



HAL
open science

Influence of forest tree species composition on bryophytic diversity in mixed and pure pine (*Pinus sylvestris* L.) and oak (*Quercus petraea* (Matt.) Liebl.) stands

Marion Gosselin, D. Fourcin, Yann Dumas, Frédéric Gosselin, Nathalie Korboulewsky, M. Toïgo, P. Vallet

► To cite this version:

Marion Gosselin, D. Fourcin, Yann Dumas, Frédéric Gosselin, Nathalie Korboulewsky, et al.. Influence of forest tree species composition on bryophytic diversity in mixed and pure pine (*Pinus sylvestris* L.) and oak (*Quercus petraea* (Matt.) Liebl.) stands. *Forest Ecology and Management*, 2017, 406, pp.318-329. 10.1016/j.foreco.2017.09.067 . hal-02499868

HAL Id: hal-02499868

<https://hal.science/hal-02499868v1>

Submitted on 5 Mar 2020

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

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

1 Influence of forest tree species 2 composition on bryophytic diversity in 3 mixed and pure pine (*Pinus sylvestris* L.) 4 and oak (*Quercus petraea* (Matt.) Liebl.) 5 stands

6 Marion Gosselin, Deki Fourcin, Yann Dumas, Frédéric Gosselin, Nathalie Korboulewsky, Maude Toïgo,
7 Patrick Vallet

8 IRSTEA, UR EFNO Ecosystèmes Forestiers, Centre de Nogent-sur-Vernisson, Domaine des Barres,
9 F-45290 Nogent-sur-Vernisson, France

10 Corresponding author: Marion Gosselin

11 Address: IRSTEA, UR EFNO Ecosystèmes Forestiers, Centre de Nogent-sur-Vernisson, Domaine des
12 Barres, F-45290 Nogent-sur-Vernisson, France

13 E-mail address: marion.gosselin@irstea.fr

14 Highlights

- 15 • Bryophyte diversity on and around tree trunks was higher for oak than for pine.
- 16 • Mixed stands enhanced bryophyte diversity for pine trees.
- 17 • At the plot level, mixed stands and pure oak stands had similar bryophyte richness.
- 18 • Nevertheless, some species were more likely to be found on pines.
- 19 • Exploratory models revealed strong effects for basal area and water supply chemistry.

20 Keywords

21 Forest biodiversity; bryophyte; mixed woods; tree composition; Oak (*Quercus petraea*); Scots pine
22 (*Pinus sylvestris*)

23 Abstract

24 The effects of mixed stands on biodiversity are increasingly being studied since they are supposed to offer higher
25 habitat heterogeneity. Nevertheless, for **tree-associated diversity, including epiphytes and terricolous species near**
26 **tree trunks**, few studies exist, and still fewer compare mixed stands with each corresponding pure tree species
27 stand. We evaluated and quantified the influence of forest composition on tree-associated bryophyte diversity
28 (species richness, abundance, composition) in mixed and pure oak-pine stands in a French lowland forest. The
29 main explanatory variables for bryophyte diversity at tree-level were the identity of the phorophyte tree species
30 and the mixture type (pure versus mixed). At the plot level, the main explanatory variable was the stand type (pure
31 oak, pure pine and mixed). We also explored the role of other variables including the chemistry of the bryophyte

32 substrates (soil, bark) and water supply (stemflow, throughfall), as well as stand abundance variables (basal area,
33 interfering plant cover). We analyzed data with Generalized Linear Models under Bayesian statistics, to take into
34 account the spatial autocorrelation between plots and any under- or over-dispersion of our data. At the tree-level,
35 bryophyte richness and abundance were higher on oak than on pine. Pine bryophyte richness was higher in mixed
36 compared to pure stands, whereas for oak, mixed stands did not enhance bryophyte richness. At the plot level,
37 mixed stands hosted bryophyte communities of similar richness to those in pure oak stands, whereas pure pine
38 stands were clearly poorer. **Our exploratory models suggested strong effects of water supply chemistry (stemflow
39 and throughfall pH or conductivity) and basal area; the latter had a strong quadratic effect on epiphytic richness at
40 the plot level.** In terms of composition, three species were more likely to be found on pine phorophytes, seven
41 species clearly occurred more frequently on oaks. Some species were more likely to be associated to pine in mixed
42 than in pure stands, and one species was found more often under pines in pure stands. Therefore, bryophyte
43 diversity at the landscape level should benefit from the simultaneous presence of the three stand composition
44 types – pure oak, pure pine and mixed stands.

45 Abbreviations

46 **SR:** species richness; **epiph:** epiphytic species; **AB:** abundance; **TF:** throughfall; **SF:** stemflow; **G:** basal
47 area; **ground:** ground-dwelling species; **glob:** both epiphytic and ground-dwelling species; **OM:**
48 organic mineral horizon; **Rec_interf_Glob:** cover percentage of interfering plants inside a ring 1meter
49 in width traced around the tree.

