Effect of woody substrate characteristics on epiphytic bryophyte species presence and richness

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Abstract

Bayesian models were used to analyze epiphytic bryophyte survey data from the GNB (Gestion, Naturalité, et Biodiversité) project. Species presence of the 20 most frequently occurring species, total species richness, and forest species richness were tested. Woody substrate type (living trees, branches, logs, and snags) was a predictive variable for species presence and richness; mean substrate diameter was a predictive variable for species presence. Total species richness had a strong positive response to both living trees and snags, a strong negative response to branches, and a negligible response to logs. Forest species richness responded in the same way except for a strong positive response to logs. Species presence responses to substrate types allowed for the categorizing of putative living wood and dead wood specialist species. Mean substrate diameter was not found to have a significant effect in predicting species presence. These initial findings are important first steps understanding the bryophyte functional groups present in France. From a management perspective, it also brings to light the importance of maintaining larger dead woody substrates in forests.

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Introduction

As is the case with most of Europe, forests in France have almost all experienced anthropogenic disturbance, particularly under the form of forest management (Vanbergen et al. 2005). In fact, according to France's national forest inventory, IFN (Inventaire Forestier National), only 30,000 hectares of the country's forests (<1%) have not had anthropogenic perturbation n the last 50 years (Ministère de l'Agriculture et de la Pêche, 2011).

Forest management practices for timber can be seen as deterministic disturbances of known frequency and intensity with biomass removal (Commarmot et al. 2005). Forest thinning consists of cutting and removing trees about once every ten years, while larger scale "harvests" can take place at frequencies of once every 50 to 200 years. This is in contrast to stochastic natural disturbances that vary in space, time, and intensity (McCarthy and Burgman 1995). Natural tree death and subsequent treefall and decomposition happen heterogeneously in space; while occasional, infrequent, intense disturbances such as storms cause large treefall events. Human perturbation happens against this background of natural disturbance, altering the forest disturbance regime and the resulting forest structure in various ways. The tree species community is homogenized to favor the tree species of management interest (Montes et al. 2005). Managed forests also show differences in microclimate due to lower large tree densities, resulting in less shade and humidity, and more frequent temperature fluctuations (Király et al. 2013). Along with fewer large living trees, managed forests also have less deadwood left undisturbed. There may be as little as 10% the natural levels of deadwood in Scandinavian forests (Stokland 2004), where management regimes remove all cut trees as well as large trees felled by natural causes such as storms. In France, managed forests have 27.82% the amount of deadwood as in unmanaged forests, although this difference is stronger in lowland plains forests than mountainous forests (Pernot et al. 2013).

This environmental change and loss of various kinds of woody substrates have a negative impact on biodiversity (Bengtsson et al. 2000). 20-25% of all forest species associate with dead wood at some point during their life cycle, including fungi, bryophytes, beetles, bats (Stokland 2004). Large trees, and large deadwood especially, are important habitats of rare and red-listed species (Berg et al. 1995, Nilsson et al. 2001). This loss in biodiversity is not only of concern in and of itself, but also risks having consequences on ecosystem functioning (Scherer-Lorenzen et al. 2005).

Therefore, it is in the interest of everyone to protect and foster biodiversity in managed forests. It is with this goal in mind that the GNB project was established, of which the work presented in this report is a part.

GNB

GNB (Gestion, Naturalité, Biodiversité) is a collaborative effort between multiple French organizations including IRSTEA (Institut National de Recherches en Sciences et Technologies pour l'Environnement et l'Agriculture), ONF (Office National des Forêts), RNF (Réserves Naturelles de France) and INRA (Institut National de la Recherche Agronomique). The project consists of completing plot surveys of seven taxa (vascular plants, bryophytes, fungi, bats, birds and carabid and saproxyllic beetles) throughout France in both managed and unmanaged forests (Figure 1).

Its objectives are twofold: firstly, these surveys explore the differences in biodiversity between managed and unmanaged forests. Is there recovery of biodiversity, both in abundance and in species richness, in the latter? In this case, the fact that France has forests reserves that have been under protection for different lengths of time, ranging from 20 to about 150 years, offers some unique insights on the dynamics of biodiversity recovery and change. Although "baseline" old-growth forests are not available in France to show how what a forest ecosystem would look like without human intervention, we can instead look at the difference between presently managed forests and neighboring reserves that were established at different times and therefore have had differing times of recovery. Secondly, these surveys, coupled with dendrometric measurements of forest structure such as tree size distribution, tree species, dead wood density within each plot, highlight what specific factors are correlated and appear to contribute to heightened biodiversity in unmanaged forests.

With an understanding of which factors are most linked to biodiversity, we can make more informed management decisions and focus efforts on imitating these specific aspects of unmanaged forests that are shown to be helpful in maintaining biodiversity.

For bryophytes, environmental characteristics at the substrate level were also analyzed. This allows us to explore the following questions:

1. Species presence per substrate: Do certain species favor certain woody substrate characteristics, such as size, species, substrate type, and decomposition? These initial findings will point us towards possible specialist species, although more thorough studies will be required to establish the more exact ecological nature of these preliminary specialists. The establishment of specialist species based on empirical data will be important especially for French bryology; no database currently exists in France of bryophyte ecological traits with regards to woody substrate characteristics. Resorting to British or German databases is the current solution, although there are discrepancies with the bryophyte niches described and those seen on the field in France.

2. Species richness per substrate: Is high species richness linked to certain woody substrate characteristics?

3. Spatial continuity: For the specialist species identified, does species presence probability increase when there is a high density of a preferred substrate in close proximity (at the plot level)?

4. Temporal continuity: Do indications that a preferred substrate was present in the past increase species presence probability? For example, the presence of very decomposed wood indicates that that particular woody substrate was once less decomposed and a possible habitat for saproxylic species specializing in dead wood of this previous level of decomposition.

In this report I focus on only epiphytic bryophytes and explore the first two questions described above. I will share my current findings on the effect of two woody substrate characteristics, substrate type and mean diameter, on bryophyte species presence and species richness.

Materials and Methods

Study area

Surveys were conducted in six French forests (Figure 1). Four of these (Auberive, Combe Lavaux, Citeaux, Fontainebleau) are lowland forests, while two are mountainous (Ballons Comtois, Ventron). A total of 92 plots were analyzed, divided equally between managed and unmanaged regions of each forest. A total of 1215 woody substrates were analyzed.

Sampling design:

Epiphytic bryophyte species were identified on various woody substrates on the 92 plots according to the protocol defined in the GNB project (Annex 1). Large woody substrates (living trees, snags, logs, and stumps) were randomly selected from a previous dendrometric inventory in the same plots, while branches were surveyed when encountered along three radial transects in each plot. Diameter was measured at breast height for living trees and snags, while the diameter of branches and fallen wood was measured at the substrate's median length. In cases where the substrate had an oblong cross-section, such as with very decomposed deadwood, two orthogonal diameter measurements were taken and averaged to give the mean diameter. Epiphytic bryophyte species were surveyed from the base to 2m in height on living trees and snags, over a length of 2m on logs, over the entire surface of branches, and on both the surface and sides of stumps.

