



HAL
open science

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

Arnault Lalanne, Jacques Bardat, Fouzia Lalanne-Amara, Thierry Gautrot, Jean-François Ponge

► To cite this version:

Arnault Lalanne, Jacques Bardat, Fouzia Lalanne-Amara, Thierry Gautrot, Jean-François Ponge. Opposite responses of vascular plant and moss communities to changes in humus form, as expressed by the Humus Index. *Journal of Vegetation Science*, 2008, 19 (5), pp.645-652. 10.3170/2007-8-18431 . hal-00495321

HAL Id: hal-00495321

<https://hal.science/hal-00495321>

Submitted on 25 Jun 2010

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Lalanne, Arnault¹; Bardat, Jacques²; Lalanne-Amara, Fouzia³; Gautrot, Thierry⁴ & Ponge,
5 Jean-François^{5*}

6

7 ¹*Office National des Forêts, Cellule Étude et Gestion de la Biodiversité, 27 rue Édouard-*
8 *Charton, 78000 Versailles, France;* ²*Muséum National d'Histoire Naturelle, CNRS UMR*
9 *5202, 57 rue Cuvier, Case Postale 39, 75231 Paris Cédex 05, France;* ³*Résidence Les*
10 *Coteaux, 3 allée des Coteaux, 95120 Ermont, France;* ⁴*Office National des Forêts, Unité*
11 *Territoriale Saint-Martin d'Aubigny, 2 place de la Préfecture, B.P. 502, 18013 Bourges*
12 *Cédex, France;* ⁵*Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du*
13 *Petit-Château, 91800 Brunoy, France*

14 **Corresponding author; E-mail jean-francois.ponge@wanadoo.fr*

15

1 **Abstract**

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

5 **Location:** temperate atlantic climate (Paris Basin, France)

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

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

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

20

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

23

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

25

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)

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

6
7 We tested this hypothesis independently in two forests exhibiting contrasted humus
8 forms, the one with nutrient-rich soils (Forêt de Brotonne, Upper Normandy), the other
9 with nutrient-poor soils (Forêt de Saint-Palais, Berry). The Humus Index was measured at
10 the scale of sites (16 and 15 sites, respectively, with five plots each), plots (400 m²) and
11 sub-plots (100 m²), and was compared with moss and vascular species richness, taking into
12 account the existence of spatial autocorrelation (Arp & Krause 1984; Riha et al. 1986;
13 Legendre & Fortin 1989). In both forests, Humus Indices were also calculated for
14 individual plant species, in order to characterize their ecological requirements (Falkengren-
15 Grerup & Tyler 1993b).

16

17 **Study sites**

18

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

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

3

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

14

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

22

23 **Methods**

24

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

7

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

12

- 13 1 Eumull (crumby A horizon, OL horizon absent, OF horizon absent, OH horizon
14 absent)
- 15 2 Mesomull (crumby A horizon, OL horizon present, OF horizon absent, OH
16 horizon absent)
- 17 3 Oligomull (crumby A horizon, OL horizon present, OF horizon 0.5 cm thick,
18 OH horizon absent)
- 19 4 Dysmull (crumby A horizon, OL horizon present, OF horizon 1 cm or more
20 thick, OH horizon absent)
- 21 5 Hemimoder (compact A horizon, OL horizon present, OF horizon present, OH
22 horizon absent)
- 23 6 Eumoder (compact A horizon, OL horizon present, OF horizon present, OH
24 horizon 0.5 cm or 1 cm thick)

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

3
4 This index, which is correlated with a wide range of soil and stand properties, as
5 mentioned above, allows a numerical treatment of otherwise purely morphological data.

6
7 The two forests investigated were treated separately, in order to account for
8 geographical distance and associated shifts in the ecological requirements of forest plant
9 species (Diekmann & Lawesson 1999, but see Prinzing et al. 2002). In each forest the
10 spatial variation of humus forms was analysed by comparing the variance of the Humus
11 Index at three scales, that of the site, that of the plot and that of the sub-plot, using the
12 Fisher-Snedecor F ratio (Sokal & Rohlf 1995) for testing for significant variation across
13 scales. When the variation of a parameter is scale-dependent, correlation studies must use
14 special tests accounting for non-independence of data, such as Mantel tests (Legendre &
15 Fortin 1989). Such tests were performed, using distance matrices between samples. The
16 distance between two samples was estimated by the algebraic difference between
17 corresponding values of Humus Index or species richness of moss or vascular vegetation.
18 Simple and partial product-moment correlation coefficients were calculated between
19 distance matrices according to the Monte-Carlo method, using 5,000 random cross-
20 permutations of rows and columns for the construction of empirical probability tables
21 (Sokal & Rohlf 1995). Statistical treatment of the data was performed using XLSTAT®
22 statistical software (Addinsoft).