50 Introduction

51 Mixed-species forest stands are increasingly being studied because of their potential benefits in
52 reconciling ecological and productivity goals, as compared to monoculture stands. These benefits
53 include biodiversity enhancement ([Barbier et al., 2008](#); [Cannell et al., 1992](#); [Cavard et al., 2011b](#);
54 [Sobek et al., 2010](#)), improved growth rates of stands ([del Rio and Sterba, 2009](#); [Pérot and Picard,
55 2012](#); [Pretzsch, 2003](#); [Vallet and Pérot, 2011](#)), more efficient water consumption ([Lubbe et al., 2016](#)),
56 better soil properties ([Brandtberg et al., 2000](#); [Brandtberg and Lundkvist, 2004](#); [Vaychis and
57 Danusyavichus, 1978](#)), reduced biotic pathogen damage ([Jactel et al., 2005](#); [Jactel and Brockerhoff,
58 2007](#); [Koricheva et al., 2006](#); [Lygis et al., 2004](#); [Watt, 1992](#)) and better tree growth compensation
59 following insect damage ([Perot et al., 2013](#)).

60 Nevertheless, mixed stands are not always better than pure ones with regard to these criteria since
61 other variables also play a role, like site conditions ([Toïgo et al., 2015](#); [Zilliox and Gosselin, 2014](#)), tree
62 species composition of the mixture ([Parrotta, 1999](#); [Simmons and Buckley, 1992](#)) and, as far as
63 biodiversity is concerned, the taxonomic or ecological groups under study (see [Migge et al. \(1998\)](#) for
64 oribatid mite diversity, [Scheu et al. \(2003\)](#) for soil microfauna biomass, [Smith \(1992\)](#) for bird
65 communities, [Oxbrough et al. \(2012\)](#) for arthropod fauna, [Barbier et al. \(2009b\)](#) and [Zilliox and
66 Gosselin \(2014\)](#) for vascular plants, [Cavard et al. \(2011a\)](#) for vascular plants and ground bryophyte
67 understory biomass, [Cavard et al. \(2011b\)](#) for soil organisms). Further studies are needed to better
68 assess the effects of different types of tree species mixtures on biodiversity, even for mixtures of
69 widespread species like sessile oak or Scots pine ([Barsoum et al., 2014](#)).

70 Mixing tree species increases the structural heterogeneity of the stand and habitat diversity, as
71 shown by [Cavard et al.'s review \(2011b\)](#), and allows more plant, animal or fungal species to colonize
72 the stand. The diversity of *epiphyte* communities in particular could be enhanced in mixed stands,
73 since different tree species provide different habitat substrates, through their differences in bark
74 texture and chemical properties ([Barkman, 1958](#)). Since these differences in bark chemical properties

75 also influence soil acidity and nutrient contents in the vicinity of the trunk ([Gustafsson and Eriksson,](#)
76 [1995;](#) [Chang and Matzner, 2000b](#)), mixed stands may also enhance habitat diversity for ground-
77 dwelling species around the trunk.

78 Bryophytes are of interest for studying the effect of mixed stands on biodiversity precisely because
79 they include **both** epiphytes **and** ground dwelling species **near trunks, which we will designate as**
80 **tree-associated bryophytes**. Epiphytic, terricolous and epixylic cryptogams are an important
81 component of overall forest biodiversity; their richness is greater than that of vascular plants in many
82 forest types ([Kriebitzsch et al., 2013](#)). In addition, they contribute to overall biodiversity as primary
83 producers and serve as food resources and habitat for mammals ([Virtanen et al., 2000](#)), molluscs,
84 insects like the Byrrhidae, and tardigrads who live and feed essentially in mosses.

