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1 **Local and regional trends in the ground vegetation of beech forests**

2

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17

1 **Abstract**

2

3 We sampled moss and vascular forest vegetation in five ancient beech forests from
4 northwest France, embracing in each a wide array of environmental conditions. Indirect
5 (PCA) and direct (RDA) gradient analysis were used to discern local and regional ecological
6 factors which explain the observed variation in species composition. Our results point to a
7 global factor encompassing a large array of soil and light conditions, unravelled when local
8 particularities of studied forests are partialled out. The humus form, numerically expressed by
9 the Humus Index, explains a large part of the observed variation in ground vegetation. Our
10 study confirmed opposite trends in vascular and moss species richness according to humus
11 condition. Ecological factors to which vascular and moss forest species respond at the
12 regional level can be estimated directly on the field by visually inspecting humus forms and
13 vegetation strata despite of the confounding influence of local factors.

14

15 **Keywords:** Beech forests; Ground vegetation; Humus Index; Regional and local factors;
16 Species groups; Species richness

17

18 **Introduction**

19

20 It is widely recognized that forest vegetation varies according to soil fertility and
21 acidity, temperature, light and moisture (Watt, 1934; Ellenberg, 1974; Diekmann and
22 Lawesson, 1999), and is a fairly good indicator of potential growth (Bergès et al. 2006) and
23 ecological integrity (Aubin et al., 2007) of managed forests. It is also admitted that
24 management practices may modify the composition of understory plant communities through
25 their influence on the abovementioned factors (Thomas et al., 1999; Gillet et al., 1999; Van

1 Calster et al., 2007). Once the ecological requirements of plant species are documented and
2 indexed over wide environmental gradients (Diekmann, 2003), then lists of plant species and
3 their ecograms (Härdtle et al., 2004) can be used to achieve a thorough assessment of site
4 conditions, often in conjunction with humus types (Bartoli et al., 2000; Wilson et al., 2001,
5 but see Wamelink et al., 2002). However, the composition of forest plant communities may
6 also vary locally due to historical heritage (Dupouey et al., 2002; Gachet et al., 2007),
7 dispersal limitation (Bossuyt et al., 1999; Graae and Sunde, 2000; Honnay et al., 2002), biotic
8 interactions (Thompson et al., 1993; Britton et al., 2003; Klanderud and Totland, 2007) and
9 landscape features (Dufour et al., 2006), and thus is in a constant state of change (Wiens,
10 1984). Among a regional pool, each forest, for past as well as present-day reasons, will select
11 or favour a subsample of species and species traits which will be redistributed according to
12 niche requirements of species, assembly rules and disturbance effects (Keddy, 1992; Zobel,
13 1997; Rajaniemi et al., 2006). Stable although distinct forest communities may develop on
14 similar sites (McCune and Allen, 1985) as a consequence of attraction domains (Beisner et al.,
15 2003).

16

17 We need tools for disentangling the joint influence of stable and variable
18 environmental factors on vegetation (Ehrenfeld et al., 1997) and to discern environmental
19 gradients of regional importance when plant communities vary locally to a great extent
20 (Ricklefs, 1987; Huston, 1999; Hillebrand, 2005): does the presence of a species indicate the
21 same thing in one and another forest? The present study is an attempt to fulfil this gap within
22 the domain of European beech (*Fagus sylvatica* L.) forests. For that purpose we selected five
23 ancient forests (Peterken and Game, 1984; Hermy et al., 1999) in Northwest France, where
24 two Atlantic forest habitats, the neutrophile *Endymio-Fagetum* or EU priority habitat type
25 41.132 (EUR25, 2003) and the acidiphilous *Ilici-Fagetum* or EU priority habitat type 41.12

1 (EUR25, 2003), are well-represented (Bardat, 1993). These beech habitats were described in
2 West and Northwest France as two associations by Durin et al. (1967). We sampled moss and
3 vascular forest vegetation in 995 plots (400 m²) embracing a wide array of canopy,
4 understory, stand age, humus type, soil disturbance, climate and atmospheric deposition
5 conditions. Indirect (PCA) and direct (RDA) gradient analysis were used to discern main local
6 and regional ecological factors which could explain the observed variation in species
7 composition. A particular attention will be given to the humus type, which is both a cause and
8 a consequence of vegetation development (Ponge, 2003; Godefroid et al., 2005) and to which
9 beech forest plant species are highly sensitive (Le Tacon and Timbal, 1973; Falkengren-
10 Grerup and Tyler, 1993; Lalanne et al., 2008).

11

12 **Materials and methods**

13

14 **Study sites**

15

16 Five forests, attested at least from the Roman period (except Compiègne attested from
17 the 14th century only) have been selected in Picardy and Upper Normandy (Table 1). The
18 choice of these forests was dictated by the need to assess the influence of local particularities
19 in the studied region, while remaining in the same plant associations, *Endymio-Fagetum* (EF)
20 and *Ilici-Fagetum* (IF) on neutral to acid soils, respectively. All these forests belonged to the
21 royal domain then acquired a national status after the French revolution. After the strong
22 deforestation which occurred during Middle Ages they were submitted to the Forest Law and
23 were managed as coppices-with-standards from 16th to 19th century, then they were
24 progressively converted to full-grown mixed forests. European beech is dominant, but sessile
25 oak (*Quercus petraea*) or pedunculate oak (*Quercus robur*) are subordinate or co-dominant in

1 the canopy. All these lowland forests (altitude < 250 m) are established on cretaceous
2 limestone tables of the 'Bassin Parisien'. The calcareous substrate is covered with tertiary and
3 quaternary deposits of varying depth and nature, which were eroded on slopes, providing a
4 variety of strongly acid to alkaline soils. The Brotonne forest is established mainly on a fossil
5 meander of river Seine made up of many quaternary gravel-sand alluvial terraces dated from
6 Riss to Wurm (Quaternary Age). Eawy and Lyons forests occupy especially plates with a
7 thick cover of loess (Quaternary Age). The Compiègne forest is located on a sandy slope
8 (Cuisian stage) and on Sparnacian marls of the alluvial river Oise valley (Tertiary Age). The
9 Retz forest is established on loess (Quaternary Age) and sand (Tertiary Age, Stampian stage)
10 deposits. The annual rainfall decreases and the mean temperature increases from Brotonne
11 and Eawy to Compiègne and Retz, Lyons being intermediate, according to a decreasing
12 Atlantic influence from West to East, without any marked North-South trend (Table 1).
13 Sulphur deposition is higher in Brotonne and Eawy, which are not far from oil refineries
14 located in Le Havre and Rouen, respectively. Nitrogen deposition, mostly of industrial origin
15 in Eawy, and of agricultural origin in Retz, is higher in these two forests. Values reported on
16 Table 1 were interpolated from a national grid of continuous measurements of atmospheric
17 dry deposition, except for Brotonne where measurement was direct (Croisé et al., 2005).

18

19 As abovementioned, our study focused on two types of beech habitats, in which beech
20 is associated with holly (*Ilex aquifolium*) in the understory on most acidic soils (upslope sites
21 with Podzols and Luvisols at pH < 5) and with bluebell (*Hyacinthoides non-scripta*) on
22 moderately acidic to neutral soils (downslope sites with Luvisols and Cambisols at pH
23 between 5 and 7). Both habitats are present in the five studied forests, but their species
24 composition varies locally according to climate and geomorphology. Bardat (1993) described
25 numerous sub-associations and variants ('sylvo-facies') on the basis of moss and vascular

1 forest vegetation. Following preliminary investigations, study sites were selected in each
2 forest in order to encompass the widest possible variety of environmental, management and
3 stand age conditions. More sites were sampled in Eawy, the smallest forest investigated, in
4 order to compensate for the relative homogeneity of site conditions. The choice of a non-
5 random selection of forests and stands within forests was dictated by the need to avoid severe
6 biases in the representativeness of sampling sites. More details about the selection of sites
7 according to stand age classes are given in Lalanne (2006).

8

9 **Sampling design and data analysis**

10

11 At each site five plots 20 x 20 m, four at angles of a 1 ha square and one at its centre
12 (Lalanne et al. 2008) were surveyed for ground vegetation and environmental factors. In each
13 plot vascular plants (herbs, ferns) and mosses were identified at the species level (Appendix
14 1) and quantified according to the Braun-Blanquet method. Kerguelen (1993), lastly updated
15 at <http://www2.dijon.inra.fr/flore-france/index.htm>, was used for the nomenclature of vascular
16 plants, and Hill et al. (2006) for mosses. Species living in aboveground micro-habitats (trunk
17 bases, boulders, dead branches and trunks) were not recorded. Previous to numerical
18 treatment Braun-Blanquet cover-abundance data were transformed in percentage values
19 according to Van der Maarel (1979). Species which were present in less than 10 sample plots
20 were excluded from further analyses, except for the calculation of species richness.

21

22 Ellenberg's indices (Light, Wetness, Fertility, pH) were affected to each plant species
23 (Appendix 1). For vascular plant species we used indicator values calculated for the British
24 Isles (Hill et al., 1999). For moss species we used a table prepared by one of us (J.B.), which
25 was partly published in Bardat and Aubert (2007). The Fertility Index was equivalent to the N

1 ('Stickstoff') index of Ellenberg (1974). Ellenberg's indices were averaged for each plot
2 according to Wamelink and Van Dobben (2003), in order to provide a global assessment of
3 ecological requirements of vegetation units on the base of auto-ecological characters.

4
5 Environmental descriptors were recorded at each sampling plot (Appendix 2). Canopy
6 cover, as well as sub-canopy cover and shrub cover when present, were estimated by cover-
7 abundance values according to the Braun-Blanquet scale and subsequently transformed into
8 cover percentages as abovementioned. The Humus Index was estimated by scoring humus
9 forms according to Ponge et al. (2002). Four measurements of the Humus Index were
10 averaged after subdividing each 400 m² plot into four 100 m² sub-plots, at the centre of which
11 as small pit was dug off. The choice of a regular grid rather than of a random selection of
12 points was due to the combined need for representativeness and minimum digging of the soil.
13 The ground surface was thoroughly observed and classified into several categories of topsoil
14 disturbance and dead wood deposition (Appendix 2), the cover percentage of which was
15 estimated visually in each plot. For the need of calculation, categories of topsoil disturbance
16 were pooled into gross categories (undisturbed = Surf1, weak disturbance = Surf2 to Surf8,
17 severe disturbance = Surf9 to Surf14). Stem density and basal area were estimated by
18 counting and measuring the diameter at breast height (DBH) of all trees and shrubs with a
19 stem diameter higher than 7.5 cm. The age of dominant trees (crowns extending above the
20 general level of the canopy) was estimated by classifying them into 'regeneration', 20-40
21 years, 70-90 years, 120-140 years and 170-200 years.