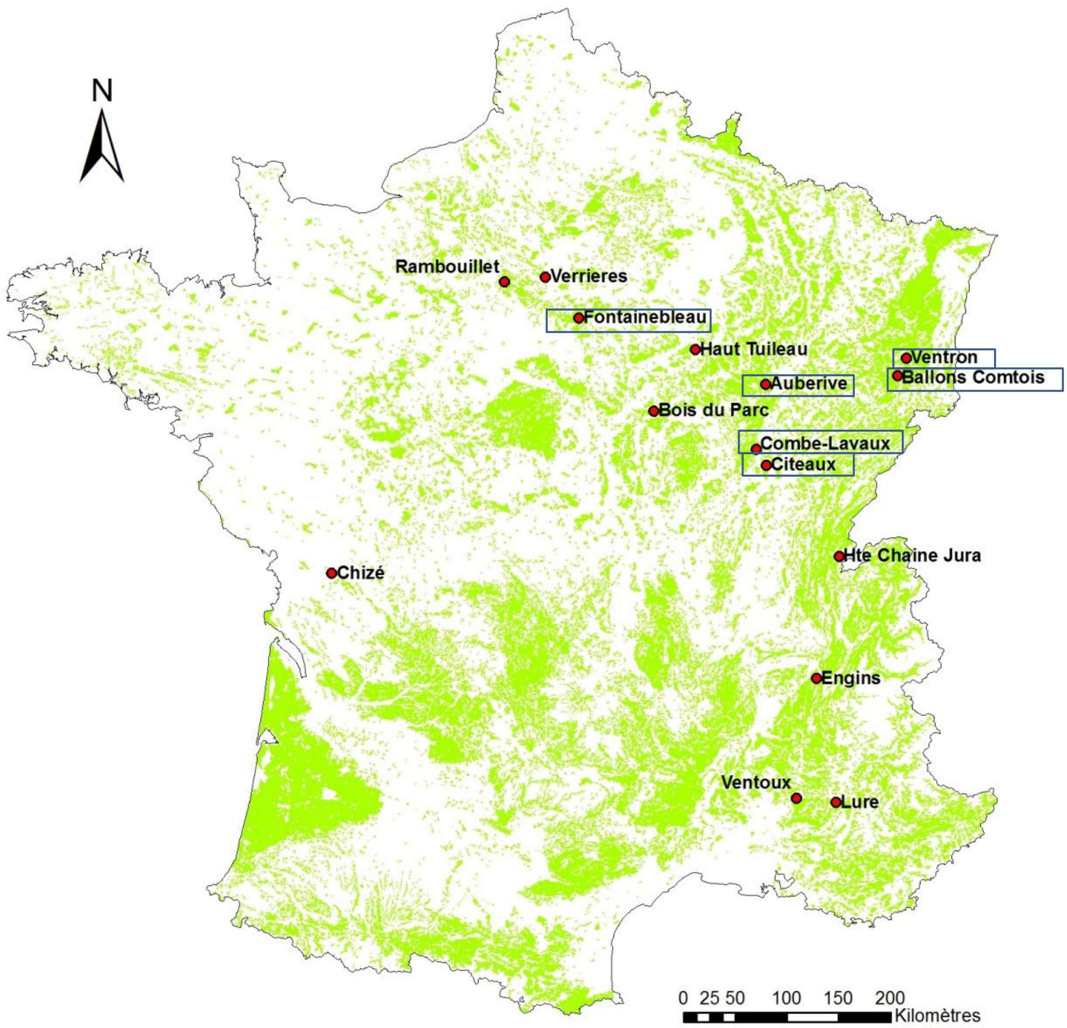

Figure 1. Location of the 15 forests studied in the GNB survey. The forests analyzed for this report are boxed.

Data analyses

Analyses were carried out in R 2.15.1 (R Core Team, 2012). Response variables were 1) total bryophyte species richness per substrate, 2) species richness per substrate of forest species as classified by Schmidt et al. (2013), and 3) individual species presence for the 20 most frequent species of the 121 bryophyte species surveyed, i.e. species observed on over 60 different logs (Table 1). Although species occurrence decreased gradually without a clear cut-off after the eighth most common species (Annex 2), these 20 species were chosen for several reasons. Firstly, this selection allowed for the comparison of congenerics of very common species to see if there are noted ecological differences between related species of differing frequency. Secondly, common species are likely to be generalists, and extending the number of analyzed species increased our chances of coming across a specialist species. Unfortunately, rare or red-listed species - who conversely are likely to be specialists (Laaka

1992) - could not be analyzed because of their necessarily low occurrence. Specialist species were determined according to criteria of habitat association similar to the work of Julliard et al. (2006) on birds.

Species code	Species	Occurrence	Bryophyte group
HYPCUP	*Hypnum cupressiforme*	1022	moss
ISOALO	*Isothecium alopecuroides*	443	moss
METFUR	*Metzgeria furcata*	407	liverwort
BRARUT	*Brachythecium rutabulum*	278	moss
DICSCOP	*Dicranum scoparium*	251	moss
RADCOM	*Radula complanata*	244	liverwort
FRUDIL	*Frullania dilatata*	194	liverwort
HOMSER	*Homalothecium sericeum*	178	moss
CHIPRO	*Chiloscyphus profundus*	98	liverwort
EURSTR	*Eurhynchium striatum*	91	moss
PTEFIL	*Pterigynandrum filiforme*	85	moss
NECCOM	*Neckera complanata*	84	moss
THUTAM	*Thuidium tamariscinum*	74	moss
ULOCRI	*Ulota crispa*	72	moss
FRUTAM	*Frullania tamarisci*	72	liverwort
ULOBRU	*Ulota bruchii*	69	moss
BRYCAP	*Bryum capillare*	67	moss
ISOMYO	*Isothecium myosuroides*	64	moss
DICMON	*Dicranum montanum*	64	moss
ORTLYE	*Orthotrichum lyellii*	61	moss

Table 1. Description of the 20 most frequent epiphytic bryophyte species analyzed for species presence.

Predictive variables were habitat characteristics at the woody substrate level: 1) substrate type (living trees, branches, dead fallen trees or logs, and dead standing trees or snags - stumps were removed from analysis on account of missing substrate characteristics in the data), and 2) mean substrate diameter. Because the focus of our analyses were characteristics at the substrate level, environmental characteristics at the forest scale such as climate and lowland versus mountainous terrain, were combined into a qualitative “forest” variable. Analyses were conducted with Bayesian models using Gibbs Sampling with the function WinBUGS (Lunn et al. 2000). Species presence probability was modeled as the logit of odds ratios (p/(1-p), where p is the species presence probability) as a linear combination of fixed and random effects. A first random effect – the plot effect – was systematically included in the models. This effect was the same in each plot, was normally distributed according to a constant variance and a covariance structure that declined exponentially with the distance between plots according to an intensity parameter. We used Bernoulli probability distributions to test species presence probabilities and a modified Poisson probability distribution to test species richness. We modeled different response types: fixed linear, where the predictive variable has a consistent effect regardless of the value of the forest variable; random linear, where the predictive variable may have different effects depending on the forest variable; or quadratic, where the response is expected to be unimodal and reach a maximum. Initial parameter values were generated randomly within a defined distribution, with iteration values of at least 50000, burn-in values of at least 5000, and the thinning parameter set at 30. Three Monte-Carlo Markov chains (MCMC) were set to converge, and models were considered to have well converged when the effect number of all parameters equaled at least 500.

Model selection

Models were first tested with only substrate type and forest effects as predictive variables. Values of DIC (deviance information criterion), an analogue of AIC (Akaike information criterion) used to compare the fit of Bayesian models, were calculated and compared to choose whether substrate type was best modeled as a fixed linear response or as a randomized linear response. The DIC values compared were not those calculated during model generation but were calculated apart to account for the unique characteristics of overdispersed count data in Bayesian models (Millar 2009).

Once the best model (fixed linear or random linear) for substrate type was determined with regards to each of the three response variables (species presence, total species richness, forest species richness), the combined effects of forest, substrate type and mean substrate diameter were analyzed for species presence. Since mean substrate diameter is a quantitative variable, its effect was tested as a fixed linear response or as a quadratic response. DIC values were calculated to determine which response type best suited mean diameter. This results with the selection of a model in which 1) substrate type has either a fixed linear or random linear structure, and 2) mean diameter has either a fixed linear or quadratic structure.

Magnitude of variable response

While DIC determined the model that best fit the data, the effect magnitude and significance of each predictive variable on the response variables were also calculated. This allows a richer interpretation than with solely statistical significance (Barbier et al. 2009). In particular, it allows us to distinguish whether effects are judged negligible or not, and whether the effects in non-negligible cases are positive or negative. For substrate type, the effect signifies the multiplicative factor by which the response variable will increase or decrease when comparing the mean value of the entire data set to a specific substrate type. For mean diameter, the effect shows how much the response variable will change when mean diameter is increased by one standard deviation (in our case, 23.8617cm). The effect magnitude shows whether or not the response distribution is negligible according to two arbitrarily defined odds ratio factors thresholds. In the case of species presence, response qualifies as weakly positive (+) or negative (-) when 95% of the simulated effects change the response variable's odds ratio by a factor of +.2 or -.2, respectively. The threshold for strongly positive (++) or negative (--) effects is a factor of +.4 or -.4, respectively. A negligible effect (0) is designated when 95% of simulated effects fall within the range of -.4 to +.4, such that a clear effect in one direction or another cannot be determined. A very negligible effect (00) is designated when 95% of simulated effects fall within the range of -.2 to +.2, such that the effect is both unclear and weak (Table 2). These values were chosen as opposed to threshold values of ± .1 and ± .2 because these lower values corresponded to differences in species presences of less than 5% when at initial frequencies of 50%. Species richness thresholds were ± .1 and ± .2 for weak and strong effects, respectively, as in Barbier et al. 2009.

Symbol	Meaning	95% simulated response distribution of species presence	95% simulated response distribution of species richness
++	Strong positive response	response > .4	response > .2
+	Weak positive response	.2 ≤ response	.1 ≤ response
0	Negligible response	-.4 ≤ response < .4	-.2 ≤ response < .2
00	Very negligible response	-.2 ≤ response < .2	-.1 ≤ response < .1
-	Weak negative response	response < -.2	response < -.1
--	Strong negative response	response < -.4	response < -.2

Table 2. Description of effect magnitudes. The two thresholds in odds ratio factors for weak and strong effects are ± .2 and ± .4 for species presence, and ± .1 and ± .2 for species presence.

Results

Responses of species presence and species richness to woody substrate type

In analyses of species richness, DIC comparisons showed a preference for models with substrate type included over null models; species richness differed depending on substrate type (Table 3). When substrate type was included, models predicting total species richness more closely fit the data when substrate type was considered as a random linear variable. For forest species richness, on the other hand, substrate type showed a better fit when treated as a fixed linear variable.