23
24 In the two forests investigated, mean Humus Indices were calculated for moss and
25 vascular plant species which were present in at least three samples (sub-plots). For that

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

4 5 **Results**

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

15
16 The variation of the Humus Index did not vary from the scale of the sub-plot to that
17 of the plot, plot/subplot F values being low and not significant (Table 2). However,
18 although not significant at 0.05 level ($P = 0.06$), the passage from the scale of the plot to
19 that of the site displayed F values far higher than when passing from the sub-plot to the
20 plot scale. As a consequence, we considered that values of the Humus Index were spatially
21 dependent, two distinct sites exhibiting a higher variation of their mean H.I. than plots
22 sampled within the same site. However, it remains true that H.I. did not vary more at 50 m
23 distance (between plots) than at 10 m distance (between sub-plots).

24

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

12
13 When censused at the sub-plot scale, the number of vascular species decreased
14 when the Humus Index increased, contrary to moss species (Fig. 3). The same trend was
15 depicted by both forests, although some differences were observed. The number of moss
16 species per sub-plot was higher in Saint-Palais than in Brotonne, and the decrease in the
17 number of vascular species was less abrupt in Brotonne than in Saint-Palais. In Saint-Palais
18 the number of moss species exceeded that of vascular species at H.I. 7 (Dysmoder), while
19 it remained always far lower than that of vascular species in Brotonne.

20
21 We tested the correlation between the Humus Index and the species richness of
22 vascular and moss communities by the Mantel test. For technical reasons, sub-plot values
23 could not be used, because of their high number (300 in Saint-Palais, 320 in Brotonne).
24 Rather, we used plot values, i.e. the mean of four H.I. values and the total number of
25 vascular and moss species censused in 400 m², which gave 75 and 80 values in Saint-Palais

1 and Brotonne, respectively. Simple Mantel tests showed that at the plot level the Humus
2 Index was positively correlated with the number of vascular species, and negatively with
3 the number of moss species, whatever the forest (Table 2). As expected, moss and vascular
4 species were negatively correlated (Mantel test, $P < 0.0001$) but no correlation between
5 both plant groups was displayed when the Humus Index was used as a covariate (partial
6 Mantel test, $P = 0.27$). When moss species richness was used as a covariate, the correlation
7 between H.I. and vascular species richness remained negative and significant (Mantel test,
8 $P < 0.0001$). When vascular species richness was used as a covariate, the correlation
9 between H.I. and moss species richness remained positive and significant (Mantel test, $P =$
10 0.0002). According to Legendre & Fortin (1989) this indicates that positive and negative
11 interactions exist between the Humus Index and moss and vascular communities,
12 respectively, without any additional interaction between both plant groups.

13

14 **Discussion**

15

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

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

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

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

7

8 Differences in Humus Index values for vascular and moss species are prominent
9 between both forests, but should be considered with caution, at least for some species the
10 distribution of which is skewed towards one or the other side of the humus form gradient.
11 For instance, *Deschampsia flexuosa*, which is commonly considered as acidophilic
12 (Rameau et al. 1999), exhibits a mean Humus Index of 4.2 in Saint-Palais (Dysmull), and
13 6.0 (Eumoder) in Brotonne. This does not mean that the ecological requirements of this
14 species vary according to its geographical position, and that it loses its acidophily in Saint-
15 Palais. Rather, its ecological range is better expressed in SaintPalais, where the humus
16 form gradient is longer than in Brotonne (Fig. 2). It is suggested that indices based on the
17 presence of individual plant species must be interpreted with caution. Such limits have
18 been noted for Ellenberg's indices (Hill et al. 1999; Diekmann 2003; Wamelink & Van
19 Dobben 2003) and may obscure geographical changes in ecological requirements
20 (Diekmann & Lawesson 1999; Prinzing et al. 2002). Given that the Brotonne forest
21 exhibited a much more restricted array of ecological conditions (here expressed by the
22 Humus Index) than the Saint-Palais forest (Fig. 2), it is easy to understand why mean
23 Humus Indices varied on a much wider scale in Saint-Palais than in Brotonne. In the
24 aforementioned example, *D. flexuosa* expresses better its ecological amplitude in Saint-

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

3

4 **Acknowledgements**

5

6 The study was financially supported by a grant given to the junior author by the
7 Office National des Forêts, which is greatly acknowledged. Authors are also grateful to
8 local authorities for access to the sites and commodities.