22
23 The whole ground vegetation data set was submitted to Principal Components
24 Analysis (PCA), after standardization of cover percentage values to mean = 0 and variance
25 =1, thereby equalling Euclidean distances between plant species to product-moment

1 correlation coefficients. Plant species, coded as in Appendix 1, were projected on bi-plots of
2 factorial axes. Other bi-plots were used to show the projection of some additional variables on
3 the same factorial axes. Although somewhat neglected by plant ecologists after the rise of
4 methods derived from Correspondence Analysis (CoA), PCA with standardized variables was
5 chosen because of the ease with which it may reveal gradients as well as clusters in a complex
6 data matrix, without being influenced by rare species nor by preconceived hypotheses (Chae
7 and Warde, 2006; Bakkestuen et al., 2008). Comparisons done by Kenkel (2006) over a large
8 array of multivariate methods, including the commonly used Detrended Correspondence
9 Analysis (DCA) concluded to the superiority of PCA to decrease the number of dimensions of
10 large data sets. Ellenberg's indices and several measured environmental descriptors were
11 projected as additional (passive) variables in order to facilitate the ecological interpretation of
12 PCA axes.

13

14 In each studied forest and in each beech habitat (*Endymio-Fagetum* and *Ilici-Fagetum*)
15 the between-sample floristic variation was measured by summing up variance components of
16 sample scores along the first three PCA components. This was used as a measure of β -
17 diversity according to Ter Braak (1983).

18

19 In order to verify whether gradients and clusters revealed by indirect gradient analysis
20 (PCA) could be defined on the basis of environmental parameters measured at each sampling
21 plot a Redundancy Analysis (RDA) was performed, using two matrices, (i) ground vegetation
22 data used for PCA, (ii) environmental data listed in Appendix 2. Note that Ellenberg's indices
23 were not used in this analysis, given that they give only an indirect view of the environment.
24 Thereafter a partial Redundancy Analysis (partial RDA) was performed, in order to verify that
25 the composition of ground vegetation could be explained by stand and ground properties

1 when the confounding influence of geographical distance was discarded. For that purpose the
2 five forests were added as five qualitative variables which were coded as 1 or 0 according to
3 sample location.

4

5 Given that spatial autocorrelation was expected due to our nested sampling design, we
6 used Signed Mantel tests (Oberrath and Böhning-Gaese, 2001) to investigate several plant-
7 environment relationships within each of the studied forests.

8

9 All calculations were done under Microsoft® EXCEL® using the Addinsoft®
10 XLSTAT® statistical software.

11

12 **Results**

13

14 **Principal Components Analysis: the F1-F2 bi-plot**

15

16 The vegetation data matrix which was analysed by PCA was comprised of 995 rows
17 (sample plots) and 141 columns (species). The first three components of PCA (those which
18 were interpretable in terms of ecological factors as a rule of thumb) extracted 11% of the total
19 variance, a weak although significant percentage (Kaiser criterium for eigen values and
20 Bartlett's test of sphericity) which is explained by the high number of variables (141)
21 included in the analysis and the ground noise caused by scarcely represented plant species.
22 The projection of plant species in the plane of the first two components of PCA (eigen values
23 7.61 and 4.55, respectively) showed three directions over which the cloud of species was
24 stretched (here called 'branches'), which were noted A, B and C (Fig. 1). The A branch was
25 stretched along the positive side of factor F1. Species projected far from the origin along the

1 A branch were considered characteristic of this branch and were noted as A group (Table 2).
2 All these species were positively correlated with F1. No branch was visible on the negative
3 side of this factor. Branches B and C were stretched on opposite sides of F2, not far from the
4 origin along F1. Two groups of characteristic species, which were positively and negatively
5 correlated with F2, respectively, were noted as B and C groups (Table 2). *Fagus sylvatica*
6 (*Fga*) and *Rubus fruticosus* agg. (*Rfr*) were projected in an intermediate position between A
7 and B branches, both species being correlated positively with F1.

8

9 The calculation of variable scores (Table 3) and the projection (Fig. 1) of additional
10 variables in the F1-F2 species plane showed that F1 was positively correlated with Fertility,
11 pH and Wetness Ellenberg's indices, while it was negatively correlated with Ellenberg's Light
12 index and Humus Index. Among canopy and sub-canopy descriptors, F1 was positively
13 correlated with canopy and sub-canopy hornbeam cover and total canopy cover. Factor F1
14 was positively correlated with vascular and total species richness and negatively with moss
15 richness. Gross disturbance categories (undisturbed, weak disturbance, severe disturbance) of
16 the ground floor were poorly correlated with F1.

17

18 Factor F2 was positively correlated with Humus Index and with Ellenberg's Light
19 index (Table 3, Fig. 1), while it was negatively correlated with pH and Fertility Ellenberg's
20 indices. Among canopy and sub-canopy descriptors, F1 was positively correlated with canopy
21 beech cover and total canopy cover. Factor F1 was negatively correlated with vascular and
22 total species richness. Gross disturbance categories were poorly correlated with F1.

23

24 The projection of samples in the F1-F2 bi-plot showed that A, B and C species groups
25 were not equally distributed in the five studied forests and in the two studied beech habitats

1 (Fig. 2, compare with Fig. 1). The B group (positive values of F2) was mostly represented in
2 the *Ilici-Fagetum* (IF) and its characteristic species were better displayed in Brotonne. The A
3 and C groups (positive values of F1 and negative values of F2, respectively) were mostly
4 represented in the *Endymio-Fagetum* (EF) and their characteristic species were better
5 displayed in Retz and Compiègne, respectively. Lyons EF was intermediate between A and C
6 species branches. It should be noted that EF and IF formed a continuum, without any clear-cut
7 limit between them, and that Brotonne EF was projected at the same position (i.e. exhibited
8 the same correlation with F1 and F2) than Eawy IF and Retz IF.

9

10 **Principal Components Analysis: the F2-F3 bi-plot**

11

12 While B and C branches were projected on opposite sides of F2, as mentioned above,
13 an additional branch D was displayed on the negative side of F3, while B and C were both
14 projected on its positive side (Fig. 3). The characteristic group of species corresponding to the
15 D branch (D group) shared two species with the A group: *Lamium galeobdolon* agg. (Lga)
16 and *Athyrium filix-femina* (Afi) (Table 2).

17

18 Contrary to F1 and F2, factor F3 (eigen value 3.42) was associated with ground
19 disturbance cover variables, being positively correlated with weak and severe disturbance
20 cover and negatively correlated with undisturbed cover (Table 3, Fig. 3). Factor F3 was
21 negatively correlated with moss species richness and subcanopy cover.

22

23 The projection of samples on the F2-F3 bi-plot (Fig. 4, compare with Fig. 3) showed
24 that the D group (negative values of F3) was mostly represented in Lyons EF and Eawy EF.
25 Other factors were not considered, because they did not exhibit any new species group, but

1 rather subdivided and reassembled A, B, C and D branches, without any clear-cut association
2 with environmental variables. We considered them as belonging to ground noise.

3

4 **Floristic heterogeneity**

5

6 Table 4 showed that floristic heterogeneity, as ascertained from the variance of sample
7 scores along the first three components of PCA, varied to a great extent according to forests
8 and according to EF and IF beech habitats. More between-sample variation was depicted by
9 the *Endymio-Fagetum* compared to the *Ilici-Fagetum* in Compiègne, Retz and Lyons. Eawy
10 remained at a very low level of floristic heterogeneity, whatever beech habitats and despite a
11 higher sampling effort (Table 1). In Brotonne the *Ilici-Fagetum* exhibited a higher floristic
12 heterogeneity than the *Endymio-Fagetum*.

13

14 **Redundancy Analysis**

15

16 Permutation tests (Monte-Carlo simulation) showed that the vegetation data matrix
17 and the environmental data matrix were not independent (Pseudo-F = 0.31, $P < 0.0001$)
18 despite of the fact that constrained variation (explained by environmental variables) was only
19 13% of total variation. The first three canonical axes extracted 46% of the constrained
20 variation (22%, 14%, 10%, respectively). Indirect and direct gradient analyses gave similar
21 results. A comparison between corresponding species bi-plots of RDA (Fig. 5) and PCA
22 (Figs. 1, 3) showed that the same four species groups were depicted by both analyses.
23 Correlation coefficients between RDA scores and PCA coordinates of plant species along the
24 first three axes were highly significant ($r = 0.94, 0.93, 0.72$, respectively, all with $P < 0.0001$).

25

1 A much simpler pattern was exhibited when the effect of geographical distance (and
 2 associated factors such as climate and past history) was eliminated (partial RDA). The two
 3 habitats EF and IF were clearly separated along Axis 1 (17.6% of constrained variation),
 4 *Endymio-Fagetum* samples being projected on its positive side while *Ilici-Fagetum* samples
 5 were projected on its negative side (Fig. 6). Among forest vegetation plant species, *Milium*
 6 *effusum* (Mef), *Athyrium filix-femina* (Afi), *Lamium galeobdolon* agg. (Lga), *Kindbergia*
 7 *praelonga* (Kpr), *Hyacinthoides non-scriptus* (Hno) and *Carpinus betulus* (Cpe) were
 8 projected far from the origin on the positive side of Axis 1, while *Ilex aquifolium* (Iaq),
 9 *Pteridium aquilinum* (Paq), *Deschampsia flexuosa* (Dfl), *Molinia caerulea* (Mca), *Carex*
 10 *pilulifera* (Cpi) and *Polytrichastrum formosum* (Pfo) were projected far from the origin on its
 11 negative side (Fig. 6). Mantel tests on the set of plant species showed that Ellenberg's indices
 12 for pH and Fertility were positively correlated with Axis 1 ($r_M = 0.41$, $P < 0.001$ and $r_M =$
 13 0.31 , $P < 0.001$, respectively), and Light Index was negatively correlated with the same axis
 14 ($r_M = -0.31$, $P < 0.001$). The Wetness index exhibited a weak (although significant) negative
 15 correlation with Axis 1 ($r_M = -0.02$, $P < 0.01$).

16

17 The projection of environmental variables (listed in Appendix 2) showed that Axis 1
 18 of partial RDA was positively correlated with hornbeam canopy cover (Cov1, $r = 0.36$) and
 19 hornbeam subcanopy cover (Cov5, $r = 0.23$), and was negatively correlated with Humus
 20 Index (H.I., $r = -0.42$) and holly (*Ilex aquifolium*) shrub cover (Cov14, $r = -0.31$).

21

22 The architecture of the cloud of samples in the plane of the first two axes of partial
 23 RDA (Fig. 6) showed a parabolic arrangement which is reminiscent of a Guttman effect (also
 24 called 'arch' or 'horseshoe' effect), well-known in gradient analysis when most significant

1 information is provided by the first canonical axis (Hill and Gauch, 1980). As a consequence
2 further canonical axes were not taken into account: they were considered as ground noise.

3

4 **The indicator value of the Humus Index at regional and local level**

5

6 Among other environmental variables measured in our study sites, the Humus Index
7 was given a prominent position by partial RDA: its strong negative score along the main
8 gradient (Axis 1) and the subordinate gradient (Axis 2) depicted by this analysis indicated that
9 it explained a large part of variation in the composition of beech forest plant habitats. We
10 tested the relationships between the Humus Index and several community indices calculated
11 at the sample level: species richness of vascular plants and mosses, average Ellenberg's
12 indices and percent cover by species belonging to the four groups depicted by PCA. In order
13 to avoid the confounding influence of discrepancies between forests (as exemplified by PCA
14 bi-plots) Mantel statistics were calculated in each forest, separately (Table 5). In all five
15 forests the Humus Index was positively correlated with moss richness and negatively
16 correlated with vascular richness. In Eawy the correlation was weak, although still significant.
17 In all forests, the Humus Index was negatively correlated with pH and Fertility Ellenberg's
18 indices. The correlation between the Humus Index and the Light Ellenberg's index was
19 positive in four out of five forests, Eawy being the exception with a weak (although
20 significant) negative value. The correlation between the Humus Index and the Wetness
21 Ellenberg's index was negative in four out of five forests, Retz being the exception with a
22 weak (although significant) positive value).

