the same trend of increased moss and decreased vascular species richness when the Humus Index increased, i.e. when humus forms shifted from mull to moder. Besides the well-known fact that a range of forest plant species are adapted to more or less acidic conditions (Falkengren-Grerup & Tyler 1993a; Lee 1999; Roem & Berendse 2000), this points to contrasted behaviour of vascular vs non-vascular species when humus forms and related factors select. That the bulk of moss species seem to be better adapted to moder than to mull, and the contrary for the bulk of vascular species, could be explained by the way they capture nutrients. While vascular root systems, connected or not to mycorrhizal hyphal systems, permeate the soil and allow higher plant species to capture nutrients liberated by litter decomposition and mineral

1 weathering, mosses capture them directly from rain, throughfall and aerosols, thus do not
 2 lie on soil for their nutrition (Oechel & Van Cleve 1986; Bates 1987). This is a first
 3 plausible explanation. Second, the better tolerance of moss species to scarcity of nutrients,
 4 soil acidity and associated aluminum toxicity can be inherited from the time at which they
 5 evolved in terrestrial habitats (Labandeira 2005). As hypothesized by Ponge (2003), and
 6 based on phylogenetic conservatism (Ponge 2000; Prinzing et al. 2001), present-day taxa
 7 may still reflect in their ecological requirements those of their Palaeozoic ancestors. Before
 8 the Carboniferous era primitive humus forms were probably of the mor type, , then of the
 9 moder type when land became colonized by invertebrates (Retallack 1985). Mull did
 10 probably not appear before the advent of angiosperms in the Cretaceous (Crepet et al.
 11 1991), which cope with its present-day association with nutrient-rich ecosystems (Schaefer
 12 & Schauermann 1990; Ponge et al. 1997). We are aware that the humus form (and closely
 13 associated factors such as soil acidity and nutrient availability) interact with many other
 14 factors, among them soil moisture, throughfall, light and micro-habitats are of paramount
 15 importance for the distribution of moss as well as vascular species. However, keeping in
 16 mind the existence of complex relationships between environmental factors which may
 17 flaw causality inferred from co-occurrence data (Mazlack 2004) it must be argued that (i)
 18 within each of the two studied forests our selection of sites was balanced between all
 19 developmental stages of beech-oak stands (Table 1), (ii) trunk bases, dead branches,
 20 boulders and other particular habitats thought more favourable to mosses than to vascular
 21 plants but not related to humus forms were avoided, and (iii) the strong negative
 22 correlation between moss and vascular species richness disappeared totally when the
 23 Humus Index was kept at a constant level. As a matter of fact, our data does not give
 24 evidence of any causality between humus forms (quantified by the Humus Index) and plant
 25 species richness but rather of a close association between them.

Although the two studied forests displayed the same phenomenon of contrasted responses of moss and vascular species to forest floor condition, differences were exhibited in the extent of colonization by these two plant groups. At the local scale (Fig. 3) as well as at the regional scale (Table 3), the species richness of moss communities was always lesser in Brotonne than in Saint-Palais, despite a more frequent occurrence of Moder and Dysmoder in the former site (Fig. 2). Several possible causes can be invoked to explain this phenomenon. First, the Forêt de Brotonne is known for its high level of atmospheric pollution, mostly by sulphur (Ulrich et al. 2002), to which mosses as a group are especially sensitive (Zechmeister et al. 2003). Second, the acidification of the soil by beech, which was grown in even-aged full-grown stands in previous mixed deciduous forests of Upper Normandy, as in other parts of Western Europe (Greig 2002), must be highlighted. The detrimental influence of pure beech on forest soils and plant biodiversity has been reported by several authors (Falkengren-Grerup 1989; Aubert et al. 2004; Godefroid et al. 2005). If the acidification-by-beech hypothesis is true, then the time needed for the floristical cortege of acid soils to colonize chalk soils of Upper Normandy may not allow the existence of a complete acidophilic moss flora. Similar hypotheses have been erected for explaining why some local, regional or continental pools of species may be poorer than others in a context of fragmentation (Rescia et al. 1995; Huston 1999; Honnay et al. 2002). Another plausible explanation is the impact of heavy machinery in Saint-Palais (Lalanne, unpublished doctorate thesis) which, added to the activity of mull-forming animal species (see Fig. 2 for the distribution of humus forms), create micro-habitats for terricolous species such as *Atrichum undulatum*, *Dicranella heteromalla* and *Fissidens taxifolius* (Table 3). At the sub-plot scale, wheel tracks, earthworm casts and mole mounds (all associated with litter disappearance) may allow these species to find a variety of suitable