9

10 **References**

11

12 Arditì, R., Michalski, J. & Hirzel, A.H. 2005. Rheagogies: modelling non-trophic effects in
13 food webs. *Ecological Complexity* 2: 249-258.

14

15 Arp, P.A. & Krause, H.H. 1984. The forest floor: lateral variability as revealed by
16 systematic sampling. *Canadian Journal of Soil Science* 64: 423-437.

17

18 Aubert, M., Bureau, F., Alard, D. & Bardat, J. 2004. Effect of tree mixture on the humic
19 epipedon and vegetation diversity in managed beech forests (Normandy, France).
20 *Canadian Journal of Forest Research* 34: 233-248.

21

22 Bates, J.W. 1987. Nutrient retention by *Pseudoscleropodium purum* and its relation to
23 growth. *Journal of Bryology* 14: 565-580.

24

- 1 Brêthes, A., Brun, J.J., Jabiol, B., Ponge, J.F. & Toutain, F. 1995. Classification of forest
2 humus forms: a French proposal. *Annales des Sciences Forestières* 52: 535-546.
3
- 4 Bridges, E.M., Batjes, N.H. & Nachtergaele, F.O. 1998. *World reference base for soil*
5 *resources*. Food And Agriculture Organization of the United Nations, Rome, Italy.
6
- 7 Crepet, W.L., Friis, E.M. & Nixon, K.C. 1991. Fossil evidence for the evolution of biotic
8 pollination. *Philosophical Transactions of the Royal Society of London, Series B,*
9 *Biological Sciences* 333: 187-195.
10
- 11 Diekmann, M. 2003. Species indicator values as an important tool in applied plant ecology.
12 A review. *Basic and Applied Ecology* 4: 493-506.
13
- 14 Diekmann, M. & Lawesson, J.E. 1999. Shifts in ecological behaviour of herbaceous forest
15 species along a transect from Northern Central to North Europe. *Folia Geobotanica*
16 34: 127-141.
17
- 18 Durin, L. Géhu, J.M., Noirfalise, A. & Sougnez, N. 1967. Les hêtraies atlantiques et leur
19 essaim climatique dans le nord-ouest et l'ouest de la France. *Bulletin de la Société*
20 *Botanique du Nord de la France Numéro Spécial* 20: 59-89.
21
- 22 Falkengren-Grerup, U. 1989. Effect of stemflow on beech forest soils and vegetation in
23 southern Sweden. *Journal of Applied Ecology* 26: 341-352.
24

- 1 Falkengren-Grerup, U. & Tyler, G. 1993a. Experimental evidence for the relative
2 sensitivity of deciduous forest plants to high soil acidity. *Forest Ecology and*
3 *Management* 60: 311-326.
- 4
- 5 Falkengren-Grerup, U. & Tyler, G. 1993b. Soil chemical properties excluding filed-layer
6 species from beech forest mor. *Plant and Soil* 148: 185-191.
- 7
- 8 Fargione, J., Tilman, D., Dybzinski, R., Hille, J., Lambers, R., Clark, C., Harpole, W.S.,
9 Knops, J.M.H., Reich, P.B. & Loreau, M. 2007. From selection to
10 complementarity: shifts in the causes of biodiversity–productivity relationships in a
11 long-term biodiversity experiment. *Proceedings of the Royal Society of London,*
12 *Series B, Biological Sciences* 274: 871-876.
- 13
- 14 Godefroid, S., Massant, W. & Koedam, N. 2005. Variation in the herb species response
15 and the humus quality across a 200-year chronosequence of beech and oak
16 plantations in Belgium. *Ecography* 28: 223-235.
- 17
- 18 Greig, J. 2002. When the Romans departed... evidence of landscape change from
19 Metchley Roman Fort, Edgbaston, Birmingham. *Acta Palaeobotanica* 42: 177-184.
- 20
- 21 Grime, J.P. & Hodgson, J.G. 1987. Botanical contribution to contemporary ecological
22 theory. *The New Phytologist* 106 (Suppl.): 283-295.
- 23