23

24 The four groups of species depicted by PCA exhibited homogeneous trends whatever
25 the forest considered. The surface covered by species belonging to A, C and D groups was

1 negatively correlated with the Humus Index, while the correlation was positive for the B
2 group (Table 5).

3

4 **Discussion**

5

6 Our study confirmed that the humus form, considered as a synthetic indicator of the
7 soil nutrient regime (Wilson et al., 2001; Pyatt et al., 2001; Ponge et al., 2002), can explain a
8 large part of the observed variation in the floristic composition of beech forests established on
9 acid to neutral soils. Over a large set of beech stands, belonging to two common habitats,
10 *Endymio-Fagetum* (EF) and *Ilici-Fagetum* (IF), our study confirmed the opposite trends in
11 vascular and moss species richness which had been shown in Brotonne and Saint-Palais IF
12 beech stands (Lalanne et al., 2008): at the sampling plot level, when the Humus Index
13 increases, passing from mull (Humus Index 1-4) to moder (Humus Index 5-7) then to mor
14 (Humus Index 8), moss species richness increases and vascular species richness decreases,
15 thereby reinforcing the view of phylogenetic conservatism of the ecological niche (Prinzing et
16 al., 2001). This observation is in agreement with Brunet et al. (1997) and Roem and Berendse
17 (2000) who showed that at local level vascular plant species richness decreases when soil
18 acidity increases in woodland and grassland, respectively. It should be highlighted, however,
19 that this observation holds for plot scale only and does not preclude the existence of an
20 opposite trend at larger scales (Levin, 2000; Gering and Crist, 2002; Rajaniemi et al., 2006).
21 Given a regional species pool (Zobel, 1997) more fertile, less acidic soils, will allow more
22 vascular species to cohabit at small scale and share a dearth of nutrients through common
23 mycelial networks and facilitation mechanisms (Bruno et al., 2002; Hart et al., 2003).

24

1 In all studied forests; the Humus Index was positively correlated with pH and Fertility
2 Ellenberg's indices, reinforcing the view expressed by Ulrich (1994) and Ponge (2003) that
3 humus forms, nutrient levels and soil acidity are strongly interconnected and interact with
4 vegetation types according to a limited number of ecosystem strategies (Odum, 1969) or
5 assembly rules (Belya and Lancaster, 1999). In a comprehensive study of understory
6 vegetation comparing 99 even-aged oak forests located in northern France, Bergès et al.
7 (2006) showed that humus forms, Ellenberg's Reaction and Nitrogen indices (here called pH
8 and Fertility), H^+ , Ca and P concentrations explained the main part of the observed floristic
9 variation. Similar results were obtained by Wilson et al. (2001) in 70 sites covering the range
10 of soil nutrient conditions prevailing in plantation forests of the United Kingdom. In both
11 cases nitrogen acted as a pollutant rather than as a nutrient and was not associated with this
12 soil fertility gradient. This further justifies that the 'Nitrogen index' of Ellenberg (1974) was
13 renamed 'Fertility Index' by Hill et al. (1999).

14

15 In all but one studied forests the Humus Index was positively and negatively
16 correlated with Light and Wetness Ellenberg's indices, respectively. In terms of causality this
17 seems to indicate that moisture disfavours and light favours the accumulation of organic
18 matter. That optimum (but not excess) moisture availability favours the circulation of
19 nutrients is a matter of fact (Austin et al., 2004) and the exception of the Retz forest, which
20 does not follow this general trend, can be explained by the high frequency of waterlogging,
21 which is currently associated with organic matter accumulation (Låg, 1971; Tate et al., 1995).
22 The observed (and at first sight surprising) correlation between light and organic matter
23 accumulation can be explained if we take into account that beech stands on more acidic soils
24 are less productive (Ponge et al., 1997), have less hornbeam and more oak, bracken and
25 heather in the understory (Lawesson, 2000), thereby shed more light on the ground. If this

1 hypothesis is true, it can be said that soil conditions (including humus form, acidity and
2 nutrient level) influence light conditions (Endler, 1993) by decreasing the influence of shade-
3 casting easy-to-decay species such as hornbeam and favouring light-demanding hard-to-decay
4 species such as oak, bracken, bilberry and heather, thereby reinforcing contrasts between
5 vegetation types (Miles, 1985). Rather than simple causal effects, our results point to the
6 existence of a global factor encompassing a large array of microclimate and soil conditions,
7 which will be discussed further below.

8
9 Among the four groups of forest vegetation species depicted by PCA in beech forests
10 of north-western France, the B group was the only one to be positively correlated with the
11 Humus Index, thus to be favoured by more acidic soils with a high Humus Index (mor and
12 moder). Species of this group (*Carex pilulifera*, *Deschampsia flexuosa*, *Holcus mollis*, *Ilex*
13 *aquifolium*, *Lonicera periclymenum*, *Polytrichastrum formosum*, *Pteridium aquilinum*,
14 *Thuidium tamariscinum*) are known for a long time for their preference for acid soils in a
15 wide array of oak and beech European forests (Olsen, 1925; Le Tacon and Timbal, 1973;
16 Ellenberg, 1974) and H-concentration was shown to be the driving factor (Falkengren-Grerup
17 and Tyler, 1993), although many other related processes may be involved, too (Lee 1999).
18 Among the sub-associations and variants of the *Ilici-Fagetum* described by Bardat (1993) in
19 the same region, this group is better represented by the *Ilici-Fagetum holcetosum*, which is
20 typically observed in forests on alluvial terraces of the Seine valley (Brotonne, Eawy, Lyons).
21 This is congruent with our results (Figs. 1, 2) except that this group was also present in Retz
22 IF and at least partially in Compiègne IF, two forests which were not covered by the study
23 cited above. Despite the vascular vs moss trend mentioned above, acidotolerant species of the
24 B group are not phylogenetically and physiognomically related (a shrub, a liana, two grasses,
25 a sedge-grass, a fern and two mosses). Within the limits of present knowledge, they rather

1 have in common to be perennial, to exhibit strong interference competition and anti-herbivore
2 defence (Jarvis, 1964; Coley et al., 1985; Dolling et al., 1994) and to excrete a variety of
3 organic acids with chelating properties in reaction to Al-toxicity (Schöttelndreier et al., 2001).
4 These characters stem in patch occupancy (Ovington, 1953; Watt, 1976), thereby decreasing
5 species coexistence at the plot level while allowing it over wide areas.

6

7 Beside these results, the case of Brotonne should be highlighted. Figure 2 showed that
8 most samples taken in the *Endymio-Fagetum* had positive values for F2, thus exhibited a
9 floristic composition which did not resemble that of the same habitat in other forests of the
10 same region. The shift of Brotonne EF towards an acidotolerant species distribution (B
11 branch) can be explained by the particular abundance of *Deschampsia flexuosa*, known to
12 thrive in the presence of atmospheric deposition of varied origin (Scale, 1980; Falkengren-
13 Grerup, 1986; Britton et al., 2003), in this air-polluted forest downwind of Le Havre (Solmon
14 et al., 2004; Croisé et al., 2005). The better representation of acidotolerant vegetation in
15 Brotonne was also reflected in a higher level of floristic variation (β -diversity) of the *Ilici-*
16 *Fagetum* (Table 4).

17

18 All other species groups exhibited by PCA (A, C, D) were negatively correlated with
19 the Humus Index, thus they were favoured by mull and less acidic soil conditions. However,
20 they diverged in their species composition, according to other environmental or geographical
21 factors which act as filters selecting subsets of species within regional pools (Weiher and
22 Keddy, 1995).

23

24 The A group (Table 2) included a liana (*Hedera helix*), three grasses (*Melica uniflora*,
25 *Milium effusum*, *Poa nemoralis*), three sedge-grasses (*Carex pendula*, *C. remota*, *C.*

1 *sylvatica*), ten forbs, among which two were annual (*Geranium robertianum*, *Moehringia*
 2 *trinervia*) and eight were perennial (*Circaea lutetiana*, *Euphorbia amygdaloides*, *Galium*
 3 *odoratum*, *Geum urbanum*, *Lamium galeobdolon* agg., *Oxalis acetosella*, *Veronica montana*,
 4 *Viola reichenbachiana*) and two ferns (*Athyrium filix-femina*, *Dryopteris filix-mas*). All these
 5 plants are commonly associated with nutrient-rich and moderately moist environments
 6 (Rameau et al. 1989). This group is better represented by the *Endymio-Fagetum typicum*,
 7 typically observed on loess deposits north of the river Seine (Bardat 1993). PCA showed that
 8 it was mostly present in Retz EF (Fig. 2), which exhibited a high level of β -diversity (Table
 9 4).

10

11 The C group included three trees (*Acer campestre*, *A. platanoides*, *Tilia platyphyllos*),
 12 two shrubs (*Crataegus monogyna*, *Evonymus europaeus*), eight forbs, among which four were
 13 annual or biennial (*Aethusa cynapium*, *Alliaria petiolata*, *Galium aparine*, *Mycelis muralis*)
 14 and four were perennial (*Fragaria vesca*, *Mercurialis perennis*, *Potentilla sterilis*, *Urtica*
 15 *dioica*), and a moss (*Rhytidiadelphus squarrosus*). These plants are commonly associated with
 16 nutrient-rich soils, but they tolerate drier conditions than the A group and are often found on
 17 calcareous soils (Rameau et al., 1989). The C group was better represented by the *Mercurialo-*
 18 *Aceretum* (Bardat, 1993), which is a xerothermophilic and basocline association, located on
 19 well-drained colluvial soils with admixture of limestone. It is known for its high vascular
 20 richness, as attested by the projection of the corresponding vector in the F1-F2 plane (Fig. 1).
 21 The C group was mostly present in Compiègne EF (Figures 3, 4).

22

23 The increase in the part played by annual herbs (0→2→4) along the B→A→C
 24 gradient is worthy to notice: it indicates an increasing nutrient availability, allowing the rapid

1 growth and reproduction of plants which are unable to store nutrients in perennial organs
2 (Fédoroff et al., 2005).

3
4 The D group, which was mostly present in Lyons EF and Eawy EF (Figures, 3, 4), was
5 comprised of two species which already belonged to the A group: the fern *A. filix-femina* and
6 the perennial forb *L. galeobdolon*. Other species were the trees *Acer pseudoplatanus* and
7 *Carpinus betulus*, the shrubs *Rubus idaeus*, *Ruscus aculeatus* and *Taxus baccata*, the sedge-
8 grass *Carex ovalis*, the perennial forbs *Anemone nemorosa*, *Callitriche sp.*, *Digitalis*
9 *purpurea*, *Hyacinthoides non-scripta*, *Lotus pedunculatus*, *Polygonatum multiflorum*,
10 *Stellaria graminea*, *Stellaria nemorum* and *Viola riviniana*, the annual forb *Galeopsis tetrahit*
11 agg., and the mosses *Atrichum undulatum*, *Brachythecium rutabulum*, *Hypnum cupressiforme*
12 agg., *Isothecium myosuroides*, *Kindbergia praelonga* and *Plagiothecium denticulatum*. Most
13 remarkable features are the diversity of mosses (see the projection of the moss richness vector
14 on Figure 3) and of spring-flowering geophytes. Several species (*C. ovalis*, *Callitriche sp.*, *L.*
15 *pedunculatus*, *Stellaria nemorum*) are known for their affinity to wet environments. The D
16 group was better represented by the *Endymio-Fagetum aretosum* (Bardat, 1993), which is the
17 most hygrophilic sub-association of the *Endymio-Fagetum*, established in bottom woodland
18 within the study region. The D group of species was projected on the negative side of Factor
19 F3 (Fig. 3), which was positively correlated with weak disturbance and negatively correlated
20 with undisturbed ground cover, thereby indicating that corresponding plots were poorly rutted
21 by exploitation traffic. In the absence of straightforward data on management practices it may
22 be thought that wetter environments, given the difficulty of timber extraction with modern
23 vehicles, have been undisturbed for the last 50 years.