For species presence probabilities, DIC comparisons showed that for the majority of species tested (13/20), support type was best modeled as a fixed linear variable. For *H. cupressiforme, D. scoparium,* and *F. tamarisci*, the best fit model was with substrate type as a random linear effect. The best fit for *T. tamariscinum, I. myosuroides, D. montanum, O. lyellii* was the null model, where the only predictive variable present was the forest variable.

Species code	DIC null	DIC fixed linear	DIC random linear
Forest species richness	3578.026	**3289.172**	3292.866
Total species richness	5647.694	5266.995	**5238.501**
HYPCUP	1260.739	1247.049	**1216.691**
ISOALO	1323.369	**1002.696**	1012.109
METFUR	1261.003	**1067.747**	1079.595
BRARUT	1143.409	**1070.099**	1072.502
DICSCOP	1076.0195	985.2932	**974.7243**
RADCOM	1002.4465	**860.4988**	891.2604
FRUDIL	988.7420	**882.6711**	902.5636
HOMSER	922.7875	**858.0902**	874.1981
CHIPRO	521.9893	**450.3636**	452.9286
EURSTR	501.9680	**485.9962**	528.9237
PTEFIL	362.4812	**317.2156**	366.0323
NECCOM	519.5576	**490.7345**	535.5911
THUTAM	**467.6048**	467.9118	590.5722
ULOCRI	541.3285	**515.1394**	556.3818
FRUTAM	419.5590	410.7674	**387.1093**
ULOBRU	450.5168	**438.5331**	612.1801
BRYCAP	384.5150	**371.3145**	414.2398
ISOMYO	**373.0707**	394.3658	452.724
DICMON	**381.7772**	390.4124	428.5431
ORTLYE	**416.1115**	420.1131	496.4617

Table 3. DIC values for models of species presence and species richness as a response to forest and woody substrate type. The lowest DIC values are marked in bold.

When modeled as a fixed linear variable, the effects of woody substrate types on both total species richness and forest species richness are similar in magnitude, although estimator values were almost twice as high for forest species richness (Table 4). Living trees and snags both have a strong positive effect on both sets of species richness, while branches had a strong negative effect. For logs, total species richness has a negligible response, while forest species richness has a weak but positive response.

Response Variable	Living tree	Branches	Logs	Snags
Total species richness (all forests)	0.286 [0.23;0.344] (++)	-0.774 [-0.867;-0.684] (--)	0.135 [0.0366;0.227]	0.354 [0.276;0.428] (++)
AUB	0.38 [0.256;0.527] (++)	-0.621 [-0.797;-0.43] (--)	0.0226 [-0.298;0.31]	0.227 [-0.0583;0.442]
BC	0.224 [0.117;0.336] (+)	-0.867 [-1.07;-0.69] (--)	0.32 [0.139;0.49] (+)	0.328 [0.2;0.462] (++)
FBL	0.389 [0.284;0.495] (++)	-0.85 [-1.02;-0.698] (--)	0.0352 [-0.142;0.205] (0)	0.428 [0.304;0.559] (++)
CIT	0.0279 [-0.154;0.218] (0)	-0.559 [-0.824;-0.313] (--)	0.236 [-0.056;0.5]	0.298 [0.0966;0.494] (+)
VEN	0.0181 [-0.118;0.155] (0)	N/A	-0.213 [-0.407;-0.0355]	0.196 [0.0572;0.349]
CL	0.425 [0.232;0.662] (++)	-0.805 [-1.07;-0.561] (--)	0.323 [-0.212;0.78]	0.077 [-0.356;0.404]

Forest species richness (all forests)	0.454 [0.349;0.56] (++)	-1.41 [-1.64;-1.2] (--)	0.305 [0.137;0.464] (+)	0.655 [0.522;0.786] (++)
AUB	0.492 [0.338;0.684] (++)	-1.36 [-1.63;-1.05] (--)	0.232 [-0.224;0.598]	0.64 [0.344;0.9] (++)
BC	0.444 [0.306;0.584] (++)	-1.46 [-1.77;-1.21] (--)	0.408 [0.148;0.673] (+)	0.617 [0.433;0.8] (++)
FBL	0.503 [0.36;0.692] (++)	-1.41 [-1.71;-1.16] (--)	0.247 [-0.076;0.528]	0.668 [0.455;0.878] (++)
CIT	0.395 [0.158;0.554] (+)	-1.47 [-1.8;-1.19] (--)	0.442 [0.0506;0.846] (+)	0.642 [0.392;0.922] (++)
VEN	-0.0077 [-0.167;0.151] (0)	N/A	-0.269 [-0.54;-0.0329]	0.277 [0.0977;0.492] (+)
CL	0.457 [0.266;0.645] (++)	-1.38 [-1.66;-1.02] (--)	0.437 [-0.0872;0.968]	0.51 [-0.0288;0.778]

Table 4a, b. Effects of substrate type on a) total species richness and b) forest species richness. The 95% confidence interval is in brackets. The odds ratio factor thresholds shown by the symbols in parentheses are as follows: (++) = .2; (+) = .1; (-) = -.1 (--) = -.2.

When modeled as a random linear variable, the effect of branches on species richness stayed strongly negative in both cases - branches in the Ventron forest were removed from the analysis because of a lack of information on other substrate characteristics like substrate diameter. Substrate type effects showed some differences between forests for both total forest species richness and forest species richness, but the discrepancies are more pronounced for total species richness. For this response variable, living trees and snags have a weaker effect magnitude (+, 0, or uncertain) for three to four out of the six forests when substrate type is modeled as a random linear effect. Meanwhile, in the fixed linear model living trees and snags both showed strongly positive effect magnitudes (++). These differences also exist in forest species richness, but effect magnitude here differs for only two out of the six forests. The inconsistent responses of woody substrate type on total species richness show that each forest has a particular effect. This is further supported by the DIC values favoring the random linear structure. Therefore, we chose to model total species richness with the woody substrate type variable as a random linear effect, while forest species richness will be modeled with woody substrate type as a fixed linear effect.

Species code	Living trees	Branches	Logs	Snags
HYPCUP	-0.0877 [-0.319;0.14] (0)	-0.5 [-0.765;-0.238] (-)	0.204 [-0.187;0.609]	0.38 [0.0408;0.752]
ISOALO	1.79 [1.5;2.07] (++)	-2.44 [-2.99;-1.93] (--)	-0.408 [-0.962;0.119]	1.07 [0.693;1.45] (++)
METFUR	1.61 [1.31;1.95] (++)	-2.02 [-2.77;-1.39] (--)	-0.272 [-0.862;0.281]	0.692 [0.289;1.1] (+)
BRARUT	-0.357 [-0.601;-0.119]	-1.13 [-1.48;-0.809] (--)	1.13 [0.773;1.48] (++)	0.364 [0.03;0.685]
DICSCOP	0.3 [0.0339;0.589]	-1.82 [-2.43;-1.31] (--)	0.269 [-0.142;0.689]	1.26 [0.934;1.6] (++)
RADCOM	1.75 [1.4;2.17] (++)	-0.766 [-1.31;-0.258] (-)	-0.181 [-0.964;0.493]	-0.782 [-1.57;-0.123] (-)
FRUDIL	1.68 [1.27;2.22] (++)	-0.457 [-1.06;0.193]	-1.19 [-2.63;-0.212] (-)	0.00787 [-0.708;0.697]
HOMSER	0.931 [0.631;1.26] (++)	-1.01 [-1.53;-0.539] (--)	0.412 [-0.112;0.901]	-0.317 [-0.892;0.19]
CHIPRO	-1.16 [-1.65;-0.704] (--)	-1.08 [-1.74;-0.514] (--)	1.2 [0.748;1.64] (++)	1.06 [0.639;1.48] (++)
EURSTR	-0.675 [-1.1;-0.243] (-)	-0.791 [-1.32;-0.299] (-)	0.504 [-0.156;1.14]	0.962 [0.426;1.5] (++)
PTEFIL	1.75 [1.19;2.44] (++)	-1.29 [-2.92;-0.267] (--)	-0.583 [-1.78;0.365]	0.21 [-0.541;0.981]
NECCOM	1.14 [0.599;1.78] (++)	-1.98 [-3.45;-0.929] (--)	0.674 [-0.28;1.53]	0.221 [-0.701;1.06]
THUTAM	0.387 [-0.0997;1.01]	-0.547 [-1.31;0.203]	-0.745 [-2.31;0.234]	0.962 [0.292;1.71] (++)
ULOCRI	1.48 [0.831;2.45] (++)	0.844 [0.0657;1.9]	-1.36 [-3.9;0.0192]	-0.854 [-2.36;0.406]
FRUTAM	55 [4.22;174] (++)	52.2 [1.49;172] (++)	-161 [-519;-8.6] (--)	53.8 [2.91;173] (++)
ULOBRU	6.78 [1.46;23.7] (++)	5.44 [0.0713;22.4] (+)	-17.5 [-68.2;-1.65] (--)	5.26 [-0.218;22.2]
BRYCAP	0.674 [0.234;1.14] (+)	-0.871 [-1.66;-0.212] (-)	0.177 [-0.595;0.86]	0.0554 [-0.635;0.69]
ISOMYO	54.3 [3.66;177] (++)	-162 [-531;-10.1] (--)	53.4 [2.79;177] (++)	54.4 [3.73;177] (++)
DICMON	0.00213 [-0.527;0.635]	-1.59 [-3.1;-0.594] (--)	0.279 [-0.511;1.05]	1.36 [0.794;2] (++)
ORTLYE	54 [4.09;177] (++)	52.9 [2.99;175] (++)	51.9 [1.9;174] (++)	-159 [-526;-8.85] (--)

Table 5. Effects of substrate type on species presence probability. The 95% confidence interval is in brackets. The odds ratio factor shown by the symbols in parentheses are as follows: (++) = .4; (+) = .2; (-) = -.2; (--) = -.4.