- 1 Heemsbergen, D.A., Berg, M.P., Loreau, M., Van Hal, J.R., Faber, J.H. & Verhoef, H.A.
2 2004. Biodiversity effects on soil processes explained by interspecific functional
3 dissimilarity. *Science* 306: 1019-1020.
4
- 5 Hill, M.O., Bell, N., Bruggeman-Nannenga, M.A., Brugués, M., Cano, M.J., Enroth, J.,
6 Flatberg, K.I., Frahm, J.P., Gallego, M.T., Garileti, R., Guerra, J., Hedenäs, L.,
7 Holyoak, D.T., Hyvönen, J., Ignatov, M.S., Lara, F., Mazimpaka, V., Muñoz &
8 Söderström, L. 2006. An annotated checklist of the mosses of Europe and
9 Macaronesia. *Journal of Bryology* 28: 198-267.
10
- 11 Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. 1999. *Ellenberg's indicator*
12 *values for British plants*. Institute of Terrestrial Ecology, Huntingdon, UK.
13
- 14 Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. & Hermy, M. 2002.
15 Possible effects of habitat fragmentation and climate change on the range of forest
16 plant species. *Ecology Letters* 5: 525-530.
17
- 18 Huston, M. 1993. Biological diversity, soils, and economics. *Science* 262: 1676-1680.
19
- 20 Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for
21 understanding variation in the diversity of plants and animals. *Oikos* 86: 393-401.
22
- 23 Jonsson, B.G. & Esseen, P.A. 1998. Plant colonisation in small forest-floor patches:
24 importance of plant group and disturbance traits. *Ecography* 21: 518-526.
25

- 1 Labandeira, C.C. 2005. Invasion of the continents: cyanobacterial crusts to tree-inhabiting
2 arthropods. *Trends in Ecology and Evolution* 20: 253-262.
3
- 4 Lambinon, J., De Langhe, J.E., Delvosalle, L. & DuVigneaud, J. 1999. *Nouvelle flore de la*
5 *Belgique, du Grand-Duché de Luxembourg, du Nord de la France et des régions*
6 *voisines (Ptéridophytes et Spermatophytes)*, 4^{ème} ed. Jardin Botanique National de
7 Belgique, Meise, Belgium.
8
- 9 Lee, J.A. 1999. The calcicole-calcifuge problem revisited. *Advances in Botanical Research*
10 29: 1-30.
11
- 12 Legendre, P. & Fortin, M.J. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:
13 107-138.
14
- 15 Mazlack, L. 2004. Discovery of causality possibilities. *International Journal of Pattern*
16 *Recognition and Artificial Intelligence* 18: 63-73.
17
- 18 Oechel, W.C. & Van Cleve, K. 1986. The role of bryophytes in nutrient cycling in the
19 taiga. In: Van Cleve, K., Chapin (F.S.III), Flanagan, P.W., Viereck, L.A. &
20 Dyrness, C.T. (eds.) *Forest ecosystems in the Alaskan taiga: a synthesis of*
21 *structure and function*, pp. 121-137. Springer, New York, NY.
22
- 23 Olsen, C. 1925. Studies on the hydrogen ion concentration of the soil and its significance
24 to the vegetation, especially to the natural distribution of plants. *Comptes-Rendus*
25 *des Travaux du Laboratoire Carlsberg* 15: 1-166.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Ovington, J.D. 1954. Studies of the development of woodland conditions under different trees. II. The forest floor. *Journal of Ecology* 42: 71-80.

Ponge, J.F. 2000. Acidophilic Collembola: living fossils? *Contributions from the Biological Laboratory, Kyoto University* 29: 65-74.

Ponge, J.F. 2003. Humus forms in terrestrial ecosystems: a framework to biodiversity. *Soil Biology and Biochemistry* 35: 935-945.

Ponge, J.F., André, J., Zackrisson, O., Bernier, N., Nilsson, M.C. & Gallet, C. 1998. The forest regeneration puzzle. Biological mechanisms in humus layer and forest vegetation dynamics. *BioScience* 48: 523-530.

Ponge, J.F., Arpin, P., Sondag, F. & Delecour, F. 1997. Soil fauna and site assessment in beech stands of the belgian Ardennes. *Canadian Journal of Forest Research* 27: 2053-2064.