24

1 All species groups depicted by PCA were confirmed by RDA, on the basis of stand
2 properties (age, basal area, stem density, composition of canopy, subcanopy and shrub layers)
3 and ground disturbance (traffic cues, wood deposits). This seems to indicate that in the
4 context of the studied region ground vegetation responded to local factors which could be
5 described fairly well by a visual inspection of ground and above strata. As a corollary, this
6 points to the existence of a common regional species pool without any additional filter than
7 described by plot-scale local environment.

8
9 Once local environmental particularities have been ruled out by partialling out the
10 geographical position of sampling plots, a simpler pattern arose, with a single gradient of soil
11 fertility/acidity/light which was exemplified by Axis 1 of partial RDA (Fig. 6). The
12 distribution of species showed a gradient from acidophily to acido-intolerance which
13 corresponded to a continuum from the *Ilici-Fagetum* (species of the B group) to the *Endymio-*
14 *Fagetum* (species of A, C and D groups). The two dominant species of these habitats,
15 respectively *I. aquifolium* (Iaq) and *H. non-scripta* (Hno), were projected far from the origin,
16 on negative and positive sides of Axis 1, respectively. This gradient of decreasing acidity and
17 light and increasing fertility and Humus Index was associated with an increase in hornbeam
18 cover, both in canopy (Cov 1) and subcanopy (Cov 5). Whether hornbeam is a cause of
19 decreasing light for forest-floor vegetation is out of doubt, given its dense canopies strongly
20 select shade-tolerant species (Kwiatkowska et al., 1997). Whether hornbeam is a cause or a
21 consequence of variation in soil fertility/acidity and humus form does not deserve any
22 straightforward answer, although feed-back relationships can be suspected (Ponge, 2003).
23 Most studies comparing forest stands with and without hornbeam did not take into account
24 historical or environmental reasons why hornbeam was present or absent and they ascribed to
25 silviculture only the observed effects (Aubert, et al. 2004; Decocq et al., 2005). Similar flaws

1 can be found in comparisons between coppice woods of varying nature and adjoining full-
2 grown forest stands (Hölscher et al., 2001). This lack of account for the spontaneous
3 establishment of *C. betulus* in natural or managed forests (Kwiatkowska et al., 1997;
4 Lawesson, 2000) is not so important for explaining variations in corticolous assemblages
5 (Bardat and Aubert, 2007) but it may flaw any conclusion about the impact of hornbeam on
6 forest-floor plant assemblages when mature forests of unknown past history are compared. As
7 shown by Decocq (2000) working on 157 sample plots distributed over the widest possible
8 range of geological substrates prevailing in northern France mixed-hardwood forests, forest-
9 floor vegetation was more influenced by the geological substrate than by the composition of
10 the overstory. However, when care is taken for substrate conditions being identical, the
11 positive impact of hornbeam on the soil fertility of beech forests, which is mainly due to
12 better litter quality of hornbeam compared to beech (Lemée and Bichaut, 1973), and
13 consequent influences on forest-floor vegetation, can be assessed less ambiguously (Decocq
14 et al., 2004; Ponge and Chevalier, 2006; Van Calster et al., 2007). Awaiting further
15 clarification of the ‘hornbeam’ effect, it can be hypothesized that the combined influence of
16 geological substrate, natural establishment of hornbeam and silviculture (in particular
17 coppicing) results in a feed-back loop in favour of mull humus forms and associated
18 vegetation.

19

20 The variation of ground vegetation can thus be explained by a combination of humus
21 quality, soil fertility, soil acidity and light along a single environmental gradient from poorly
22 productive (and species-poor) to highly productive (and species-rich) forest ecosystems, in
23 accordance with some (but far from all) theoretical studies (Ulrich, 1994; Bruno et al., 2002)
24 and in line with experimental and descriptive studies (Falkengren-Grerup and Tyler, 1993;
25 Brunet et al., 1997; Rodríguez-Loinaz et al., 2008). To these rather simple effects, due to

1 multiple but strongly interconnected factors stemming in a limited number of stable states
2 (Perry, 1995; Ponge, 2003; Beisner et al., 2003), are superimposed local effects of a more
3 complex (i.e. harder to discern) nature. Climate (Bakkestuen et al., 2008), atmospheric
4 deposition (Brandt and Rhoades, 1972; Falkengren-Grerup, 1986), past history (Peterken and
5 Game, 1984; Koerner et al., 1997; Gachet et al., 2007), management practices (Thomas et al.,
6 1999; Decocq, 2000; Godefroid and Koedam, 2004), dispersal from sources of migration
7 (Björkman and Bradshaw, 1996; Bossuyt et al., 1999) and succession (Watt, 1934; Myster
8 and Pickett, 1992; Godefroid et al., 2005) are supposed to act more or less independently in
9 different forests (McCune and Allen, 1985), thereby creating the variegated forest habitats
10 which could be described (but not necessarily fully explained) locally (Rol, 1937; Ricklefs,
11 1987; Huston, 1999).

12

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14

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20

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7

1 **Figure legends**

2

3 **Figure 1.** Principal Components Analysis. F1-F2 bi-plot of plant species and some additional
4 variables. For the sake of clarity, arrows have not been indicated for plant species
5 vectors. Species names coded as in Appendix 1 and Table 2

6

7 **Figure 2.** Principal Components Analysis. F1-F2 bi-plots of sampling plots in the five studied
8 forests

9

10 **Figure 3.** Principal Components Analysis. F2-F3 bi-plot of plant species and some additional
11 variables. For the sake of clarity, arrows have not been indicated for plant species
12 vectors. Species names coded as in Appendix 1 and Table 2

13

14 **Figure 4.** Principal Components Analysis. F2-F3 bi-plots of sampling plots in the five studied
15 forests

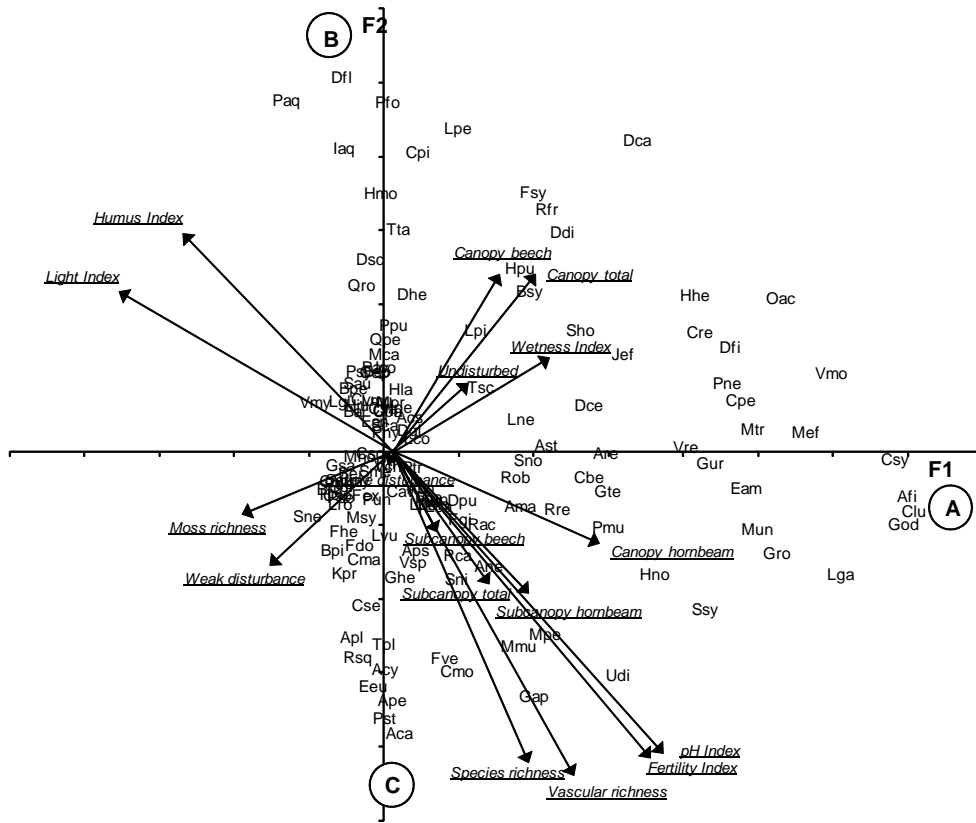
16

17 **Figure 5.** Redundancy Analysis. Axis 1-Axis 2 (top) and Axis 2-Axis 3 (bottom) bi-plots of
18 plant species. For the sake of clarity, arrows have not been indicated for plant species
19 vectors. Species names coded as in Appendix 1 and Table 2

20

21 **Figure 6.** Partial Redundancy Analysis. Axis 1-Axis 2 bi-plots of plant species (top left),
22 sampling plots (top right) and environmental variables (bottom). For the sake of
23 clarity, arrows have not been indicated for plant species and environmental vectors.
24 Species names coded as in Appendix 1 and Table 2. Environmental variables coded as
25 in Appendix 2