habitats, thus increasing moss species richness. Jonsson & Esseen (1998) showed that most severe disturbances of the forest floor (appearance of the mineral soil) favoured moss species richness. At last, the more humid climate in Saint-Palais (940 mm annual rainfall, compared to 752 mm in Brotonne) favours the establishment on the forest floor of corticolous/epilithic moss species such as *Isoetecium myosuroides* (Table 3), which are limited to tree trunk bases (and thus absent from our census) in Brotonne.

Differences in Humus Index values for vascular and moss species are prominent between both forests, but should be considered with caution, at least for some species the distribution of which is skewed towards one or the other side of the humus form gradient. For instance, *Deschampsia flexuosa*, which is commonly considered as acidophilic (Rameau et al. 1999), exhibits a mean Humus Index of 4.2 in Saint-Palais (Dysmull), and 6.0 (Eumoder) in Brotonne. This does not mean that the ecological requirements of this species vary according to its geographical position, and that it loses its acidophily in Saint-Palais. Rather, its ecological range is better expressed in Saint-Palais, where the humus form gradient is longer than in Brotonne (Fig. 2). It is suggested that indices based on the presence of individual plant species must be interpreted with caution. Such limits have been noted for Ellenberg's indices (Hill et al. 1999; Diekmann 2003; Wamelink & Van Dobben 2003) and may obscure geographical changes in ecological requirements (Diekmann & Lawesson 1999; Prinzing et al. 2002). Given that the Brotonne forest exhibited a much more restricted array of ecological conditions (here expressed by the Humus Index) than the Saint-Palais forest (Fig. 2), it is easy to understand why mean Humus Indices varied on a much wider scale in Saint-Palais than in Brotonne. In the aforementioned example, *D. flexuosa* expresses better its ecological amplitude in Saint-

Palais, where humus forms from Mesomull to Dysmoder are represented, than in Brotonne, where humus forms are nearly always of the moder type.

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Figure captions

Fig. 1. Sampling design used in each site for describing vegetation and humus forms

Fig. 2. Distribution of humus forms, ranked from most active to most inactive forms, in the two studied forests, together with the corresponding Humus Index

Fig. 3. Plot-scale variation of moss and vascular species richness according to the Humus Index in the two studied forests

Table 1. Main silvicultural features of the investigated sites.

	Saint-Palais	Brotonne
Number of sites	15	16
Number of plots	75	80
Developmental stages		
20-40-yr	25	20
60-90-yr	20	20
120-140-yr	15	25
170-200-yr	15	15

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Table 2. Variation of Humus Index values at different scales (site, plot 400 m², sub-plot 100 m²) and relationships with vascular and moss plant species richness. Probability values are given between parentheses.

	Saint-Palais	Brotonne
Mean Humus Index	3.87	6.01
Variance among sub-plots	0.75	0.16
Variance among plots	0.51	0.15
Variance among sites	0.9	0.28
F plot/subplot (P)	0.68 (0.98)	0.97 (0.54)
F site/plot (P)	1.76 (0.06)	1.79 (0.06)
Mantel r Humus Index x mosses (P)	0.36 (0.0001)	0.29 (0.0002)
Mantel r Humus Index x vascular plants (P)	-0.29 (<0.0001)	-0.12 (<0.0001)

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Table 3. List of vascular and moss species which were censused in at least three samples (sub-plots) in each of the two studied forests, together with their average Humus Index (mean±standard error).