Ponge, J.F. & Chevalier, R. 2006. Humus Index as an indicator of forest stand and soil properties. *Forest Ecology and Management* 233: 165-175.

Ponge, J.F., Chevalier, R. & Loussot, P. 2002. Humus Index: an integrated tool for the assessment of forest floor and topsoil properties. *Soil. Science Society of America Journal* 66: 1996-2001.

- 1 Prinzing, A., Durka, W., Klotz, S. & Brandl, R. 2001. The niche of higher plants: evidence
2 for phylogenetic conservatism. *Proceedings of the Royal Society of London, Series*
3 *B, Biological Sciences* 268: 2383-2389.
- 4
- 5 Prinzing, A., Durka, W., Klotz, S. & Brandl, R. 2002. Geographic variability of ecological
6 niches of plant species: are competition and stress relevant? *Ecography* 25: 721-
7 729.
- 8
- 9 Rameau, J.C., Mansion, D. & Dumé, G. 1989. *Flore forestière française. I. Plaines et*
10 *collines*. Institut pour le Développement Forestier, Paris, France.
- 11
- 12 Rescia, A.J., Schmitz, M.F., Martin de Agar, M.P., Pablo, C.L. de & Pineda, F.D. 1995.
13 Ascribing plant diversity values to historical changes in landscape: a
14 methodological approach. *Landscape and Urban Planning* 31: 181-194.
- 15
- 16 Retallack, G.J. 1985. Fossil soils as grounds for interpreting the advent of large plants and
17 animals on land. *Philosophical Transactions of the Royal Society of London, Series*
18 *B, Biological Sciences* 309: 105-142.
- 19
- 20 Riha, S.J., James, B.R., Senesac, G.P. & Pallant, E. 1986. Spatial variability of soil pH and
21 organic matter in forest plantations. *Soil Science Society of America Journal* 50:
22 1347-1352.
- 23

- 1 Roem, W.J. & Berendse, F. 2000. Soil acidity and nutrient supply ratio as possible factors
2 determining changes in plant species diversity in grassland and heathland.
3 *Biological Conservation* 92: 151-161.
4
- 5 Schaefer, M. & Schauermaun, J. 1990. The soil fauna of beech forests: comparison
6 between a mull and a moder soil. *Pedobiologia* 34: 299-314.
7
- 8 Sokal, R.R. & Rohlf, F.J. 1995. *Biometry. The principles and practice of statistics in*
9 *biological research, 3rd ed.* Freeman, New York, NY.
10
- 11 Ulrich E., Coddeville P. & Lanier M. 2002. *Les retombées atmosphériques en France entre*
12 *1993 et 1998.* ADEME, Paris, France.
13
- 14 Wamelink, G.W.W. & Van Dobben, H.F. 2003. Uncertainty of critical loads based on the
15 Ellenberg indicator value for acidity. *Basic and Applied Ecology* 4: 515-523.
16
- 17 Wilson, S.McG., Pyatt, D.G., Malcolm, D.C. & Connolly, T. 2001. The use of ground
18 vegetation and humus type as indicators of soil nutrient regime for an ecological
19 site classification of British forests. *Forest Ecology and Management* 140: 101-116.
20
- 21 Yachi, S. & Loreau, M. 2007. Does complementary resource use enhance ecosystem
22 functioning? A model of light competition in plant communities. *Ecology Letters*
23 10: 54-62.
24

- 1 Zechmeister, H.G., Grodzińska, K. & Szarek-Lukaszewska, G. 2003. Bryophytes. In:
- 2 Markert, B.A., Breure, A.M. & Zechmeister, H.G. (eds.) *Bioindicators and*
- 3 *biomonitors: principles, concepts and applications*, pp. 329-375. Elsevier,
- 4 Amsterdam, The Netherlands.
- 5

1 **Figure captions**

2

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

4

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

7

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

10

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

1

2

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)

1

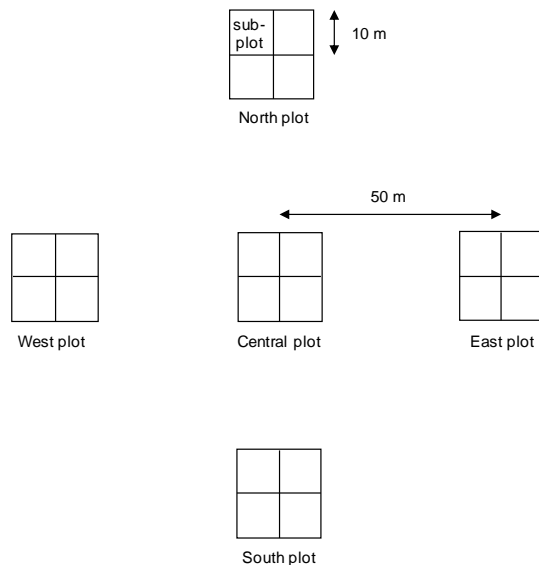
2

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
Isoetes 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				