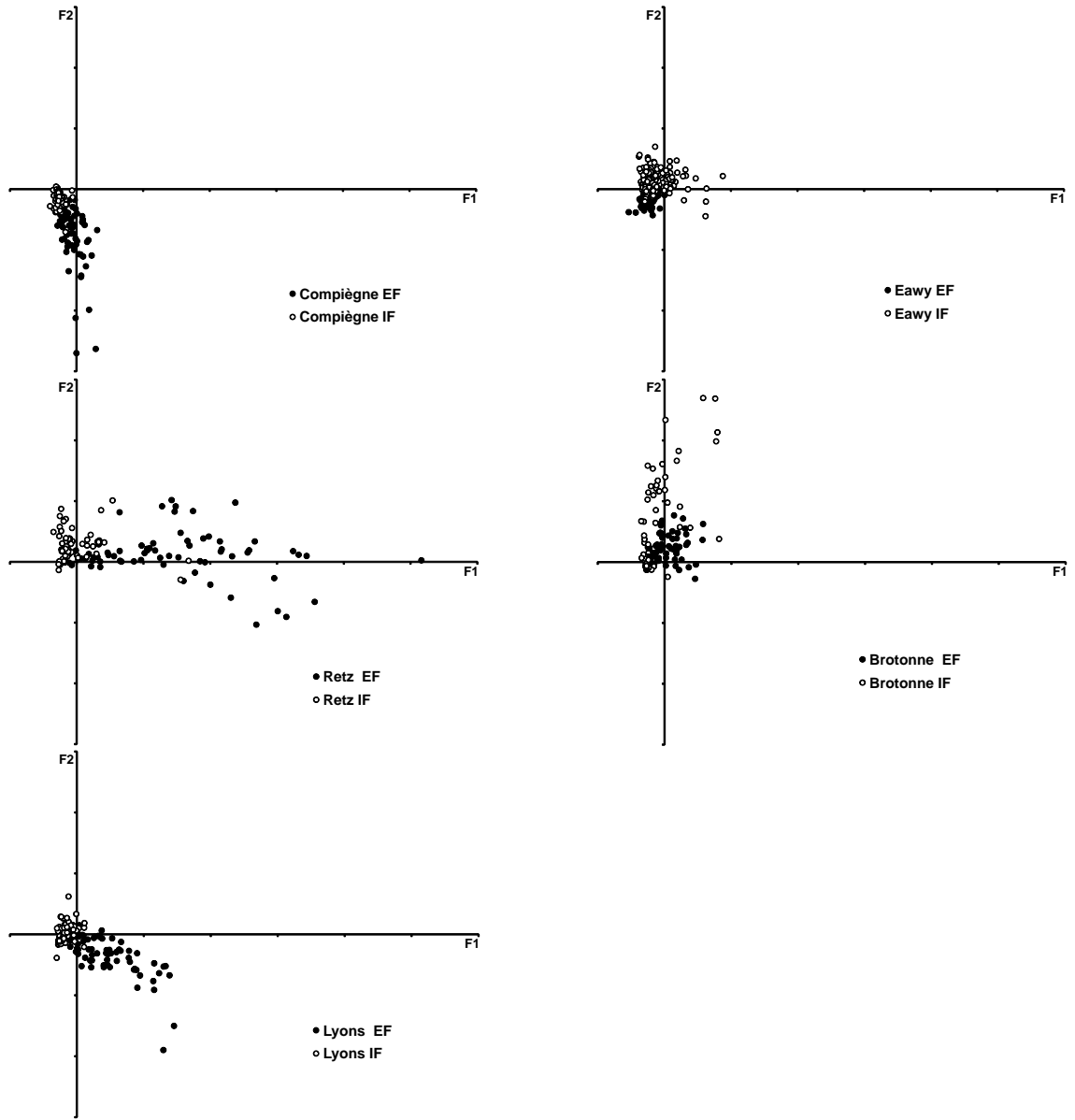
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2 Fig. 1

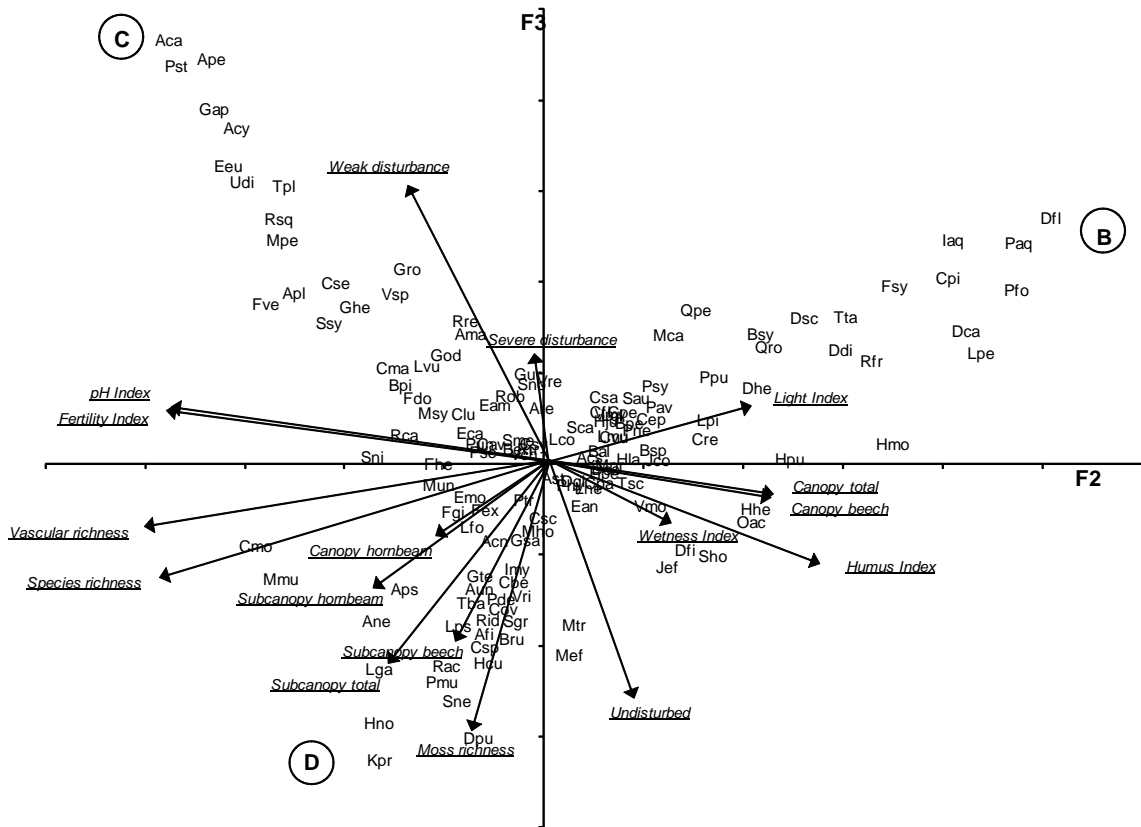
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2 Fig. 2