85 Overall bryophyte diversity on a local scale is affected **both by the regional macroclimate and by the**
86 **microclimate and other local variables** ([Raabe et al., 2010](#)), among which the composition of the
87 **stand. Indeed, as far as tree-associated bryophytes are concerned, bryophyte diversity** may be
88 influenced by both phorophyte and overall stand characteristics. **Concerning phorophyte**
89 **characteristics, tree-associated bryophyte diversity** is **firstly** explained by substrate structure and
90 chemistry ([Cleavitt et al., 2009](#)), light ([Aude and Poulsen, 2000;](#) [Tinya et al., 2009](#)) and wind and
91 precipitation exposure; and secondly, by the phorophyte species ([Cleavitt et al., 2009](#)). Although
92 epiphytic bryophytes are not host-tree-specific – each bryophyte species can be found on various
93 host-tree species ([Bates and Brown, 1981;](#) [Cleavitt et al., 2009;](#) [Gonzalez-Mancebo et al., 2003](#)),
94 bryophyte community composition can significantly differ among host tree species in mixed stands
95 ([Odor et al., 2013;](#) [McGee and Kimmerer, 2002](#)), depending on the structural and chemical
96 characteristics of the substrate. In particular, bryophytes are known to be sensitive to the pH of their
97 substrate – whether bark, rock or soil ([Barkman, 1958;](#) [Bates and Brown, 1981;](#) [Bates, 1992;](#) [Fritz and](#)
98 [Heilmann-Clausen, 2010](#)) as well as to the pH and nutrient content of their water supply. Some
99 authors have also used conductivity of water supplies or soil solutes as a proxy for their nutrient
100 content (e.g. [Sutinen et al., 2002](#)). In forest stands, bryophyte water supplies consist of either
101 throughfall, for ground species, or stemflow for trunk epiphytes: throughfall is the rainwater that
102 falls to the ground through the canopy, and stemflow is rainwater that runs down the trunk of the
103 tree ([Barkman, 1958;](#) [Bates and Brown, 1981;](#) [Farmer et al., 1991;](#) [Leith et al., 2008;](#) [Nagano, 1972](#)).
104 Stemflow acidity can also affect the ground assemblages (vascular flora or bryophytes) at the base of
105 the trunks, with more acidic indicator species adjacent to the tree ([Neite and Wittig, 1985;](#) [Wittig and](#)
106 [Neite, 1985](#)). Indeed, Beniamino et al. (1991), Chang and Matzner (2000b) and [Vellak et al. \(2003\)](#)
107 studied mean stemflow pH for different tree species and found that the acidic effects of stemflow
108 decrease with distance from the tree. **Among overall stand characteristics**, stand density and cover of
109 interfering plants (i.e. competing and covering vascular plants like *Pteridium aquilinum* (L.) Kuhn,
110 *Molinia caerulea* (L.) Moench or *Calluna vulgaris* (L.) Hull ([Dumas, 2006](#))) may also affect both
111 ground-dwelling and epiphytic bryophytes **because they are related to light and substrate availability:**
112 the higher the stand density or the interfering plant cover, the less light reaches the forest floor;
113 smaller trunk diameters and low density may limit available habitats for epiphytes. In addition,
114 increasing diameter is known to be positively correlated with epiphytic bryophyte richness
115 ([Gustafsson and Eriksson, 1995](#) or [McGee and Kimmerer, 2002](#) cited by [Marialigeti et al., 2009](#)).

116 **In order to study the stand composition effect on the diversity of tree-associated bryophytes,**
117 **bryophyte assemblages** can be considered at both tree (**alpha**) and stand (**gamma**) levels. **Few**

118 publications have been specifically designed to compare this bryophyte diversity on individual tree
119 species between pure and mixed stands. They indicate that *epiphytic* bryophyte diversity was higher
120 in mixed stands at both tree and plot levels than in at least one corresponding pure stand, most often
121 the coniferous one (Cleavitt et al. (2009) in mixed maple - spruce stands, Kiraly and Odor (2010) in
122 Hungarian oak and pine forests, Felton et al. (2010) for spruce and birch). For *ground* bryophytes,
123 Marialigeti et al. (2009) found that the presence of oak in a pine forest had a positive effect on the
124 diversity of forest floor bryophytes at the stand level.

125 In this study, we investigated the effects of stand composition on the richness, abundance and
126 composition of tree-associated bryophyte assemblages, i.e. epiphytic bryophytes at the trunk base
127 and ground bryophytes in the trunk vicinity. We compared pure oak and pine stands with mixed oak-
128 pine stands in a lowland temperate forest with homogeneous acidic site conditions.

129 We addressed hypotheses for bryophyte diversity at both tree and plot level. The sampling design
130 was balanced to assess tree species and stand composition effects, according to the following main
131 hypotheses (see Table SM1):

132 H1 – tree-level bryophyte diversity (species richness and abundance) will be higher on oak than on
133 pine and bryophyte species composition will differ between oak and pine (Barkman, 1958; Kiraly and
134 Odor, 2010);

135 H2 – for a given phorophyte-species, tree-level bryophyte diversity (richness, abundance and
136 composition) will differ between pure and mixed stands (Cleavitt et al., 2009; Kiraly et al., 2013);

137 H3 – plot level bryophyte diversity (richness and abundance) will be higher in mixed stands than in
138 pure ones and bryophyte composition will differ between pure and mixed stands (Cavard et al.,
139 2011b; Cleavitt et al., 2009; Kiraly and Odor, 2010).

140 For exploratory purposes and to further reflect on the mechanisms involved, we also checked if other
141 variables such as the physical and chemical characteristics of the substrates (soil or bark) or the
142 water supplies (throughfall or stemflow) had an effect (see Table SM1 - exploratory hypothesis H4).
143 In addition to simple tree species identity and the interactive “species identity x stand composition
144 type”, we also investigated other stand variables (tree density, interfering plant cover) which might
145 contribute to differences in bryophyte diversity (see Table SM1 - exploratory hypotheses H5 and H6).