1

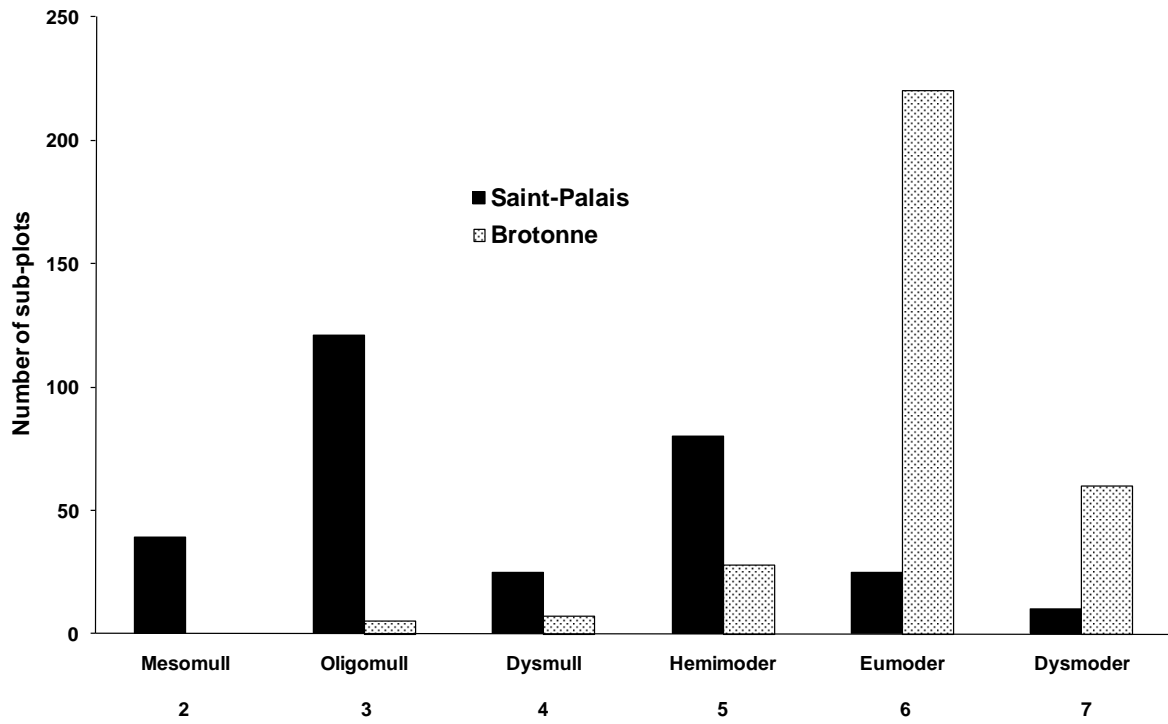
2



1

2 Fig. 1

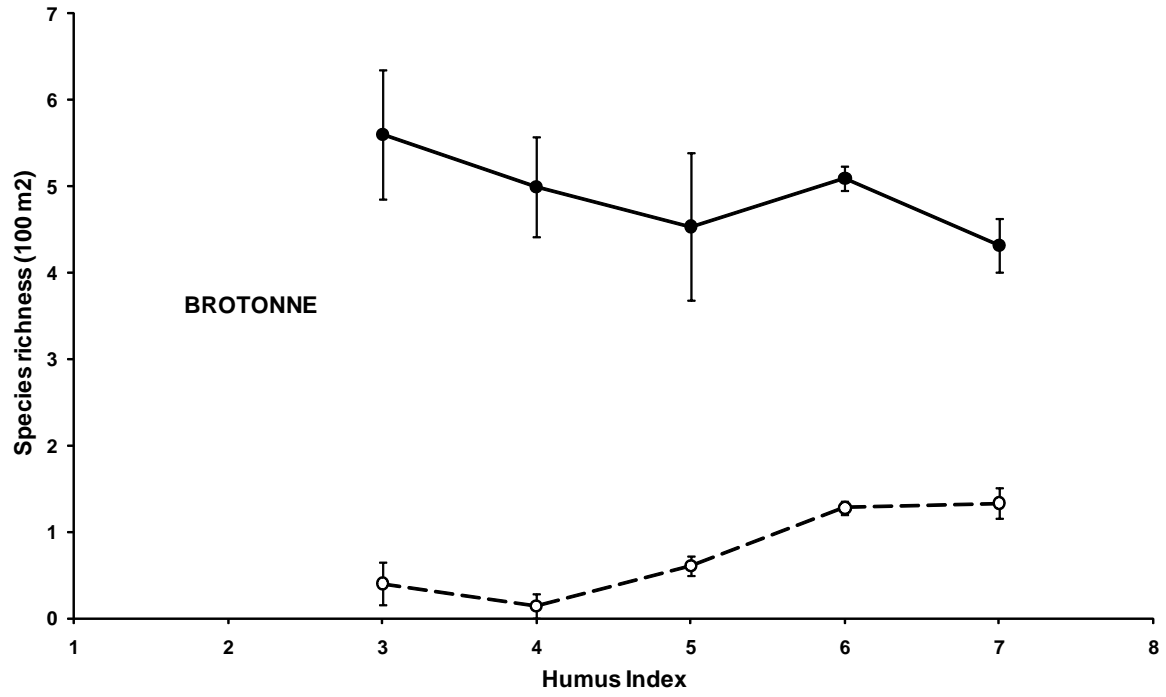