Despite the different preferences for substrate type responses according to DIC values, we chose to analyze the effect of substrate type on species presence as a fixed linear variable for ease of comparison between the 20 different species (Table 5). General trends for species presence by substrate type showed that species are more likely to be found on living trees and snags, and less on branches. Proposed living tree specialists are species that show a positive correlation to living trees and a negative or negligible correlation to either snags or logs; these species include *R. complanata, F. dilatata, P. filiforme, N. complanata, U. crispa, U. bruchii*, and *B. capillare*. Proposed dead wood specialists are species showing a disinclination towards living trees and a preference for either logs or snags; these species include *C. profundus* and *E. striatum*; *B. rutabulum* and *D. scoparium* and may be log and snag specialists, respectively. *I. myosuroides* particularly avoided branches and *O. lyellii,* snags.

Responses of species presence to woody substrate type and mean substrate diameter

The effect of mean substrate diameter on species presence was modeled both as a fixed linear effect and a quadratic effect (Table 6). The quadratic response type had better DIC values for the majority of species (13/20). When compared with models without mean diameter (Table 3), DIC values preferred models with mean diameter in only six species (*N. complanata*, *F. tamarisci*, *U.bruchii*, *I. myosuroides*, *D. scoparium*, and *O. lyellii*); these models all had mean diameter modeled as a quadratic response. The response of species presence probability to substrate type in models containing both substrate type and mean substrate diameter variables were very similar in effect magnitude as compared to models testing only substrate type (not shown). The numeric value of the effects of the multivariate model were slightly weaker, as expected since these models also had mean substrate diameter to explain a portion of the variation in species presence probability. Other differences between substrate effects when models include the mean diameter variable include the weakening of the effect magnitude of branches in *P. filiforme* and *B. capillare*, and the weakening of the effect magnitude of snags in *T. tamariscinum*. In one species, *U. bruchii*, including the mean diameter variable caused the positive effect magnitudes of branches and snags to increase from (+) and (0) to (++).

Species code	DIC fixed linear	DIC quadratic
HYPCUP	**1248,148**	1250,659
ISOALO	1013,124	**1008,238**
METFUR	1074,617	**1070,964**
BRARUT	1083,595	**1071,346**
DICSCOP	985,5882	**983,0569**
RADCOM	870,9629	**867,963**
FRUDIL	**886,1184**	891,8179
HOMSER	**859,8117**	881,7041
CHIPRO	**455,2288**	463,5708
EURSTR	**488,9391**	489,7188
PTEFIL	337,5843	**326,4668**
NECCOM	491,0696	**485,2287**
THUTAM	**486,8303**	510,6602
ULOCRI	**532,6015**	556,4199
FRUTAM	396,2314	**364,2911**
ULOBRU	462,3377	**435,5014**
BRYCAP	481,9592	**424,611**
ISOMYO	363,9044	**332,033**
DICMON	397,8193	**375,3009**
ORTLYE	412,6563	**409,0964**

Table 6. DIC values for models of species presence as a response to forest, woody substrate type, and mean diameter. The lowest DIC values are marked in bold.

All effects of mean substrate diameter, once substrate type was accounted for, on species presence were negligible or inconclusive (Table 7). The one exception is *P. filiforme* whose presence was found to increase slightly (+) when substrate diameter is increased from initially small values.

Species code	Diameter (fixed linear)	Diameter (quadratic)		
		Quantile 1	Median	Quantile 3
HYPCUP	1,03 [0,866;1,23] (00)	-	-	-
ISOALO	-	1,17 [0,784;1,8]	1,17 [0,911;1,5] (0)	1,16 [0,972;1,38] (0)
METFUR	-	1,14 [0,764;1,69]	1,14 [0,902;1,46] (0)	1,15 [0,969;1,37] (0)
BRARUT	-	1,03 [0,666;1,61]	1,01 [0,775;1,31] (0)	0,984 [0,805;1,2] (0)
DICSCOP	-	0,886 [0,572;1,36]	0,949 [0,723;1,23] (0)	1,01 [0,844;1,21] (00)
RADCOM	-	1,09 [0,686;1,83]	1,05 [0,801;1,39] (0)	1,01 [0,794;1,27] (0)
FRUDIL	0,961 [0,776;1,17] (0)	-	-	-
HOMSER	1,08 [0,882;1,32] (0)	-	-	-
CHIPRO	0,941 [0,689;1,24] (0)	-	-	-
EURSTR	0,939 [0,655;1,34] (0)	-	-	-
PTEFIL	-	2,96 [1,15;8,9] (+)	1,68 [1,05;2,77]	0,994 [0,647;1,45]
NECCOM	-	1,14 [0,642;2,06]	1,26 [0,858;1,85]	1,38 [1,03;1,83]
THUTAM	1,07 [0,756;1,51] (0)	-	-	-
ULOCRI	0,811 [0,586;1,11]	-	-	-
FRUTAM	-	1,3 [0,669;2,55]	1,36 [0,89;2,14]	1,43 [1,07;1,9]
ULOBRU	-	0,602 [0,3;1,28]	0,834 [0,549;1,27]	1,13 [0,771;1,6]
BRYCAP	-	1,47 [0,699;3,46]	1,27 [0,788;2,1]	1,1 [0,785;1,54] (0)
ISOMYO	-	1,05 [0,49;2,25]	1,21 [0,74;1,99]	1,38 [0,998;1,91]
DICMON	-	0,985 [0,418;2,49]	0,959 [0,587;1,6]	0,937 [0,648;1,32] (0)
ORTLYE	-	2,64 [1,02;8,41]	1,51 [0,925;2,5]	0,901 [0,428;1,58]

Table 7. Effects of mean substrate diameter on species presence probability. Mean diameter was shown as fixed linear or quadratic depending on the DIC results in Table 6. The 95% confidence interval is in brackets. The odds ratio factor shown by the symbols in parentheses are as follows: (++) = .4; (+) = .2; (-) = -.2; (--) = -.4; (0) = 95% of simulated effects fall between -.4 and -.4; (00) = 95% of simulated effects fall between -.2 and -.2.

Discussion

Model comparisons for species richness

When modeled as either fixed linear or random linear, the woody substrate type variable's response type of best fit differed between total species richness and forest species richness. For total species richness, substrate type was best modeled as a random linear variable because substrate types had different effects depending on the forest. This could be an indication of the beta species diversity between forests if these differences between forests are due to different bryophyte communities in each forest responding to substrate types in different ways. Conversely, if bryophyte communities in each forest are very similar, the differences in woody substrate type effects may come from environmental differences between forests that in turn alter the capacity of substrates to sustain of bryophyte species. This has been shown to be the case for vascular plants (Zilliox and Gosselin 2014). Forest species richness's preference for substrate type as a fixed linear variable suggests that the different forests' environmental characteristics did not greatly impact woody substrate type effects. Forest species are a smaller group, of more particular ecological characteristics, so it could be expected that forest species communities respond similarly from one forest to another, even if these communities have high beta species diversity between forests.

Substrate effects on species richness

For the effect of each substrate type on species richness, we see that logs have a positive effect on forest species diversity, but a negligible effect on total species richness. This could denote a difference in the ecology of forest species compared to all epiphytic bryophytes. We may expect this difference in forest species diversity if it were particularly rich in saproxylic species that associate with dead wood, but of the 69 species comprising of the forest species subgroup (as classified by Schmidt et al. 2013 for Germany), only 23 species are particularly associated to dead wood (as classified by Hill et al. 2007 for Britain Isles). Therefore it is not clear why there is a particular preference for logs in forest species richness.
This could be due to the fact that the databases of ecological attributes we used are not completely accurate for French forests and the bryophytic associations therein.

Meanwhile, branches had a consistent negative effect on species richness compared to the strongly positive effects of living trees and snags. The difference between branch, snag, and log effects brings to bear the importance of substrate size on species richness. A question for forest management practices is how much and what kind of dead wood to leave behind when removing trees to mitigate biodiversity loss. These findings suggest that branches are not an optimal woody substrate to leave behind, but that larger standing or fallen dead wood offer a stronger biodiversity benefit.