146 We mainly stressed management-related variables (stand composition, tree density) in order to help
147 translate results for forest managers paying attention to biodiversity conservation.

148 **Materials and methods**

149 **Study area**

150 The study was carried out in the National Forest of Orléans in central France. This temperate lowland
151 forest stretches over 60 km to the North of the Loire river (2°29' E; 47°49' N) and covers around
152 35,000 hectares. The elevation is between 107 and 174 meters above sea level. The dominant tree
153 species are sessile oak (*Quercus petraea* Liebl.) and Scot's pine (*Pinus sylvestris* L.). The climate is
154 temperate continental with an oceanic influence. Mean annual temperature is about 11.3°C, with an
155 average minimum temperature of 0.7°C in February and an average maximum temperature of 25°C
156 in July. The mean annual rainfall is 740 mm (1981-2010 data from the weather station at Nogent-sur-

157 Vernisson, France, about 20 km east of the study area). Soils are relatively poor and acidic with a
158 sandy upper layer on a clayey stratum; temporary waterlogging occurs in winter (planosol).

159 **Study design and bryophyte sampling**

160 Our sampling design was balanced according to the two main explanatory variables: tree species
161 (oak, pine) and mixture type (pure or mixed). We selected 21 plots, corresponding to seven
162 repetitions for each level of the combined factors (pure oak, pure pine, mixed oak-pine) – see
163 Supplementary Material, Figure SM 1. All the plots belonged to a restricted range of similar site
164 conditions and were located in even-aged stands managed by the French National Forest Office. Each
165 plot was circular with a radius of 15 meters. Plots were split into three equal parts (delimited by the
166 directions 0, 133 and 167 grades) and the largest tree of the given study species (oak and/or pine) in
167 each part was selected to record bryophytes. We selected the largest trees to better estimate
168 potential bryophyte richness, which is known to increase with tree diameter. Thus, we collected data
169 on three trees per species and per plot, leading to a total of 84 trees (21 oaks in pure stands, 21 pines
170 in pure stands, 21 oaks and 21 pines in mixed stands).

171 Data were collected between October and November, 2012. The bryophyte inventory **was carried**
172 **out at the tree level**. Epiphytic bryophytes were recorded on the entire trunk from its base up to a
173 height of 2 meters. We listed all bryophyte species present and assessed their abundance in cover
174 classes. Ground bryophytes were recorded on six 50-by-50 cm² quadrats. These quadrats were
175 located in three directions (azimuth 90, 210 and 330 degrees from magnetic North) around each
176 phorophyte and were centered at two distances from the trunk (25 and 75 cm). For each distance
177 from **a trunk**, data were combined, giving us separate composite records for bryophyte species at 25
178 cm and 75 cm from the tree. An additional composite record for all under-tree ground species was
179 obtained by combining the data from all six quadrats. We listed all bryophyte species present and
180 assessed their total abundance (estimated in cm²).

181 Bryophytes were identified at species level, either in the field when possible or in the laboratory on
182 collected samples, if necessary. Nomenclature follows the list established by **Gargominy et al. (2015)**.
183 It was not possible to identify *Ulota* at the species level in the absence of a capsule and in this case,
184 they were recorded at the genus level as *Ulota* sp.

185 For each phorophyte, the final bryophyte data set included data of species richness (number of
186 species on trunks or on soil), ground species abundance (cover in cm², which cannot exceed 15,000
187 cm² for any given tree), epiphyte species abundance (cover classes ranked in increasing order) and
188 species binomial presence data. Data were calculated either at tree or plot level. To obtain plot level
189 data, we had an unbalanced sampling effort between pure and mixed stands – three trees in pure
190 stands and six trees in mixed stands. We therefore randomly selected three trees in each of the
191 seven mixed-stand plots – forcing a selection of either two oaks and one pine or one oak and two
192 pines; we then calculated the plot level data on the basis of these three randomly selected trees and
193 used the three remaining trees to build seven “additional” mixed stand plots for which we also
194 calculated the plot level data. We thus obtained a dataset of 28 plots: seven pure oak stands, seven
195 pure pine stands and 14 mixed stands.

196 **Environmental data**

197 In addition to the main variables (tree species and stand composition), we collected data for trunk
198 diameter and inclination, stand density (basal area in $\text{m}^2 \text{ha}^{-1}$ for trees with dbh greater than 7.5 cm),
199 chemical characteristics of bryophyte substrate and water supply in October, 2012 and February,
200 2013. For the substrate and water supply, soil and throughfall were used in the analysis of forest
201 floor species; whereas bark and stemflow were related to epiphytic bryophyte species.

202 We attributed an estimated cover percentage to interfering plant cover present under breast height
203 in two concentric 50 cm-wide rings around each tree, centered 25 and 75 cm away from the trunk.
204 Additionally, we estimated the global interfering plant cover percentage within a 1m-radius circle
205 around the tree.