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2 Fig. 3

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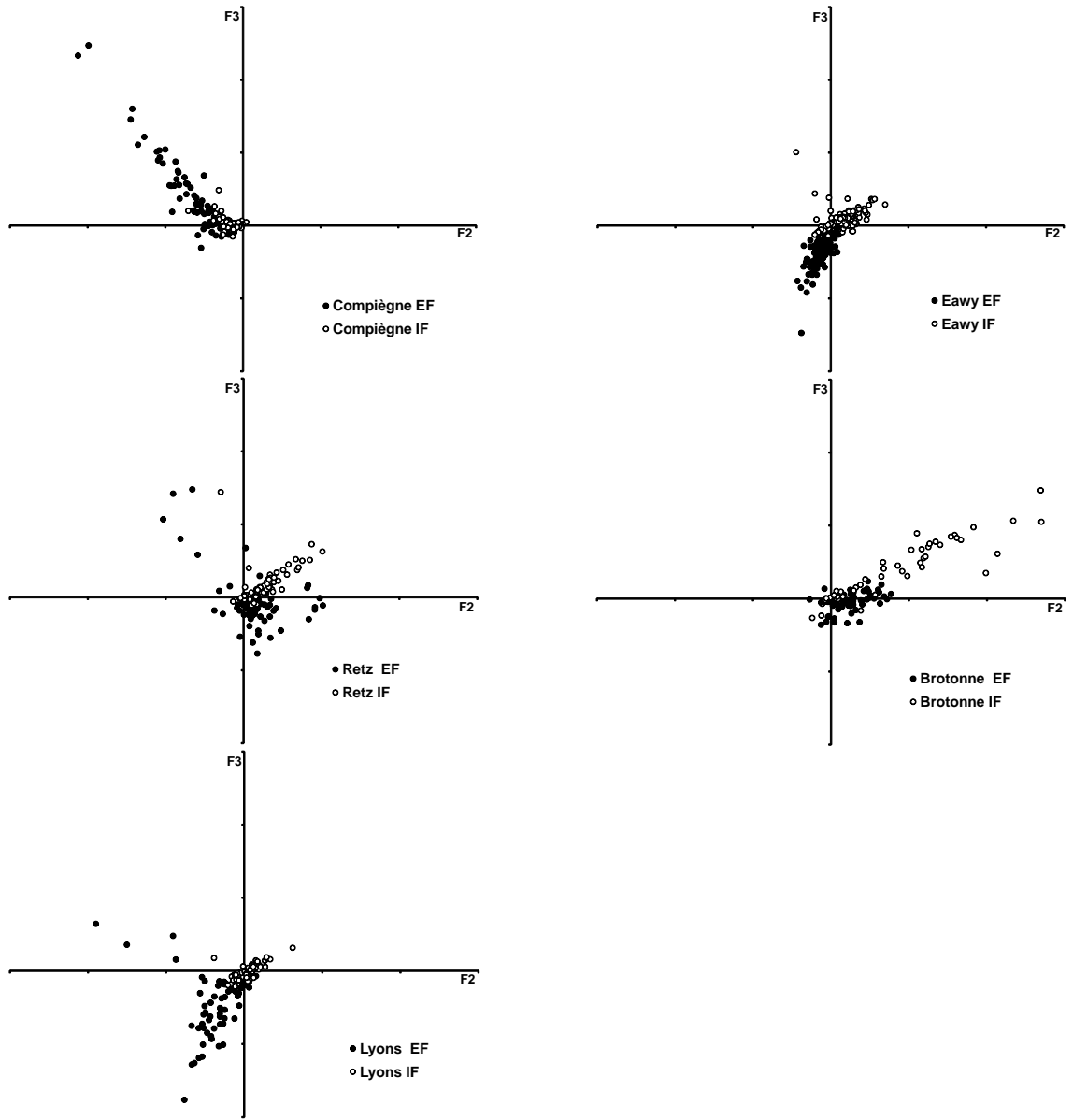
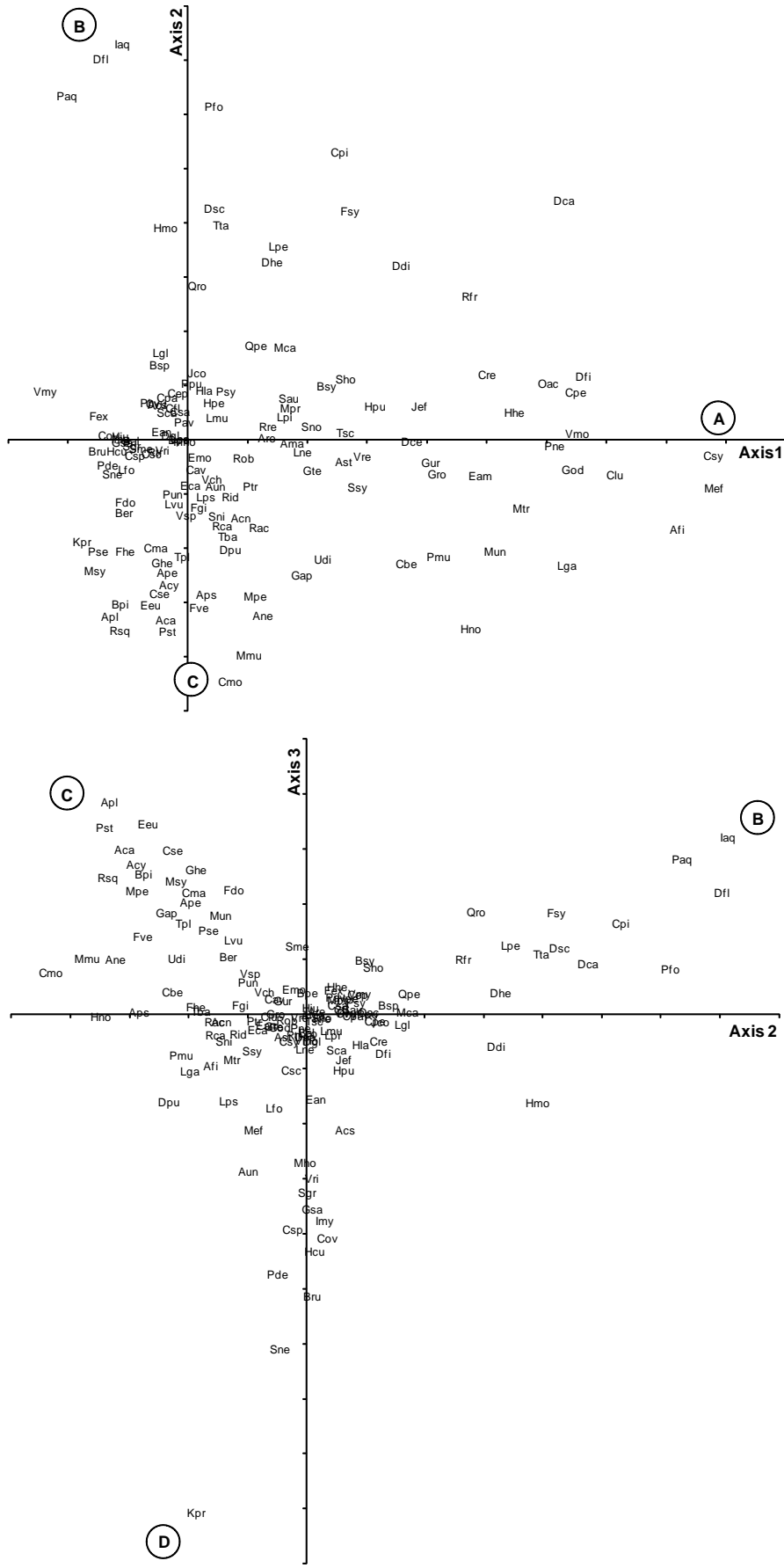
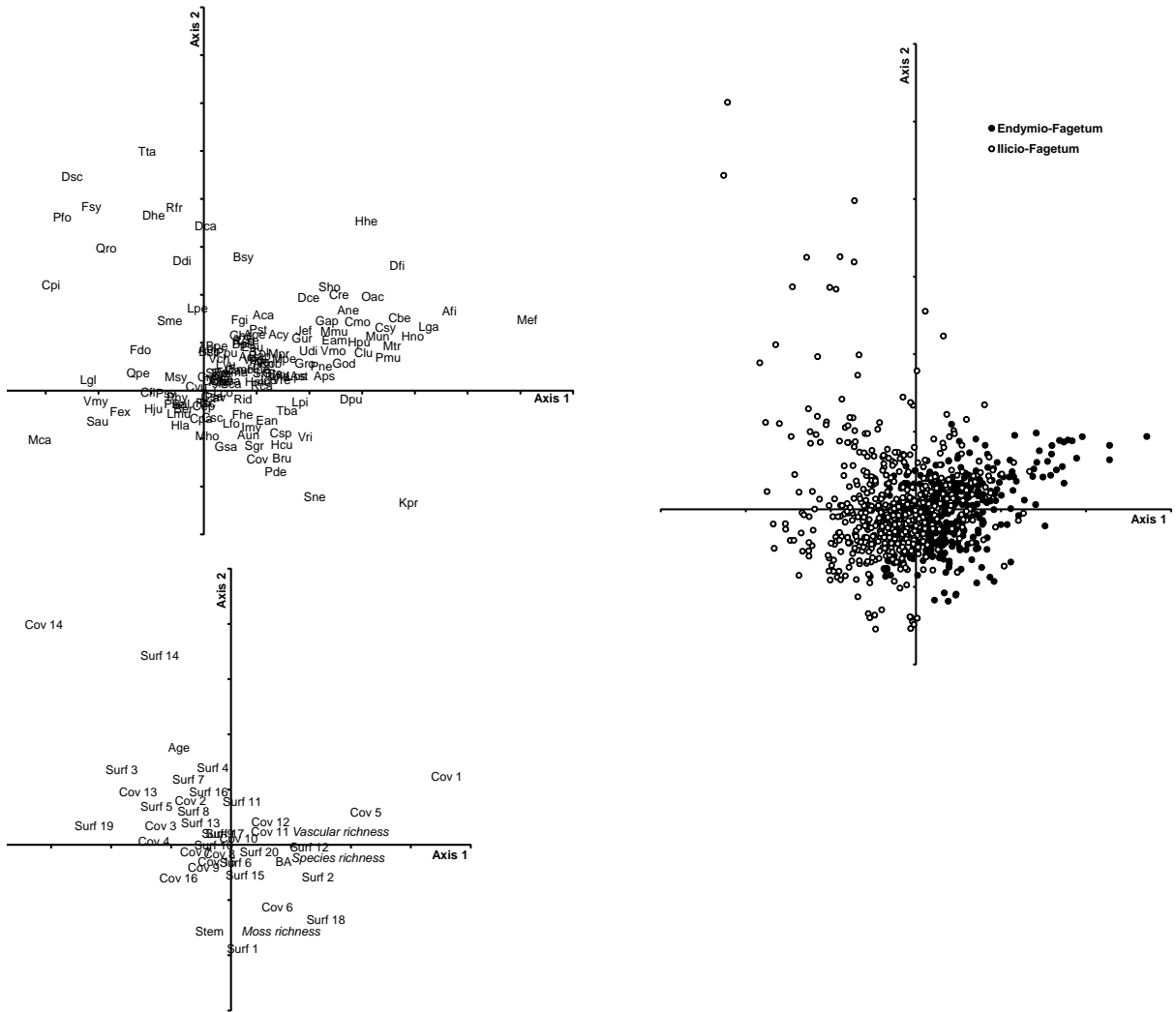


Fig. 4



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2 Fig. 5



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2 Fig. 6

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Table 1. Mean features of the five studied forests. Climate data averaged over 1978-2007. Atmospheric deposition data averaged over 1993-2004

| | Compiègne | Eawy | Retz | Brotonne | Lyons |
|---|------------------|-------------|-------------|-----------------|--------------|
| Number of sites | 33 | 74 | 25 | 34 | 33 |
| Number of plots | 165 | 370 | 125 | 170 | 165 |
| Latitude | 49°30' N | 49°35' N | 49°14' N | 49°36' N | 49°18' N |
| Longitude | 2°55' E | 1°21' E | 2°48' E | 0°44' E | 1°37' E |
| Surface | 14,400 ha | 6,550 ha | 13,000 ha | 7,200 ha | 10,700 ha |
| Altitude | 32-148 m | 130-230 m | 155-241 m | 10-60 m | 67-178 m |
| Annual rainfall | 749 mm | 904 mm | 719 mm | 950 mm | 780 mm |
| Mean temperature | 10.9°C | 10.1°C | 10.7°C | 10.4°C | 10.9°C |
| Annual warming | 0.038°C | 0.077°C | 0.064°C | 0.070°C | 0.065°C |
| S deposition (kg.ha ⁻¹ .yr ⁻¹) | 4.6 | 6.9 | 4.6 | 6.8 | 5.9 |
| N deposition (kg.ha ⁻¹ .yr ⁻¹) | 7.8 | 9 | 8.1 | 7.9 | 7.9 |

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Table 2. List of plant species placed in characteristic position by Principal Components Analysis, with their corresponding floristic groups

| Code | Species name | A group | B group | C group | D group |
|------|-----------------------------------|---------|---------|---------|---------|
| Aca | <i>Acer campestre</i> | | | + | |
| Apl | <i>Acer platanoides</i> | | | + | |
| Aps | <i>Acer pseudoplatanus</i> | | | | + |
| Acy | <i>Aethusa cynapium</i> | | | + | |
| Ape | <i>Alliaria petiolata</i> | | | + | |
| Ane | <i>Anemona nemorosa</i> | | | | + |
| Afi | <i>Athyrium filix-femina</i> | + | | | + |
| Aun | <i>Atrichum undulatum</i> | | | | + |
| Bru | <i>Brachythecium rutabulum</i> | | | | + |
| Csp | <i>Callitriche</i> sp. | | | | + |
| Cov | <i>Carex ovalis</i> | | | | + |
| Cpe | <i>Carex pendula</i> | + | | | |
| Cre | <i>Carex remota</i> | + | | | |
| Cpi | <i>Carex pilulifera</i> | | + | | |
| Csy | <i>Carex sylvatica</i> | + | | | |
| Cbe | <i>Carpinus betulus</i> | | | | + |
| Clu | <i>Circaea lutetiana</i> | + | | | |
| Cmo | <i>Crataegus monogyna</i> | | | + | |
| Dfl | <i>Deschampsia flexuosa</i> | | + | | |
| Dpu | <i>Digitalis purpurea</i> | | | | + |
| Dfi | <i>Dryopteris filix-mas</i> | + | | | |
| Eam | <i>Euphorbia amygdaloides</i> | + | | | |
| Eeu | <i>Evonymus europaeus</i> | | | + | |
| Fve | <i>Fragaria vesca</i> | | | + | |
| Gte | <i>Galeopsis tetrahit</i> | | | | + |
| Gap | <i>Galium aparine</i> | | | + | |
| God | <i>Galium odoratum</i> | + | | | |
| Gro | <i>Geranium robertianum</i> | + | | | |
| Gur | <i>Geum urbanum</i> | + | | | |
| Hhe | <i>Hedera helix</i> | + | | | |
| Hmo | <i>Holcus mollis</i> | | + | | |
| Hno | <i>Hyacinthoides non-scripta</i> | | | | + |
| Hcu | <i>Hypnum cupressiforme</i> | | | | + |
| Iaq | <i>Ilex aquifolium</i> | | + | | |
| Imy | <i>Isoetes myosuroides</i> | | | | + |
| Kpr | <i>Kindbergia praelonga</i> | | | | + |
| Lga | <i>Lamium galeobdolon</i> | + | | | + |
| Lpe | <i>Lonicera periclymenum</i> | | + | | |
| Lps | <i>Lotus pedunculatus</i> | | | | + |
| Mun | <i>Melica uniflora</i> | + | | | |
| Mpe | <i>Mercurialis perennis</i> | | | + | |
| Mef | <i>Milium effusum</i> | + | | | |
| Mtr | <i>Moehringia trinervia</i> | + | | | |
| Mmu | <i>Mycelis muralis</i> | | | + | |
| Oac | <i>Oxalis acetosella</i> | + | | | |
| Pde | <i>Plagiothecium denticulatum</i> | | | | + |
| Pne | <i>Poa nemoralis</i> | + | | | |
| Pmu | <i>Polygonatum multiflorum</i> | | | | + |
| Pfo | <i>Polytrichastrum formosum</i> | | + | | |
| Pst | <i>Potentilla sterilis</i> | | | + | |
| Paq | <i>Pteridium aquilinum</i> | | + | | |
| Rsq | <i>Rhytidiadelphus squarrosus</i> | | | + | |
| Rid | <i>Rubus idaeus</i> | | | | + |
| Rac | <i>Ruscus aculeatus</i> | | | | + |
| Sgr | <i>Stellaria graminea</i> | | | | + |
| Sne | <i>Stellaria nemorum</i> | | | | + |
| Tba | <i>Taxus baccata</i> | | | | + |
| Tta | <i>Thuidium tamariscinum</i> | | + | | |
| Tpl | <i>Tilia platyphyllos</i> | | | + | |
| Udi | <i>Urtica dioica</i> | | | + | |
| Vmo | <i>Veronica montana</i> | + | | | |
| Vre | <i>Viola reichenbachiana</i> | + | | | |
| Vri | <i>Viola riviniana</i> | | | | + |