Model comparisons for species presence:

Although the 20 species tested for species presence did not all prefer models with support type as a fixed linear variable, this response was used for all species to streamline comparisons. Furthermore, three of the four species preferring the null model, where substrate type was not taken into account – *I. myosuroides* , *D. montanum* ,and *O. lyellii* – were the three least frequent species of the chosen set. These species were simply never observed in certain forests; *I. myosuroides*, for example, was entirely absent in Aubrive, Ballons Comtois, and Citeaux – three of the six forests surveyed. In such cases, the forest variable would be very indicative of species presence probability, which may explain why substrate type did not further explain the variation in these species according to the DIC values.

It is worth mentioning that while DIC offers insight on which model structure best fits the data, it is also important to consider response magnitude – even more so for conservation and management practices. Decisions that affect the system are done in situ without complete certainty or information (McCarthy and Burgman 1995). The role of the forest manager is one of compromise and taking risks; therefore, a statistically significant parameter that has a weak response may be of less interest from a management perspective than a less statistically certain parameter with a large response.

Substrate effects on species richness and species presence

As expected from the results on species richness, almost all individual species tested responded negatively to branches. This could an indication of a preference for substrates of larger size, because branches have the smaller surface areas than other substrates and may be able to sustain fewer species. In this case, we would expect an effect of diameter in the models that include substrate diameter as a predictive variable, but this turns out to not be the case (see next section).

Three species responded positively to branches: *F. tamarisci, U.bruchii,* and *O. lyellii.* However, each of these species also associated positively to living trees. It is therefore possible that seeing these species on fallen branches is a result of them colonizing branches in living tree canopies, before the branch fell.

A question we asked was whether congenerics would fall into the same prospective specialist group. The findings had mixed results in this regard. Both *U. crispa* and *U.bruchii* appeared as living tree specialists, whereas only one species of the other genera with two species represented (*Isothecium, Frullania,* and *Dicranum*) appeared as a specialist. Of these three pairs of species, the rarer species was the specialist in only one case, with *I. myosuroides* appearing as a branch avoider. The living wood specialist *F. dilatata* and the dead wood specialist *D. scoparium*, on the other hand, were more frequent than their more generalist congenerics. Studies on species presence according to wood decomposition reveal similar specialist groups for the species mentioned (Odor and van Hees 2004, Sabovljevic et al. 2010).

Prospective specialist species found in these analyses are not final definitions of ecological functional groups. To fully understand the unique ecology of epiphytic bryophyte species in French ecosystems, we would need to do more pointed studies on these particular species and determine their preferred habitats. The broad overview of the GNB project and my analyses thereof allows us to pinpoint species of interest that may be specialists.

Mean diameter effects on species richness

Curiously, mean substrate diameter did not show a positive non-negligible effect in species presence when increased by a notable 23.8617cm, despite our expectations to the contrary (see also Király et al. 2013, Heilmann-Clausen et al. 2005). The only species to show a non-negligible response to diameter was *P. filiforme.* A preference for larger diameters may be expected for species for which branches had a strong negative effect on species presence because branches are the smallest substrate type. However, *P. filiforme* was one of the few species to *not* have a negative response to branches.

The inherent repartitioning of substrate diameters among the different substrate types may in fact be the reason why we don't see an effect in the diameter variable. The maximum mean diameter of branches is 27cm, while for the other substrate types we may see mean diameter measurements from 30cm to 158cm. Therefore, it is possible that the negative effects seen in branches are an inadvertent combination of both substrate effect and small diameter. If this is the case, it would explain why the diameter variable explains so little additional variance after substrate type had been taken into account. To address this, it may be worth testing the effect of mean substrate diameter alone, without the effect of substrate type. Another possibility is to add an interaction variable between diameter and substrate type. This way, we may be able to determine whether – and if so, how – diameter effects change depending on the substrate type. In this case, for example, we may expect branches to still have a generally negative effect on species presence, but for large branches to have a more positive effect than small branches.

An additional problem encountered had to do with the lower ranges of diameter measurements between substrate types. According to the GNB protocol (Annex 1), logs and snags were defined as substrates measuring at least 30cm in diameter, but our data shows the logs and snags with diameters inferior to this threshold, indicating erroneously labeled branches. This error will be corrected for in future analyses. That said, this accidental blurring of substrate type effects did not prevent us from seeing a clear difference between branches and other substrate types.

Prospective analyses: next steps

As of the current writing of this report, there is still over a month in my internship during which I will continue working on this project. During this time, I will continue to explore different model structures and predictive variables to model species richness and species presence. The different response types tested so far have been fixed linear, random linear, and quadratic. Another response type for quantitative variables is the threshold response, wherein the effect of the predictive variable on the response variable stays constant up until a certain value, after which the effect jumps up or down. For example, this type of model would predict that species richness would not change with mean substrate diameter until the diameter was of a certain minimal, or threshold, value. A last possible response type for quantitative variables is the sigmoid response. Here, the effect on the response variable encounters first a lag phase as the predictive variable increase, then rises sharply at an inflection point, then finally reaches a plateau. This can be seen as a smoother, less sudden presentation of the threshold response. This more gradual response may be more biologically accurate and may provide insight on the dynamics of species richness and presence indicators. Conversely, threshold responses are of interest for management purposes, because their delineation of when an effect increases offers forest managers clear goals.

Along with different response types, there are different possible predictive variables at the substrate level to test. Although logs and snags are necessarily dead wood, an indicator of interest is the level of decomposition of the woody substrate. Different species are linked to certain decomposition stages (Odor and Van Hees 2004, Sabovljevic et al. 2010, Andersson and Hytteborn 1991). Dead woody substrates are therefore subject to species turnover as substrates decompose (Botting and DeLong 2009), and individual species presence as well as species assemblies can be studied as a function of progressive decomposition to determine saproxylic specialists.

The decomposition of the tree bark is of specific interest for studying bryophyte ecology. As nonvascular plants without a root system, bryophytes are sensitive to desiccation (Barkman 1958, Söderström 1987), and the capacity of bark to retain water is beneficial to epiphytic bryophytes (Hauck et al. 2000). Therefore, as bark degrades and becomes less present on further decomposed substrates, we can expect to see changes in species composition from species associated with living trees covered in bark to more saproxylic specialists colonizing bare wood (Jansova & Soldan 2006, but see also Botting and DeLong 2009)

We used diameter as the measure of substrate size in our current models, but it is possible to use substrate surface area or volume instead. Since epiphytic bryophytes colonize the habitable surface of a substrate, it is possible that surface area is the most telling indicator. This consideration may give a more nuanced understanding on the effects of branches, for example: if surface area is an important indicator of species presence or richness, then both diameter and branch length, which can vary, must be taken into account.

Another variable to consider is the tree species of the woody substrate. As well as having different bark texture and chemistry (Barkman 1958, Hauck and Javkhlan 2009), the different evolutionary histories of tree species allows for unique associations between epiphytic bryophytes and host trees, which can be explored for both living trees and dead woody substrates.

While decomposition is a characteristic at the substrate level, the effect of spatial continuity and variety of decomposition for species richness and species presence can be analyzed at the plot level. Possible results of spatial continuity have important implications on future forest management practices. From a logistical point of view, it is much easier to consider felling trees of needed sizes in a single zone to leave a concentrated region of deadwood that may be left undisturbed and allowed to decompose. This could be the case if colonization is only determined by habitat availability, such as when there are a high number of inactive propagules dispersed throughout the environment, waiting only the right conditions. However, if spatial continuity turns out to be an important variable for species richness, a more concerted effort will be required to assure the presence of woody substrates of varying degrees of decomposition throughout the forest. This is much more likely for ephemeral species or species with limited dispersal capacities.

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Annex 1 : GNB protocol of bryophyte surveys

PROTOCOLE BRYOPHYTES

Projet Gestion, Naturalité, Biodiversité

Résumé

But : Ce protocole est destiné à inventorier les bryophytes, un des 7 groupes taxonomiques étudiés dans le cadre du projet Gestion, Naturalité, Biodiversité (GNB ; https://gnb.cemagref.fr/), dont le but est de quantifier la réponse de la biodiversité à l'exploitation forestière en comparant des parcelles exploitées et des parcelles non exploitées.

4 types de bryophytes sont étudiés

- Bryophytes terricoles présentes sur la terre nue
- Bryophytes humicoles présentes sur les humus
- Bryophytes épixyliques présentes sur les arbres morts
- Bryophytes corticoles présentes sur les écorces des arbres

Supports : Les bryophytes sont inventoriées sur les arbres vivants et le bois mort debout ou au sol quelle que soit l'essence forestière. Ces supports sont préalablement tirés au sort à partir de l'inventaire dendrométrique. Les espèces terricoles et humicoles, quant à elles, sont relevées sur 3 cercles de 2 mètres de rayon ainsi que sur une assiette de chablis. Enfin, sur l'ensemble de la placette, un inventaire complémentaire de 30 minutes est réalisé, notamment sur des zones intéressantes telles que rochers, houppiers tombés au sol ou essences forestières peu communes (supports qui auraient pu passer entre les mailles du tirage au sort).