206 A 2.5 cm-high soil coring ring was used to collect samples of first, the fragmented organic (OF)
207 surface horizon, then the underlying organo-mineral (A) horizon at the base of each sampling tree.
208 Samples were taken at 25 and 75 cm from the trunk in three directions (at the center of each ground
209 bryophyte sampling quadrat). For each horizon, we combined the three samples to create two
210 composite soil samples, one for each distance from the tree. Thus, we obtained four soil samples per
211 sampling tree (one surface horizon and one organo-mineral horizon for each distance from the
212 trunk).

213 Measurements of soil pH and conductivity were carried out in the laboratory according to the ISO
214 10390 norm ([AFNOR, 1996](#)).

215 Bark outer surface was collected on 4 cm^2 from the West side of each tree at 1.10 m high, with a
216 minimum amount of lichen. Samples were air dried, broken into small pieces, then 0.4 g was added
217 to 4 ml of demineralized water. The sample was left to soak for one hour before reading the pH
218 (Eutech pH 6+ Meter). A further 15 ml of demineralized water were added to measure the
219 conductivity (Eutech Cond 6+).

220 Two series of water samples were collected for throughfall and stemflow pH and conductivity
221 measurements (ISO 10523 norms ([AFNOR, 2012](#))): one at the beginning of October (for pH
222 measurements) when the canopy was in leaf, and the second in February (pH and conductivity
223 measurements) when the deciduous trees were bare. Throughfall was collected in pots anchored in
224 the soil at 25 and 75 cm from the tree on the West side. Pots were protected by a mesh to prevent
225 leaves or small animals falling in. Stemflow was collected in a 520 ml cup attached to the West side
226 of the trunk at 1 m in height. Cups were protected by an aluminum foil so that stemflow could fall in
227 whereas direct rain could not.

228 **Statistical methods**

229 **Models**

230 We analyzed our data with Bayesian statistical models in order to estimate, analyze and compare the
231 statistical models defined in the Supplementary Material, [Table SM2](#). We chose Bayesian methods
232 for two reasons. First, they allowed us to take into account the spatial autocorrelation among plots,
233 thanks to spatially correlated plot random effects that have been found to give good results in a
234 Bayesian framework ([Saas and Gosselin, 2014](#)). Indeed, even if this was not a case of complete
235 pseudo-replication, the spatial distribution of the plots was not completely balanced since all the

236 stands for a given composition tended to grow in the same area (Figure SM1). Second, they allowed
237 us to take into account potential under- or over-dispersion of our species richness count data, thus
238 ensuring better analyses than the Poisson law under frequentist models ([Gosselin, 2011](#); [Gosselin,
239 2015](#); [Lynch et al., 2014](#)).

240 We studied the effect of tree species identity and stand composition type (two main explanatory
241 variables) on bryophyte species diversity, namely species richness, species abundance and species
242 presence probability ([Table SM1](#)). Other environmental variables were considered either as single
243 variables or as co-variables added to or in interaction with the two main variables ([Table SM2](#)).

244 Species richness being integer-value count data and being potentially under- or over-dispersed
245 relative to the Poisson distribution, we modeled this variable following a new distribution law
246 ([Gosselin, 2011](#); [Zilliox and Gosselin, 2014](#)) which allows the dispersion parameter to be <1 or >1. We
247 used the log function as the associated link function.

248 Ground species abundance data are numerical bounded between 0 and N_{\max} , where N_{\max} is the
249 maximum value for one abundance record; we therefore modeled abundance with a beta-binomial
250 or Polya distribution ([Chen et al., 2008](#)). We preferred a Polya distribution over a binomial one, since
251 binomials tend to artificially “detect” effects where actually there are none, as when bounded data is
252 over-dispersed ([Gosselin, 2015](#)). We used the logit function as the associated link function.

253 Trunk epiphyte abundance are cover class data, ranked in increasing order, characterized by values
254 bounded between 0 and 100%, asymmetric classes, and a high proportion of zeroes. They were
255 modeled with a zero-inflated cumulative beta distribution, following the MTUnlimited method
256 described in [Herpigny and Gosselin, 2015](#) (2015). We used two logit functions to link the mean of the
257 probability distributions to the linear combination of effects (one for the presence absence process,
258 and one for the mean total cover process; cf. [Herpigny and Gosselin, 2015](#)).

259 Species presences are numerical data taking the values 0 and 1: species presence probabilities were
260 modeled through logistic regressions with a binomial distribution. We used the logit function as the
261 associated link function. We modeled presence probability at both tree and plot levels and only for
262 sufficiently abundant species (more than 9 occurrences).

263 All the Bayesian models included a Gaussian spatially correlated plot random effect that was added
264 to the linear combination used to calculate the mean of the model. The shape of the spatial
265 dependence was exponential, with no nugget (function `spatial.exp` in Winbugs, with parameter $k=1$;
266 i.e. the correlation $C_{i,j}$ between plots i and j separated by a distance of $d_{i,j}$ was $C_{i,j} = \exp(-\frac{d_{i,j}}{\phi})$).