Table 3. Pearson correlation coefficients between additional (passive) variables and the first three axes of PCA on plant species (see graphical representation in Figures 1 and 3)

| | F1 | F2 | F3 |
|---------------------------------|-----------|-----------|-----------|
| Species richness | 0.19 | -0.42 | -0.13 |
| Vascular richness | 0.26 | -0.44 | -0.07 |
| Moss richness | -0.21 | -0.08 | -0.30 |
| Ellenberg's Light Index | -0.39 | 0.22 | 0.06 |
| Ellenberg's Wetness Index | 0.22 | 0.13 | -0.06 |
| Ellenberg's pH Index | 0.38 | -0.41 | 0.06 |
| Ellenberg's Fertility Index | 0.37 | -0.41 | 0.06 |
| Humus Index | -0.29 | 0.29 | -0.11 |
| Total canopy cover | 0.20 | 0.24 | -0.04 |
| Hornbeal canopy cover | 0.29 | -0.12 | -0.08 |
| Beech canopy cover | 0.15 | 0.24 | -0.04 |
| Total subcanopy cover | 0.13 | -0.18 | -0.22 |
| Hornbeam subcanopy cover | 0.19 | -0.19 | -0.14 |
| Beech subcanopy cover | 0.06 | -0.11 | -0.19 |
| Undisturbed ground cover | 0.10 | 0.09 | -0.26 |
| Weak disturbance ground cover | -0.17 | -0.15 | 0.30 |
| Severe disturbance ground cover | -0.01 | -0.01 | 0.12 |

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Table 4. Floristic heterogeneity in the six studied forests and in two beech communities. See text for calculation details. EF = Endymio-Fagetum. IF = Illicio-Fagetum

| | EF | IF |
|------------------|-----------|-----------|
| Compiègne | 17.4 | 0.6 |
| Eawy | 1.6 | 1.8 |
| Retz | 37.6 | 6.7 |
| Brotonne | 2.8 | 17.7 |
| Lyons | 11.9 | 1.0 |

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Table 5. Relationship between Humus Index and several community indices in the five studied forests. Signed Mantel test, product-moment correlation coefficient: *** = P<0.001

| | Compiègne | Eawy | Retz | Brotonne | Lyons |
|--------------------------|------------------|-------------|-------------|-----------------|--------------|
| Vascular richness | -0.56*** | -0.15*** | -0.50*** | -0.52*** | -0.33*** |
| Moss richness | 0.31*** | 0.09*** | 0.30*** | 0.29*** | 0.28*** |
| pH Index | -0.50*** | -0.14*** | -0.68*** | -0.32*** | -0.45*** |
| Fertility Index | -0.46*** | -0.12*** | -0.53*** | -0.24*** | -0.43*** |
| Light Index | 0.29*** | -0.05*** | 0.56*** | 0.19*** | 0.19*** |
| Wetness Index | -0.13*** | -0.25*** | 0.06*** | -0.12*** | -0.22*** |
| A group cover | -0.36*** | -0.33*** | -0.65*** | -0.23*** | -0.27*** |
| B group cover | 0.28*** | 0.11*** | 0.50*** | 0.09*** | 0.26*** |
| C group cover | -0.39*** | -0.13*** | -0.11*** | -0.29*** | -0.14*** |
| D group cover | -0.07*** | -0.11*** | -0.51*** | -0.41*** | -0.15*** |

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Appendix 1. List of plant species used in data analysis (species present in more than 10 samples). Vascular species names in roman, moss species names in italic type