Période

Les relevés sont à réaliser de préférence de mi-avril à mi-juin et de septembre à octobre, au moment de la saison de reproduction qui est variable selon les espèces, afin d'observer les capsules souvent essentielles pour passer du genre à l'espèce.

Principe du travail

Le protocole s'appuie sur les placettes GNB de 20 m de rayon définies dans le cadre du protocole "*Medd : protocole de suivi des espaces naturels protégés*" (Bruciamacchie, 2005)[1]. Deux principaux types de relevés sont effectués sur chaque placette :

- Relevés de la diversité spécifique sur des supports de différentes natures
    - 5 relevés sur du gros bois vivant
    - 3 relevés sur des petits bois vivants
    - 5 relevés sur du gros bois mort au sol
    - 5 relevés sur des souches
    - 5 relevés sur des chandelles

    } Préalablement tirés au sort à partir de l'inventaire dendrométrique*

    - 3 relevés au sol
    - 5 relevés sur des petits bois morts

    } Sur les transects 0 gr, 133 gr et 267 gr

    - 1 relevé sur une assiette de chablis

    } La plus proche du centre de la placette

*NB : Le tirage au sort est surnuméraire afin de parer aux imprévus (arbre tombé, billon de bois mort déplacé, etc…).

- Inventaire complémentaire chronométré de 30 min sur l'ensemble de la placette

[1] Bruciamacchie M., 2005. *Protocole de suivi d'espaces naturels protégés.* ENGREF - MEDD, Nancy, 40 p.

Il est conseillé de travailler en binôme. L'un prend les notes et met les échantillons sous enveloppe pour les analyses en laboratoire tandis que l'autre prospecte : cela permet à l'observateur de garder l'œil en continu sur le support à inventorier.

Saisie des données :

L'opérateur dispose de 2 fiches :

- La fiche "dendro" est une copie du relevé dendrométrique. Elle permet de localiser sur le terrain les supports, tirés au sort, à inventorier. Elle indique les caractéristiques de ces supports de la manière suivante :

Massif	Code du massif étudié (ex : Ventron => VEN)
Numpla GNB	Code identifiant la placette GNB
Essence	Code essence
Type objet	Nature et numéro de la pièce étudiée (ex : bois vivant => BV, arbre mort debout => BMD, bois mort au sol=> BMS)
Type BM	Précision par rapport au type de bois mort (ex : arbre avec houppier => A, chandelle => V, souche => S) et pour le type de bois vivant (ex : billon relié à un arbre presque entier ou à une galette => C, rémanent issu de l'exploitation => E)
Azimut	Valeur numérique de l'azimut de l'arbre depuis le centre de la placette exprimé en grades entre 0 et 400
Distance	Distance en mètres entre l'objet et le centre de la placette
Diam1	Valeur numérique donnée en cm. Elle correspond à la première mesure du diamètre de l'objet
Diam2	Valeur numérique donnée en cm. Elle correspond à la seconde mesure du diamètre de l'objet
Diam med	Valeur numérique donnée en cm. Elle correspond au diamètre médian pour les BMS de grande taille
Longueur	Valeur numérique donnée en m. Elle correspond à la longueur de la pièce pour BMS ou à la hauteur de la pièce pour MV

- La fiche "saisie bryo" (**Annexe I**) est utilisée pour établir la liste des espèces présentes sur chacun des supports ainsi que leur abondance.
  Lorsque les supports présentent des compartiments distincts, ils font l'objet de plusieurs relevés (un par compartiment) : la notion de support désigne la pièce étudiée (bois mort debout, souche, bois vivant...etc.) alors que la notion de compartiment correspond à une subdivision du support (tronc/branche pour les arbres debout, flanc/ section pour les souches). La légende des colonnes est la suivante :

Équipe	Nom des personnes réalisant les relevés
Date du relevé	Date de réalisation du relevé
Heure début	Heure de début du relevé
Heure fin	Heure de fin du relevé
Code massif	Code identique au code "massif" de la fiche "dendro"
Parcelle	Désignation du numéro de la parcelle forestière
Code placette	Code identique au code "numpla_GNB" de la fiche "dendro"
Durée	Durée totale de l'inventaire
Sol/arbre	Inscrire "S" pour les relevés effectués au sol et "A" pour ceux effectués sur les arbres
Type objet (support)	Reporter le code "type objet" de la fiche "dendro" pour ce qui est issu du tirage au sort. Sinon indiquer - P1, P2, P3,… pour les 5 petits bois morts au sol - AC pour l'assiette de chablis - S1, S2, S3,… pour les 3 relevés au sol

Compartiment T/B	Inscrire "T" pour les bryophytes observées sur le tronc et "B" pour celles observées sur une branche
Type BM	Ne concerne que les bois morts debout et les bois morts au sol Reporter le code de la colonne "Type BM" de la fiche "dendro" Pour BMD (ex : arbre avec houppier => A, chandelle => V, souche => S) Pour BMS (ex : billon relié à un arbre presque entier et à la galette => C, rémanent issu de l'exploitation => E)
BM F/S	Pour le bois mort de type souche, inscrire "S" pour les relevés effectués sur la section et "F" pour ceux effectués sur les flancs
N° transect	Inscrire le numéro de l'azimut du transect (0, 133 ou 267 gr) pour les bryophytes au sol et sur les petits bois morts
Surf	Classe de surface occupée (en %) par l'ensemble des bryophytes sur surface étudiée. On adoptera les classes suivantes adaptées de Bardat et Aubert (2007) : ➢ classe 0 : aucune bryophyte observée ➢ classe I : recouvrement < 5 % ➢ classe II : recouvrement 5 % ≤ R < 25 % ➢ classe III : recouvrement 25 % ≤ R < 50 % ➢ classe IV : recouvrement ≥ 50 %
Nom taxon	Nom des taxons identifiés sur les supports analysés. Les espèces sont notées autant de fois qu'elles sont présentes sur des supports ou compartiments différents
Surf espèce	Classe de surface occupée (en %) pour chaque espèce sur la surface étudiée
Angle	Colonne à renseigner pour le bois vivant et le bois mort debout type chandelle. Evaluation de l'inclinaison de l'arbre par rapport au sol en utilisant les 3 classes suivantes : ➢ classe A : inclinaison < 15° ➢ classe B : inclinaison 15° ≤ I < 45° ➢ classe C : inclinaison ≥ 45°
Distance	Par rapport au centre de la placette pour les petits bois morts au sol (P)
Dim P	Renseigner le diamètre médian et la longueur
Dim AC	Renseigner la hauteur et la largeur de l'assiette de chablis
E	Pour les petits bois morts au sol, renseigner la classe de surface recouverte par de l'écorce : E1. Écorce présente sur tout le billon E2. Présente sur plus de 50% de la surface E3. Présente sur moins de 50% du bois E4. Absente du billon
D	Pour les petits bois morts au sol, renseigner la classe de décomposition, appréciée à l'aide d'un couteau qu'on enfonce dans le bois : D1. Dur et non altéré D2. Pourriture < ¼ du diamètre D3. Pourriture comprise entre ¼ et ½ du diamètre D4. Pourriture comprise entre ½ et ¾ du diamètre D5. Pourriture supérieure à ¾ du diamètre
Support inventaire complémentaire	Indiquer la nature du support sur lequel les espèces supplémentaires ont été trouvées lors de l'inventaire chronométré de 30 min
Remarques	Rubrique libre

Placette : à partir du centre de la placette, on utilisera un télémètre afin de déterminer la limite des 20 mètres de rayon. Sinon, l'opérateur repère et matérialise cette limite sur les azimuts 0 gr, 133 gr et

267 gr à l'aide du ruban décamétrique.

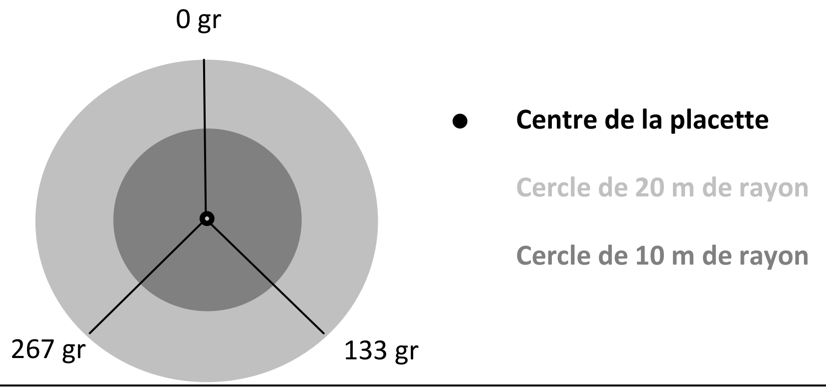


Figure n°1

Détail des tâches à réaliser

Avant de procéder à l'inventaire des espèces sur les supports désignés par le protocole, l'opérateur indique les informations générales sur la fiche "saisie bryo", à savoir : les noms des opérateurs, la date du relevé, le code massif, le numéro de la parcelle forestière, le code de la placette et enfin l'heure de début du relevé. Les informations de la fiche "dendro" sont reprises du relevé dendrométrique.