267 For mixed stand plot level data, the resulting “double data” (14 plots instead of 7) for the same plots
268 had the same coordinates and therefore the same random effect. Doubling the data for mixed stands
269 and simultaneously modeling plots’ spatial autocorrelation as a spatially structured random effect
270 was a way to use all the information provided by the six trees **sampled** in mixed stands, and yet to
271 control the sampling effort per stand (3 trees and no more at stand level).

272 Since our models were hierarchical, with one random effect per observation, we compared their
273 marginalized DIC (deviance information criterion) values ([Millar, 2009](#)) to identify the best model for
274 each given response variable. The smaller the marginalized DIC, the better the model.

275 The Bayesian models were fitted in R through the R2WinBUGS library calling WinBugs ([Lunn et al.,](#)
276 [2000](#)) (including the extensions GeoBUGS for spatial autocorrelation modelling and the WBdev
277 interface for some probability distributions). We used three trajectories of 100,000 iterations, a
278 burning period of 10,000 iterations and a thinning parameter of 30. The convergence of the model
279 was checked with Gelman and Rubin's (1992) Rhat quantity, which was smaller than 1.1.

280 The prior distribution for the parameters of the spatially auto-correlated random effects were chosen
281 as constrained, relatively non-informative values: the log of the inverse decay parameter ϕ was
282 chosen to be uniform between -11 and -3, corresponding to a range of correlations from $2 \cdot 10^{-9}$ to
283 0.99 and from 0 to 0.70 at the minimum (401 m) and maximum (21,537 m) distance between plots,
284 respectively. The logarithm of the inverse of the variance had a uniform prior between -2 and 12 –
285 corresponding to a possible standard deviation from 0.0025 and 2.72. To compare marginalized DIC
286 and select the best models, we had used a uniform distribution between -9 and -3.

287 All the main fixed effects in the models – see [Table SM2](#) – had a non-informative Gaussian prior with
288 a mean of 0 and a variance of 10,000.

289 The prior for the logarithm of the index of dispersion (ID) for *count data models* was chosen to be
290 uniform between -1 to 5 – ranging from rather strong levels of under-dispersion (ID of 0.37) to high
291 levels of over-dispersion (ID of 148) compared to the Poisson distribution. For the *zero inflated*
292 *cumulative beta distribution*, the prior for parameter δ and the logarithm of Φ , as described in
293 [Herpigny and Gosselin \(2015\)](#), were rather non-informative and chosen as Gaussian with a mean of 0
294 and a variance of 10. For the *beta-binomial Polya model*, the over-dispersion parameter (with respect
295 to the dispersion of the binomial distribution) followed a uniform distribution between 1 and 10,000.
296 Analyses were performed with the R (version Rx64 2.15.1) and the WinBUGS14 (version 1.4)
297 software.

298 **Interpreting model results: analyzing the magnitude of the effect in addition to its** 299 **statistical significance**

300 For each response variable and for both main and – if different – best models, we not only analyzed
301 the significance, but also the magnitude of the effect ([Barbier et al., 2009b](#)). We simulated a change
302 in the explanatory variable (either an increase for numeric variables or a change of level for factors)
303 and studied the magnitude of the consecutive change in the mean of the response variable. For
304 numeric explanatory variables, the simulated increases were chosen with standardized values,
305 namely the standard deviation of the variable and one fifth of its amplitude in the data set (Tables
306 [SM10](#), [SM11](#), [SM12](#)). We checked that the resulting variations could be judged realistic in forest
307 management.

308 We considered the magnitude of the effect negligible (even if statistically significant) if the variation
309 ΔX of the explanatory variable X led to a variation in the mean of the response variable that was less
310 than 10% of the mean of the response variable's initial value. We analyzed two levels of magnitude:
311 the effect was considered strong (respectively very strong) if the simulated increase in the
312 explanatory variable led to a difference of more than 10% (respectively 20%) in species number or in
313 species abundance.

314 Based on Bayesian parameter estimation as in Camp et al. (2008), the aim of the magnitude analysis
315 was to identify the following cases:

- 316 (i) When the parameter had a high probability ($\geq 95\%$) of being in the negligibility interval.
317 (ii) When the parameter had a high probability ($\geq 95\%$) of being above the negligibility
318 interval (positive, non-negligible effect).
319 (iii) When the parameter had a high probability ($\geq 95\%$) of being below the negligibility
320 interval (negative, non-negligible effect).

321 The notations we adopted for the final interpretation of the model results are presented in [Table](#)
322 [SM3](#) and can be summarized as follows for the magnitude: + (respectively ++): strong (respectively
323 very strong) positive effect (difference of more than 10%, respectively 20%), – (respectively – –):
324 strong (respectively very strong) negative effect (difference of more than 10%, respectively 20%); nc:
325 no possible conclusion about magnitude.