| Code | Latin name | Light Index | Wetness Index | pH Index | Fertility Index | Number of samples |
|------|---|-------------|---------------|----------|-----------------|-------------------|
| Aca | <i>Acer campestre</i> L. | 5 | 5 | 7 | 6 | 43 |
| Apl | <i>Acer platanoides</i> L. | 4 | 5 | 7 | 7 | 21 |
| Aps | <i>Acer pseudoplatanus</i> L. | 4 | 5 | 6 | 6 | 149 |
| Acy | <i>Aethusa cynapium</i> L. | 6 | 4 | 7 | 6 | 18 |
| Acn | <i>Agrostis canina</i> L. | 7 | 7 | 3 | 3 | 23 |
| Acs | <i>Agrostis capillaris</i> L. | 6 | 5 | 4 | 4 | 190 |
| Ast | <i>Agrostis stolonifera</i> L. | 7 | 6 | 7 | 6 | 18 |
| Are | <i>Ajuga reptans</i> L. | 5 | 7 | 5 | 5 | 13 |
| Ape | <i>Alliania petiolata</i> (Bieb.) Cavera & Grande | 5 | 6 | 7 | 8 | 57 |
| Ane | <i>Anemone nemorosa</i> L. | 5 | 6 | 5 | 4 | 171 |
| Ana | <i>Anum maculatum</i> L. | 4 | 5 | 7 | 7 | 22 |
| As | <i>Athyrium filix-femina</i> (L.) Roth | 5 | 7 | 5 | 6 | 333 |
| Aun | <i>Atrichum undulatum</i> (Hedw.) P. Beauv. | 7 | 6 | 3 | 4 | 281 |
| Bal | <i>Betula alba</i> L. | 7 | 7 | 4 | 4 | 37 |
| Bpe | <i>Betula pendula</i> Roth | 7 | 5 | 4 | 4 | 71 |
| Bsp | <i>Blechnum spicant</i> (L.) Roth | 5 | 6 | 3 | 3 | 67 |
| Bpi | <i>Brachypodium pinnatum</i> (L.) Beauv. | 7 | 3 | 8 | 3 | 44 |
| Bsy | <i>Brachypodium sylvaticum</i> (Huds.) Beauv. | 6 | 5 | 6 | 5 | 89 |
| Bru | <i>Brachythecium rutabulum</i> (Hedw.) B., S. & G. | 6 | 5 | 6 | 5 | 20 |
| Ber | <i>Bromus erectus</i> Huds. | 7 | 4 | 8 | 3 | 26 |
| Cep | <i>Callimagrostis epigejos</i> (L.) Roth | 7 | 7 | 7 | 6 | 24 |
| Csp | <i>Callitriche</i> sp. | 7 | 9 | 6 | 6 | 10 |
| Cwu | <i>Calluna vulgaris</i> (L.) Hull | 7 | 6 | 2 | 2 | 16 |
| Cse | <i>Calystegia sepium</i> (L.) R.Br. | 7 | 8 | 7 | 7 | 17 |
| Cfl | <i>Cardamine flexuosa</i> With. | 5 | 7 | 6 | 6 | 18 |
| Cov | <i>Carex ovalis</i> Good. | 7 | 7 | 5 | 4 | 21 |
| Cpa | <i>Carex pallens</i> L. | 6 | 6 | 5 | 4 | 22 |
| Cpe | <i>Carex pendula</i> Huds. | 5 | 8 | 7 | 6 | 44 |
| Cpi | <i>Carex pilulifera</i> L. | 7 | 5 | 3 | 2 | 360 |
| Cre | <i>Carex remota</i> L. | 4 | 8 | 6 | 6 | 516 |
| Ccy | <i>Carex sylvatica</i> Huds. | 4 | 5 | 6 | 5 | 267 |
| Cbe | <i>Carpinus betulus</i> L. | 4 | 5 | 5 | 6 | 326 |
| Csa | <i>Castanea sativa</i> Mill. | 5 | 5 | 5 | 5 | 65 |
| Clu | <i>Circaea lutetiana</i> L. | 4 | 6 | 7 | 6 | 177 |
| Cma | <i>Conopodium majus</i> (Gouan) Loret | 6 | 5 | 5 | 5 | 54 |
| Csv | <i>Corylus avellana</i> L. | 6 | 5 | 6 | 22 | 421 |
| Cmo | <i>Crataegus monogyna</i> Jacq. | 6 | 5 | 7 | 6 | 69 |
| Csc | <i>Cytisus scoparius</i> (L.) Link | 8 | 5 | 4 | 4 | 93 |
| Dgl | <i>Dactylis glomerata</i> L. | 7 | 5 | 7 | 6 | 52 |
| Dce | <i>Deschampsia cespitosa</i> (L.) Beauv. | 6 | 6 | 5 | 4 | 160 |
| Df | <i>Deschampsia flexuosa</i> (L.) Trin. | 5 | 2 | 3 | 3 | 421 |
| Dhe | <i>Dicranella heteromalla</i> (Hedw.) Schimp. | 9 | 3 | 4 | 1 | 163 |
| Dsc | <i>Dicranum scoparium</i> Hedw. | 9 | 3 | 4 | 1 | 154 |
| Dpu | <i>Digitalis purpurea</i> L. | 6 | 6 | 4 | 5 | 155 |
| Dca | <i>Dryopteris carthusiana</i> (Villar) H.P. Fuchs | 6 | 8 | 5 | 4 | 597 |
| Ddi | <i>Dryopteris dilatata</i> (Hoffm.) A. Gray | 5 | 6 | 4 | 5 | 330 |
| Df | <i>Dryopteris filix-mas</i> (L.) Schott | 5 | 6 | 5 | 5 | 370 |
| Ean | <i>Epilobium angustifolium</i> L. | 6 | 5 | 6 | 5 | 70 |
| Emo | <i>Epilobium montanum</i> L. | 6 | 6 | 6 | 6 | 42 |
| Eca | <i>Eupatorium cannabinum</i> L. | 7 | 8 | 6 | 7 | 10 |
| Eam | <i>Euphorbia amygdalodes</i> L. | 4 | 5 | 6 | 6 | 90 |
| Eeu | <i>Evonymus europaeus</i> L. | 5 | 5 | 8 | 5 | 23 |
| Fsy | <i>Fagus sylvatica</i> L. | 3 | 5 | 5 | 5 | 776 |
| Fgi | <i>Festuca gigantea</i> (L.) Vill. | 5 | 6 | 7 | 7 | 74 |
| Fhe | <i>Festuca heterophylla</i> Lam. | 8 | 5 | 6 | 5 | 23 |
| Fie | <i>Fragaria vesca</i> L. | 5 | 6 | 6 | 4 | 21 |
| Fdo | <i>Frangula dodonei</i> Ard. | 6 | 8 | 5 | 5 | 62 |
| Fex | <i>Fraxinus excelsior</i> L. | 5 | 6 | 7 | 6 | 149 |
| Gte | <i>Galeopsis tetrahit</i> L. agg. | 7 | 5 | 6 | 6 | 86 |
| Gsp | <i>Galium aparine</i> L. | 6 | 6 | 7 | 8 | 116 |
| God | <i>Galium odoratum</i> (L.) Scop. | 5 | 5 | 7 | 6 | 101 |
| Gsa | <i>Galium saxatile</i> L. | 6 | 6 | 3 | 3 | 12 |
| Gro | <i>Geranium robertianum</i> L. | 5 | 6 | 6 | 6 | 84 |
| Gur | <i>Geum urbanum</i> L. | 4 | 6 | 7 | 7 | 63 |
| Ghe | <i>Glechoma hederacea</i> L. | 6 | 6 | 7 | 7 | 45 |
| Hhe | <i>Hedera helix</i> L. | 4 | 5 | 7 | 6 | 435 |
| Hla | <i>Holcus lanatus</i> L. | 7 | 6 | 6 | 5 | 52 |
| Hmo | <i>Holcus mollis</i> L. | 6 | 6 | 3 | 3 | 256 |
| Hno | <i>Hyacinthoides non-scripta</i> (L.) Chouard ex Rothm. | 5 | 5 | 5 | 6 | 263 |
| Hpe | <i>Hypericum perforatum</i> L. | 7 | 4 | 7 | 5 | 17 |
| Hpu | <i>Hypericum pulchrum</i> L. | 6 | 5 | 4 | 3 | 187 |
| Hcu | <i>Hypnum cupressiforme</i> Hedw. agg. | 8 | 8 | 4 | 2 | 118 |
| Hju | <i>Hypnum julandicum</i> Holmen & Wancke | 8 | 8 | 4 | 2 | 11 |
| Iaq | <i>Ilex aquifolium</i> L. | 5 | 5 | 5 | 5 | 574 |
| Imy | <i>Isotrichum myosuroides</i> Bnd. | 7 | 9 | 5 | 3 | 12 |
| Jco | <i>Juncus conglomeratus</i> L. | 7 | 7 | 4 | 3 | 115 |
| Jef | <i>Juncus effusus</i> L. | 7 | 7 | 4 | 4 | 408 |
| Kpr | <i>Kindbergia praelonga</i> (Hedw.) Ochrya | 7 | 5 | 4 | 3 | 86 |
| Lga | <i>Lamium galeobdolon</i> (L.) Crantz agg. | 4 | 5 | 7 | 6 | 139 |
| Lco | <i>Lapsana communis</i> L. | 6 | 4 | 7 | 7 | 16 |
| Lgl | <i>Lasiochylum glaucum</i> (Hedw.) Angstr. | 8 | 4 | 7 | 4 | 83 |
| Lvu | <i>Ligustrum vulgare</i> L. | 6 | 5 | 7 | 5 | 24 |
| Lpe | <i>Lonicera periclymenum</i> L. | 5 | 6 | 5 | 5 | 398 |
| Lps | <i>Lotus pedunculatus</i> Cav. | 7 | 8 | 6 | 4 | 11 |
| Llo | <i>Luzula forsteri</i> (Sm.) DC. | 4 | 4 | 5 | 2 | 24 |
| Lmu | <i>Luzula multiflora</i> (Retz.) Lej. | 7 | 6 | 3 | 3 | 25 |
| Lpi | <i>Luzula pilosa</i> (L.) Willd. | 5 | 5 | 5 | 3 | 147 |
| Lne | <i>Lysimachia nemorum</i> L. | 5 | 7 | 4 | 5 | 46 |
| Msy | <i>Malus sylvestris</i> Mill. | 7 | 5 | 7 | 5 | 19 |
| Mpr | <i>Malampyrum pratense</i> L. | 5 | 5 | 2 | 5 | 11 |
| Mun | <i>Melica uniflora</i> Retz. | 4 | 5 | 7 | 5 | 285 |
| Mpe | <i>Mercurialis perennis</i> L. | 3 | 6 | 7 | 7 | 66 |
| Mef | <i>Milium effusum</i> L. | 4 | 5 | 6 | 5 | 490 |
| Mho | <i>Milium horum</i> Hedw. | 7 | 5 | 6 | 6 | 101 |
| Mtr | <i>Molinia tinaria</i> (L.) Csinv. | 7 | 5 | 6 | 7 | 63 |
| Mca | <i>Molinia caerulea</i> (L.) Moench | 7 | 8 | 3 | 2 | 17 |
| Mmu | <i>Mycelis muralis</i> (L.) Dum. | 4 | 5 | 7 | 5 | 58 |
| Oac | <i>Oxalis acetosella</i> L. | 4 | 6 | 4 | 4 | 266 |
| Psy | <i>Pinus sylvestris</i> L. | 7 | 6 | 2 | 2 | 38 |
| Pun | <i>Pinguicula vulgaris</i> (Hedw.) T.Kop. | 7 | 4 | 7 | 7 | 19 |
| Pde | <i>Pinguicula denticulata</i> (Hedw.) Schimp. | 7 | 4 | 7 | 7 | 16 |
| Pne | <i>Poa nemoralis</i> L. | 4 | 5 | 6 | 5 | 120 |
| Ptr | <i>Poa trivialis</i> L. | 7 | 6 | 6 | 6 | 36 |
| Pmu | <i>Polygonatum multiflorum</i> (L.) All. | 4 | 5 | 7 | 6 | 169 |
| Pty | <i>Polygonum hydropiper</i> L. | 7 | 7 | 6 | 6 | 44 |
| Plo | <i>Polytrichum formosum</i> (Hedw.) G.L.Sm. | 4 | 5 | 6 | 6 | 605 |
| Pst | <i>Potentilla sterilis</i> (L.) Garcke | 5 | 5 | 5 | 5 | 26 |
| Pav | <i>Prunus avium</i> L. | 4 | 5 | 6 | 6 | 145 |
| Pse | <i>Prunus serotina</i> Ehrh. | 6 | 5 | 4,5 | 4,5 | 121 |
| Ppu | <i>Pseudocarpodum purum</i> (Hedw.) Fleisch. Ex Broth. | 8 | 5 | 6 | 2 | 48 |
| Paq | <i>Pteridium aquilinum</i> (L.) Kuhn | 6 | 5 | 3 | 3 | 646 |
| Ope | <i>Quercus petraea</i> (Mattus.) Liebl. | 6 | 6 | 3 | 4 | 258 |
| Oro | <i>Quercus robur</i> L. | 7 | 5 | 5 | 4 | 362 |
| Rre | <i>Ranunculus repens</i> L. | 6 | 7 | 6 | 7 | 25 |
| Rsq | <i>Rhynchospora squarrosa</i> (Hedw.) Warnst. | 9 | 9 | 3 | 1 | 30 |
| Rtr | <i>Rhynchospora triquetra</i> (Hedw.) Warnst. | 9 | 9 | 3 | 1 | 10 |
| Rca | <i>Rosa canina</i> L. | 6 | 5 | 7 | 6 | 16 |
| Rfr | <i>Rubus fruticosus</i> L. agg. | 6 | 6 | 6 | 6 | 905 |
| Rid | <i>Rubus idaeus</i> L. | 6 | 5 | 5 | 5 | 23 |
| Rob | <i>Rumex obtusifolius</i> L. + <i>R. sanguineus</i> L. | 7 | 5 | 7 | 9 | 47 |
| Rac | <i>Ruscus aculeatus</i> L. | 4 | 5 | 4 | 4 | 33 |
| Sca | <i>Salix caprea</i> L. | 7 | 7 | 7 | 7 | 34 |
| Sni | <i>Sambucus nigra</i> L. | 6 | 5 | 7 | 7 | 14 |
| Sno | <i>Scrophularia nodosa</i> L. | 5 | 6 | 7 | 6 | 40 |
| Ssa | <i>Scorbus aucuparia</i> L. | 6 | 6 | 3 | 4 | 91 |
| Ssy | <i>Stachys sylvatica</i> L. | 6 | 6 | 7 | 8 | 53 |
| Sgr | <i>Stellaria graminea</i> L. | 7 | 6 | 5 | 4 | 14 |
| Sho | <i>Stellaria holostea</i> L. | 5 | 5 | 6 | 6 | 149 |
| Sme | <i>Stellaria media</i> (L.) Vill. | 7 | 5 | 6 | 7 | 30 |
| Sre | <i>Stellaria nemorum</i> L. | 4 | 6 | 6 | 7 | 33 |
| Tba | <i>Taxus baccata</i> L. | 4 | 4 | 7 | 5 | 11 |
| Tsc | <i>Teucrium scorodonia</i> L. | 6 | 4 | 4 | 3 | 25 |
| Tia | <i>Thuidium tamariscinum</i> (Hedw.) B., S. & G. | 8 | 4 | 8 | 2 | 75 |
| Tpi | <i>Tilia platyphyllos</i> Scop. | 4 | 5 | 7 | 6 | 12 |
| Udi | <i>Urtica dioica</i> L. | 6 | 6 | 7 | 8 | 190 |
| Vmy | <i>Vaccinium myrtillus</i> L. | 6 | 6 | 2 | 2 | 58 |
| Vch | <i>Veronica chamaedrys</i> L. | 6 | 5 | 6 | 5 | 15 |
| Vmo | <i>Veronica montana</i> L. | 4 | 6 | 6 | 6 | 61 |
| Vsp | <i>Vicia sepium</i> L. | 6 | 5 | 6 | 6 | 34 |
| Vre | <i>Viola reichenbachiana</i> Jord. | 4 | 6 | 7 | 6 | 5 |
| Vri | <i>Viola riviniana</i> Reichb. | 6 | 5 | 5 | 4 | 16 |

Appendix 2. List of environmental variables measured in each vegetation sample and used in data analysis

| Code | Environmental variable |
|-------------|--|
| Cov 1 | Hornbeam canopy cover |
| Cov 2 | Beech canopy cover |
| Cov 3 | Sessile oak canopy cover |
| Cov 4 | Pedunculate oak canopy cover |
| Cov 5 | Hornbeam subcanopy cover |
| Cov 6 | Beech subcanopy cover |
| Cov 7 | Pedunculate oak subcanopy cover |
| Cov 8 | Hornbeam tall shrub cover |
| Cov 9 | Beech tall shrub cover |
| Cov 10 | Sycamore tall shrub cover |
| Cov 11 | Hornbeam shrub cover |
| Cov 12 | Hawthorn shrub cover |
| Cov 13 | Beech shrub cover |
| Cov 14 | Holly shrub cover |
| Cov 15 | Black cherry shrub cover |
| Cov 16 | Pedunculate oak shrub cover |
| H.I. | Humus Index |
| Surf 1 | No topsoil disturbance |
| Surf 2 | Boulder or drain |
| Surf 3 | Litter undisplaced but traces of engine trail |
| Surf 4 | Litter undisplaced, traces of engine trail and slash remains |
| Surf 5 | Litter displaced, organic soil intact |
| Surf 6 | Soil packing, litter displaced, traces of engine trails |
| Surf 7 | Litter mixed with organic soil |
| Surf 8 | Soil deposited above litter |
| Surf 9 | Organic soil displaced, exposing the mineral soil |
| Surf 10 | Engine trail packed and managed |
| Surf 11 | Soil mixed with litter |
| Surf 12 | Rut 5-15 cm deep |
| Surf 13 | Rut 16-30 cm deep |
| Surf 14 | Mineral soil visible at the bottom of ruts |
| Surf 15 | Fallen branchwood less than 10 cm diameter |
| Surf 16 | Fallen branchwood 10-30 cm diameter |
| Surf 17 | Fallen branchwood more than 30 cm diameter |
| Surf 18 | Fallen trunkwood |
| Surf 19 | Stump |
| Surf 20 | Stump with slash remains |
| Stem | Stem density |
| BA | Basal area |
| Age | Age of dominant trees |