Saint-Palais	n	H.I.±S.E.		Brotonne	n	H.I.±S.E.
Vascular species						
Vinca minor	13	2.5±0.1		Holcus mollis	91	5.6±0.1
Teucrium scorodonia	17	2.9±0.3		Lonicera periclymenum	130	5.7±0.1
Euphorbia amygdaloides	4	3±0.4		Milium effusum	37	5.9±0.1
Potentilla erecta	3	3±0		Dryopteris filix-mas	14	5.9±0.1
Ruscus aculeatus	3	3±0.6		Carex remota	26	6±0.1
Carex remota	4	3.3±0.3		Hedera helix	80	6±0.1
Dryopteris carthusiana	38	3.3±0.2		Deschampsia flexuosa	248	6±0.1
Hypericum androsaemum	14	3.3±0.3		Hypericum perforatum	5	6±0.3
Juncus effusus	27	3.3±0.2		Calamagrostis epigeios	3	6±0
Luzula sylvatica	9	3.3±0.4		Melica uniflora	11	6±0
Athyrium filix-femina	19	3.4±0.3		Molinia caerulea	3	6±0
Hypericum pulchrum	69	3.4±0.1		Stellaria holostea	8	6±0
Carex pallescens	15	3.4±0.3		Pteridium aquilinum	292	6±0.04
Poa nemoralis	20	3.4±0.2		Rubus sp	210	6±0.1
Carex sylvatica	14	3.4±0.3		Carex pilulifera	128	6±0.1
Dryopteris filix-mas	7	3.6±0.6		Dryopteris carthusiana	136	6±0.1
Lonicera periclymenum	213	3.6±0.1		Luzula pilosa	8	6.1±0.1
Carex pilulifera	160	3.6±0.1		Juncus effusus	14	6.1±0.1
Rubus fruticosus agg.	241	3.6±0.1		Carex sylvatica	7	6.1±0.1
Luzula campestris	3	3.7±1.2		Brachypodium sylvaticum	6	6.2±0.2
Hedera helix	228	3.7±0.1		Oxalis acetosella	39	6.2±0.1
Hypericum perforatum	4	3.8±0.8		Juncus conglomeratus	16	6.2±0.1
Melampyrum pratense	9	3.8±0.4		Agrostis capillaris	5	6.2±0.2
Polygonatum multiflorum	6	4±0.5		Dryopteris dilatata	30	6.2±0.1
Pteridium aquilinum	163	4.1±0.1		Festuca gigantea	6	6.3±0.2
Deschampsia flexuosa	46	4.2±0.2		Holcus lanatus	5	6.4±0.2
Molinia caerulea	18	4.6±0.3				
Convallaria majalis	7	5.6±0.2				
Moss species						
Fissidens taxifolius	3	3±0		Polytrichum formosum	185	6.1±0.04
Atrichum undulatum	14	3.4±0.3		Scleropodium purum	18	6.1±0.1
Dicranella heteromalla	63	3.8±0.2		Dicranella heteromalla	26	6.1±0.1
Dicranum scoparium	43	4.3±0.2		Thuidium tamariscinum	47	6.2±0.1
Isoetecium myosuroides	5	4.4±0.9		Leucobryum glaucum	40	6.2±0.1
Scleropodium purum	7	4.4±0.6		Dicranum scoparium	61	6.3±0.1
Thuidium tamariscinum	108	4.4±0.1				
Hypnum cupressiforme	11	4.6±0.5				
Eurhynchium striatum	10	4.9±0.6				
Polytrichum formosum	203	5±1				
Hylocomium brevirostre	10	5.3±0.5				
Leucobryum glaucum	5	5.6±0.4				

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2 Fig. 1

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Fig. 2

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