326 The same reasoning and notations apply to Polya abundance, cumulative beta or binomial presence
327 probability data, taking into account the adapted logit link function. In each case, we report the
328 mean value of the multiplier of the mean (equivalent to $\beta \Delta X$ in our example in [Table SM3](#)), its 95%
329 confidence interval and the magnitude of the effect.

330 For statistical significance, the notations are: **=significant effect ($p < 0.01$), *=significant ($p < 0.05$), ns:
331 non-significant effect.

332 Results

333 Descriptive statistics

334 We recorded a total of 29 species (among which eight were liverworts) on 84 trees and surrounding
335 forest floor in the 21 plots – [Table SM4](#). Four species occurred only on the ground, eight only on
336 trunks while 17 species were found both on trunks and on the soil. Twenty-seven species occurred
337 on oak and 13 on pine. Two species (*Dicranum montanum* Hedw. and *Plagiothecium succulentum*
338 (Wilson) Lindb.) were found only on pine whereas 16 species were found only on oak ([Table SM4](#)).

339 **At tree level, epiphyte species** richness per tree ranged from two to seven species for oak, and from
340 one to five species for pine. On the ground within one meter around the trunks, species richness
341 ranged from one to twelve species for oak, and from one to seven species for pine ([Table SM5](#)). **At**
342 **plot level, global species richness** ranged from eight to nineteen species in pure oak stands, three to
343 eight species in pure pine stands and eight to fifteen species in mixed stands.

344 Observed pH values ([Table SM6](#)) were significantly higher on oak than on pine for bark, stemflow,
345 throughfall (t-test, $p < 0.01$) and for the organo-mineral horizon (t-test, $p < 0.05$). The difference was
346 non-significant for soil surface horizon.

347 Bark pH values varied between 4.2 and 5.4 for oak, and between 4.0 and 4.9 for pine.

348 Pine conductivity values were significantly higher than for oak for bark and February throughfall at
349 75 cm from the trunk (t-test, $p < 0.01$). The difference was non-significant for stemflow conductivity
350 ([Table SM6](#)).

351 Model results

352 Effects of tree species identity on bryophyte diversity at tree-level – H1

353 Overall bryophyte diversity was higher on oak than on pine trees (See [Table SM7](#) and Figure 1), thus
354 confirming hypothesis H1a. Richness was significantly higher on/under oak than on/under pine, with

355 a magnitude higher than 20% for both epiphytic and ground-species richness (**/++), and abundance
356 as well, but only for epiphytic species.

357 Three species clearly had a higher probability of being present on or under pine (Table 1): *Hypnum*
358 *jutlandicum* Holmen & E.Warncke, *Lophocolea heterophylla* (Schrad.) Dumort. and *Campylopus*
359 *flexuosus* (Hedw.) Brid., whereas seven species clearly occurred more frequently on or under oaks:
360 *Hypnum cupressiforme* Hedw., *Lophocolea bidentata* (L.) Dumort., 1835, *Frullania dilatata* (L.)
361 Dumort., *Frullania tamarisci* (L.) Dumort., *Orthotrichum lyellii* Hook. & Taylor, *Polytrichastrum*
362 *formosum* (Hedw.) G.L.Sm. and *Thuidium tamariscinum* (Hedw.) Schimp.

363 **Tree species identity and stand composition type effects interacted on bryophyte** 364 **diversity at tree-level – H2**

365 Tree species identity and stand composition type had clearly interacting effects on bryophyte
366 diversity (Table 2); taking this interaction into account enhanced the model in terms of marginalized
367 DIC (Table SM8).

368 Bryophyte richness, whatever the species group considered (epiphyte, ground or global richness),
369 was higher on and under pine trees in mixed stands compared to pure stands (Table 2). The
370 estimated median of global richness was 4.42 species per tree in mixed stands and 3.08 species per
371 tree in pure stands (more than 10% higher). The difference was especially clear for epiphytic
372 bryophyte richness, with 3.67 species per pine in mixed stands and 2.39 species per pine in pure
373 stands (more than a 20% difference in species number). For oak, there was no significant difference
374 between pure and mixed stands in global, epiphyte or ground species richness, and no conclusion on
375 magnitude was possible.

376 The abundance of ground bryophytes under both pine and oak trees was higher in pure stands than
377 in mixed stands (a difference of more than 20% in absolute cover under pines, 10% under oaks).
378 Epiphyte abundance was not significantly different between mixed and pure stands, whatever the
379 tree species.

380 In terms of bryophyte composition, mixture enhanced the probability of four species to be found
381 on/under pine (Table 3): *Campylopus flexuosus*, *Dicranum scoparium* Hedw., *Hypnum cupressiforme*
382 and *Leucobryum glaucum* (Hedw.) Ångstr. On the contrary, pure stands enhanced the probability to
383 find *Pseudoscleropodium purum* (Hedw.) M.Fleisch under pine trees and *Polytrichum formosum*
384 Hedw. under oak trees.