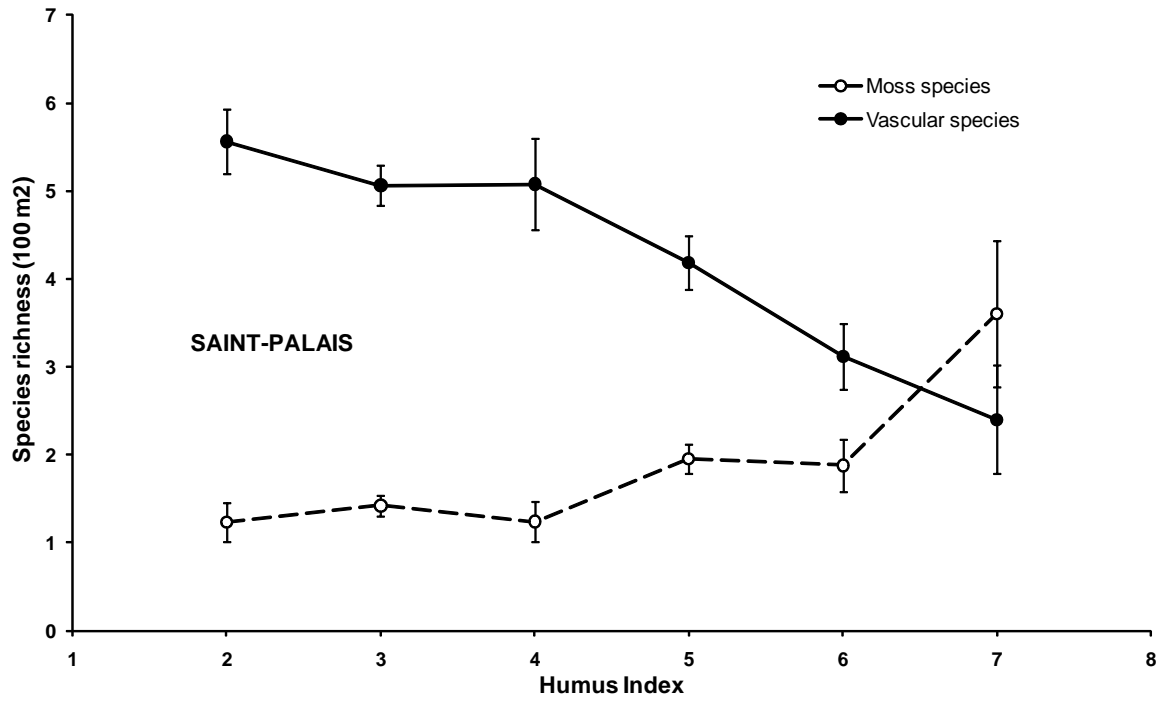
3



1

2 Fig. 2

3



1

2 Fig. 3