Récolte d'échantillons lors de l'inventaire : l'opérateur placera sous enveloppe les échantillons à déterminer, en indiquant la date, les codes Massif et placette, le support (code + identifiant) et le nom(ou numéro) provisoire de l'échantillon, suivi d'un "?".

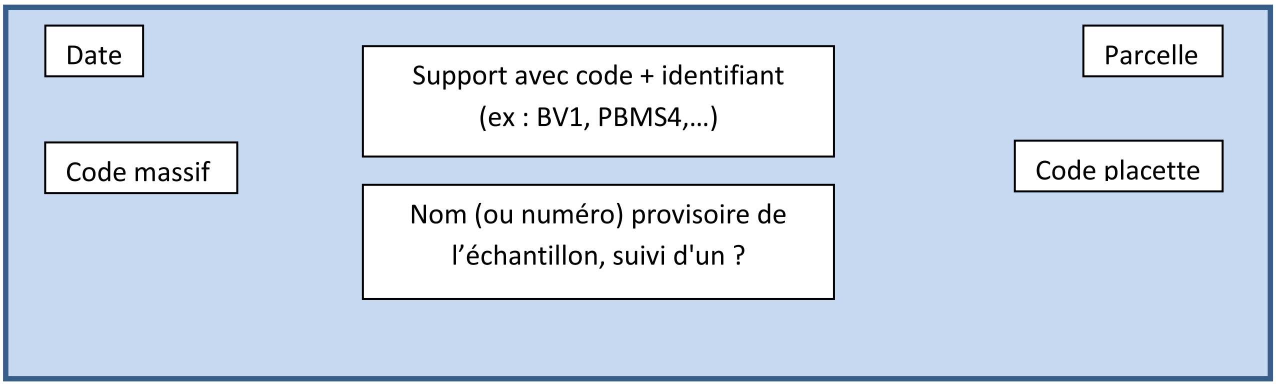


Figure n°2

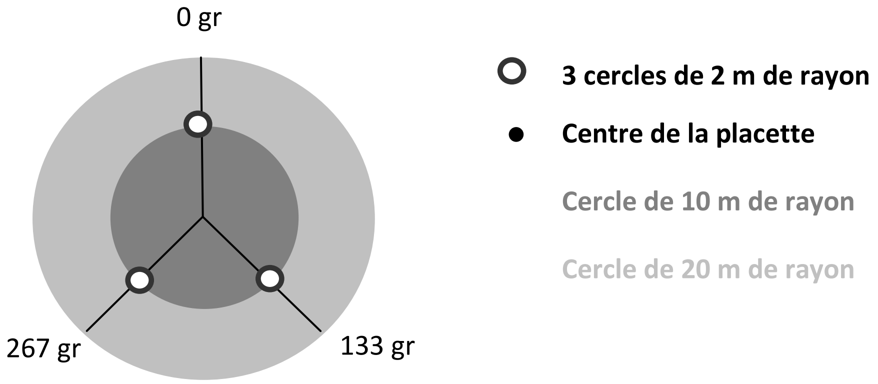
L'opérateur reportera, sur la fiche "saisie bryo", le nom (ou numéro) provisoire de l'échantillon écrit sur l'enveloppe suivi d'un point "?". Une fois l'identification de l'espèce réalisée en laboratoire, ce nom ou numéro provisoire sera remplacé par le nom validé du taxon sur la fiche "saisie bryo". Les espèces qui auront été traitées au laboratoire doivent être surlignées en rouge dans la fiche "saisie bryo" et conservées en herbier.

NB. Afin de pouvoir récolter les espèces qui nécessiteront un examen au laboratoire, Irstea et l'ONF ont fait des demandes d'autorisation de prélèvements auprès du Ministère en charge de l'Environnement, dans le cadre du projet.

Le sol : Il s'agit de la surface plus ou moins humifère exempte de bois mort identifiable. La microtopographie peut conduire à un déterminisme écologique différent dû à la présence de microhabitats liée à l'activité de la méso et macrofaune (ex : taupinière, turricules de vers de terre).

Les inventaires seront effectués sur 3 cercles de 2 m de rayon, situés à 10 m du centre de la placette, aux azimuts 0 gr, 133 gr et 267 gr.

Figure n°3



Les opérations à réaliser sont les suivantes :

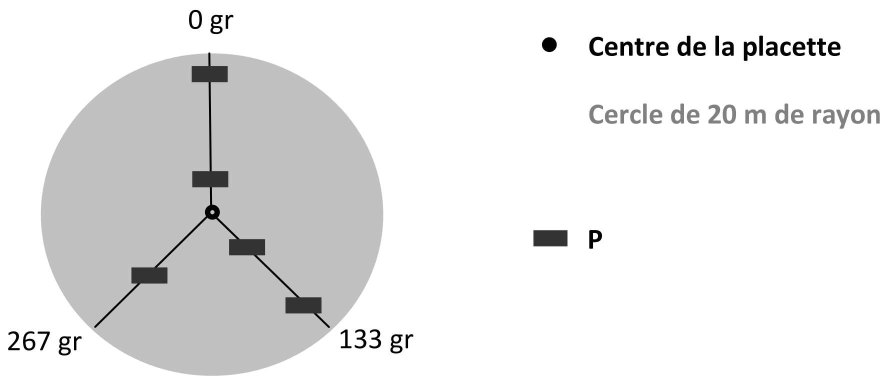
- Renseigner en premier lieu, les colonnes "type objet", "n° transect" et "sol/arbre"
- Effectuer l'inventaire, le plus complet possible, de l'ensemble des taxons (une ligne par taxon)
- À l'aide de l'abaque présentée en **Annexe II**, évaluer le recouvrement total, en %, de l'ensemble des bryophytes par rapport à la surface étudiée dans la colonne "surf" en adoptant les classes suivantes de Bardat et Aubert (2007) :
    - classe 0 : aucune bryophyte observée
    - classe I : recouvrement < 5 %
    - classe II : recouvrement 5 % ≤ R < 25 %
    - classe III : recouvrement 25 % ≤ R < 50 %
    - classe IV : recouvrement ≥ 50 %

Cette donnée est à signaler une seule fois par relevé, dès la première ligne du support étudié, dans la colonne "surf" de la fiche "saisie bryo".

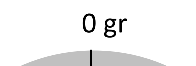
- Pour chaque taxon, on indiquera dans la colonne "surf esp" le recouvrement de l'espèce par rapport au support, selon les mêmes classes de recouvrement que ci-dessus, à l'aide de l'abaque de l'**Annexe II**.

Les petits bois morts au sol : les inventaires se réalisent sur les bois morts d'un diamètre compris entre 5 et 30 cm. Seuls les bois morts au sol interceptés par les transects des azimuts 0 gr, 133 gr et 267 gr dans le rayon de 20 m sont à considérer.

Figure n°4



Le protocole prévoit d'échantillonner 5 petits bois morts au maximum sur l'ensemble des transects. Ils pourront faire l'objet d'un examen approfondi et pourront être retournés. Il s'agit des premiers et derniers bois morts interceptés sur chaque transect. Si le nombre total de pièces ainsi définies est inférieur à 5, on pourra compléter avec les autres petits bois compris entre le premier et le dernier de chaque transect (*Figure n°5*). Ce nombre pourra être inférieur à 5 si évidemment il y a moins de 5 petits bois morts sur l'ensemble des 3 transects de la placette.



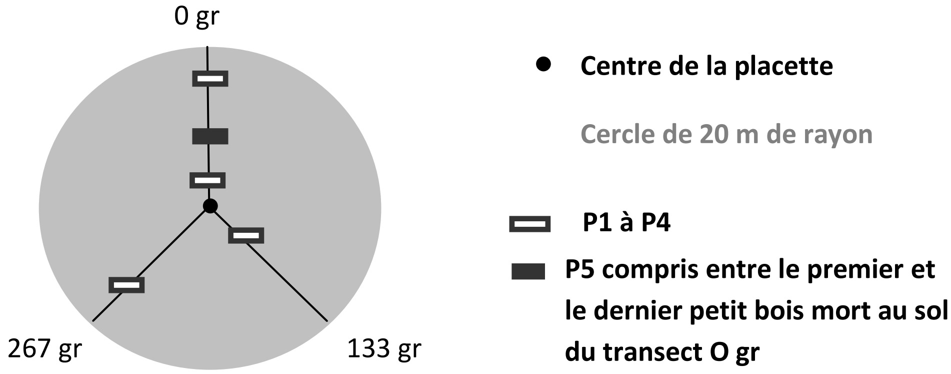


Figure n°5

Si le diamètre intercepté correspond à une branche d'un bois mort déjà étudié, l'opérateur ne retiendra pas cet objet.

Les opérations à réaliser sont les suivantes :

- Renseigner les colonnes "type objet" (tous les bois identifiés sont codés de P1 à P5 selon l'ordre dans lequel l'observateur les trouve), "n° transect", "distance", "dim P", "E" et "D". Pour ces deux dernières informations, la codification est la suivante :

Ecorce	Décomposition/Pourriture du bois
E1. Présente sur tout le billon	D1. Dur et non altéré
E2. Présente sur plus de 50% de la surface	D2. la pointe du couteau s'enfonce sur moins de ¼ du diamètre
E3. Présente sur moins de 50% du bois	D3. la pointe du couteau s'enfonce entre ¼ et ½ du diamètre
E4. Absente du billon	D4. la pointe du couteau s'enfonce entre ½ et ¾ du diamètre
	D5. la pointe du couteau s'enfonce sur plus de ¾ du diamètre

- Effectuer l'inventaire, le plus complet possible, de l'ensemble des taxons
- Évaluer le recouvrement total, en %, de l'ensemble des bryophytes par rapport à la surface étudiée dans la colonne "surf" en utilisant les mêmes classes que précédemment (Abaque **Annexe III**)
- Pour chaque taxon, on indiquera dans la colonne "surf esp" le recouvrement de l'espèce par rapport au support, selon les mêmes classes de recouvrement que précédemment (Abaque **Annexe III**)

Le bois vivant : les inventaires s'effectuent sur 5 arbres d'un diamètre supérieur ou égal à 30 cm tirés au sort dans le rayon de 20 m et 3 arbres d'un diamètre inférieur à 20 cm tirés au sort dans le rayon de 10 m. Les arbres seront étudiés depuis la base du tronc jusqu'à une hauteur de 2 m. Le nombre d'arbres inventoriés pourra être inférieur à 5 (respectivement 3) par placette si évidemment il y a moins de 5 (respectivement 3) bois vivants ≥ 30 cm de diamètre (respectivement ≤ 20 cm de diamètre).

Toute branche présente sur la hauteur étudiée sera également inventoriée. S'il y a plusieurs branches, seule la plus basse sera étudiée. L'inventaire des espèces sur cette branche s'arrêtera à la première fourche identifiée ou, à défaut, à une longueur de 1 m.

En conséquence, au cours du relevé, l'opérateur précise dans la colonne "compartiment T/B" de la fiche "saisie bryo", si l'espèce est présente sur le tronc : "T" ou sur une branche basse : "B". L'espèce est notée autant de fois qu'elle est présente sur des compartiments différents d'un même support.

Les opérations à réaliser sont les suivantes :

- Renseigner les colonnes "sol/arbre", "type objet", "compartiment T/B" et "angle". Pour renseigner la colonne angle, évaluer l'inclinaison de l'arbre par rapport au sol en utilisant les 3 classes suivantes :
    - ➢ classe A : inclinaison < 15°
    - ➢ classe B : inclinaison 15° ≤ **I** < 45°
    - ➢ classe C : inclinaison ≥ 45°
- Effectuer l'inventaire, le plus complet possible, de l'ensemble des taxons
- Évaluer le recouvrement total, en %, de l'ensemble des bryophytes par rapport à la surface étudiée dans la colonne "surf" en utilisant les mêmes classes que précédemment (Abaque **Annexe III**)
- Pour chaque taxon, on indiquera dans la colonne "surf esp" le recouvrement de l'espèce par rapport au support, selon les mêmes classes de recouvrement que précédemment (Abaque **Annexe III**)

Le bois mort debout : les inventaires s'effectuent sur 2 types de supports :

- 5 chandelles naturelles d'un diamètre ≥ 30 cm dans un rayon de 20 m.
- 5 souches d'un diamètre ≥ 30 cm telles qu'elles sont désignées par l'inventaire dendrométrique

Les inventaires seront effectués depuis la base du tronc jusqu'à une hauteur de 2 m.

Toute branche présente sur la hauteur étudiée sera également inventoriée. S'il y a plusieurs branches, seule la plus basse sera étudiée. L'inventaire des espèces sur cette branche s'arrêtera à la première fourche identifiée ou, à défaut, à une longueur de 1 m. En conséquence, l'opérateur doit préciser dans la colonne "compartiment T/B" si l'espèce est présente sur le tronc : "T" ou sur une branche basse : "B".

L'espèce sera notée autant de fois qu'elle est rencontrée sur des compartiments différents d'un même support.

Les opérations à réaliser sont les suivantes :

- Renseigner les colonnes "sol/arbre", "type objet", "compartiment T/B", "type BM".
  - Si le support est une chandelle, l'observateur doit remplir la colonne "angle" selon les classes suivantes :
    - ➢ classe A : inclinaison < 15°
    - ➢ classe B : inclinaison 15° ≤ **I** < 45°
    - ➢ classe C : inclinaison ≥ 45°

  - Si le support étudié est une souche, l'observateur doit remplir la colonne "BM F/S"
- Effectuer l'inventaire, le plus complet possible, de l'ensemble des taxons
- Évaluer le recouvrement total, en %, de l'ensemble des bryophytes par rapport à la surface étudiée dans la colonne "surf" en utilisant les mêmes classes que précédemment (Abaque **Annexe III**)
- Pour chaque taxon, on indiquera dans la colonne "surf esp" le recouvrement de l'espèce par rapport au support, selon les mêmes classes de recouvrement que précédemment (Abaque **Annexe III**)

Le gros bois mort au sol : les inventaires se réalisent sur 5 bois morts au sol d'un diamètre supérieur à 30 cm tirés préalablement au sort dans le rayon de 20 m. Les inventaires s'effectuent sur une longueur de 2 m, depuis la base du bois mort, en considérant que celle-ci correspond au plus fort diamètre.

Tous les bois identifiés sont codés BMS1, BMS2, BMS3…etc., dans la colonne "type objet ". Dans la colonne "type BM", l'opérateur précise s'il s'agit d'un billon relié à un arbre presque entier et à la galette ("C"), d'un rémanent issu de l'exploitation ("E") ou d'une branche ou bois ne constituant pas le corps de la grume proprement dite ("B").

Pour tous les bois morts au sol, toute branche présente sur la hauteur étudiée sera également inventoriée. S'il y a plusieurs branches, seule la plus proche de la base du bois mort sera étudiée. L'inventaire des espèces sur cette branche s'arrêtera à la première fourche identifiée ou, à défaut, sur une longueur de 1 m. En conséquence, au cours du relevé, l'opérateur précise dans la colonne "compartiment T/B", si l'espèce est présente sur le tronc ("T") ou sur une branche basse ("B").

L'espèce sera notée autant de fois qu'elle est rencontrée sur des compartiments différents d'un même support.

Les opérations à réaliser sont les suivantes :

- Renseigner les colonnes "sol/arbre", "type objet", "compartiment T/B", "type BM"
- Effectuer l'inventaire, le plus complet possible, de l'ensemble des taxons
- Évaluer le recouvrement total, en %, de l'ensemble des bryophytes par rapport à la surface étudiée dans la colonne "surf" en utilisant les mêmes classes que précédemment (Abaque **Annexe III**)
- Pour chaque taxon, on indiquera dans la colonne "surf esp" le recouvrement de l'espèce par rapport au support, selon les mêmes classes de recouvrement que précédemment (Abaque **Annexe III**)

Les assiettes de chablis : Une seule assiette de chablis sera inventoriée par placette ; elle sera codée "AC". Les observateurs choisiront l'assiette la plus proche du centre de la placette. Les inventaires concernent uniquement la partie du sol piégée par le système racinaire, généralement peu ou pas humifère. Ils seront réalisés sur toute la surface de l'assiette de chablis, c'est-à-dire des deux côtés.

Les opérations à réaliser sont les suivantes :

- Renseigner les colonnes "sol/arbre", "type objet", "distance" et "dim AC"
- Effectuer l'inventaire, le plus complet possible, de l'ensemble des taxons
- Évaluer le recouvrement total, en %, de l'ensemble des bryophytes par rapport à la surface étudiée dans la colonne "surf" en utilisant les mêmes classes que précédemment
- Pour chaque taxon, on indiquera dans la colonne "surf esp" le recouvrement de l'espèce par rapport au support, selon les mêmes classes de recouvrement que précédemment

Complément chronométré d'inventaire : les observateurs complèteront leurs relevés par un inventaire libre d'une durée de 30 min en indiquant pour chaque taxon relevé le type de support concerné. Ce dernier sera à indiquer dans la colonne "support inventaire complémentaire" de la fiche "saisie bryo". Ce complément permet de prospecter des zones riches telles que les rochers, les houppiers tombés au sol ou les essences forestières peu communes qui n'ont pas forcément été sélectionnées par le tirage au sort.

Les opérations à réaliser sont les suivantes :

- Renseigner les colonnes "type objet" et "support inventaire complémentaire" en indiquant dans la première Inv_Comp
- Effectuer l'inventaire, le plus complet possible, de l'ensemble des taxons

Annex 2: Occurrence of each epiphytic bryophyte species inventoried in the GNB survey