385 **Effect of stand composition type on bryophyte diversity at plot level – H3**

386 At the plot level, bryophyte communities in pure oak and mixed stands had similar richness for
387 global, epiphytic and ground- species, and similar epiphyte species abundance, and all were higher
388 (**/++) than in pure pine stands (Figure 2 and Table SM 9). Ground species abundance was higher in
389 pure oak stands, with significant differences (*/++) compared to mixed stands. Other comparisons
390 between stands were not significant.

391 **Bryophyte composition varied among stand types (Table 4).** Three bryophyte species were more
392 likely to occur in mixed stands compared to pure pine stands: *Hypnum cupressiforme*, *Frullania*
393 *dilatata* (which occurred more frequently on oak trees; Table 1), and *Campylopus flexuosus* (which
394 occurred more frequently on pine trees; Table 1). Seven species were more likely to occur in pure
395 oak than in pure pine stands: *Hypnum cupressiforme*, *Dicranum scoparium*, *Frullania dilatata*,

396 *Frullania tamarisci*, *Polytrichum formosum*, *Thuidium tamariscinum* – all of which are associated to
397 oak trees; [Table 1](#) – plus, surprisingly, *Campylopus flexuosus*, which is more frequently associated to
398 pine trees but which did not occur in any of the pure pine stands in our study.

399 **Exploratory models for bryophyte richness and abundance – H4, H5 and H6**

400 Effects of trunk and water supply characteristics on epiphytic bryophyte diversity (H4a)

401 When used as single explaining variables, bark and October stemflow pH had a strong positive effect
402 on both epiphyte abundance and richness. Trunk diameter had a negative effect on epiphyte
403 abundance. None of these effects remained significant once the tree species effect or the interaction
404 with the stand composition effect had been taken into account.

405 Whether used as a single or additional variable, bark conductivity had a negligible effect on epiphyte
406 richness and abundance. Neither stemflow conductivity nor trunk inclination had any significant
407 effect.

408 Effects of trunk diameter, soil and throughfall chemical properties on ground bryophyte diversity 409 (H4b)

410 In addition to tree species effect, trunk diameter had a significant effect on ground bryophyte
411 richness, but the magnitude analysis did not show any systematically clear strong positive effect
412 (* /nc). Adding trunk diameter to species*composition effect led to better DIC, but with no
413 significant effect. Furthermore, trunk diameter had no significant effect on ground bryophyte
414 abundance.

415 Whether used as a single or additional variable, pH and conductivity of February throughfall at 75 cm
416 from the trunk had strong effects on both ground bryophyte abundance and richness (positive effect
417 of pH **/++ , negative effect of conductivity **/– –, with a better DIC than the simple tree species
418 effect model). These effects led to the best models explaining ground richness and abundance at
419 75 cm from the trunk ([Tables SM10 and SM11](#)). Data at 25 cm from the trunk revealed strong single-
420 variable effects of February throughfall pH (* /++) on ground bryophyte abundance, but no strong
421 effect on ground bryophyte richness.

422 The pH and conductivity of October throughfall and of the substrates (organo-mineral horizon and
423 soil surface pH) had no effect on ground bryophyte richness or abundance, even though these
424 variables appeared in some best models ([Table SM10](#)).

425 Effects of stand basal area and interfering understory plant cover on bryophyte diversity (H5 – H6)

426 *Stand basal area* generally had a strongly significant effect on bryophyte richness per tree, when
427 considered in interaction with tree species identity and stand composition type. Taking basal area
428 into account led to the best explicative models for epiphyte diversity, ground species abundance and
429 global bryophyte richness per tree (see [Tables SM10 and SM11](#)). We found a very strong quadratic
430 effect (**/successively ++/0/– –) of stand basal area on epiphyte richness, in addition to tree species
431 identity and stand composition type ([Table SM10](#)).

432 At the plot level, basal area gave the best explanatory model for plot epiphytic richness, with a strong
433 quadratic effect in addition to stand composition type (see [Figure 3 and Tables SM12 and SM13](#) for

434 the marginalized DIC values). Epiphytic and ground species abundance was also best explained by
435 basal area taken as a single variable, with no possible conclusion about magnitude, however.

436 The *cover of interfering plants* had a strongly negative effect (*/-) on ground bryophyte abundance
437 at 75 cm from the trunk, and gave the best explanatory model for under-tree ground bryophyte
438 richness (See [Table SM10](#)) **in addition** to the species-composition interacting effect. However, **the**
439 **effect of** interfering plant cover on total ground species abundance **was negligible**.

440 At the plot level, interfering plant cover used as a single variable had a significant effect on bryophyte
441 richness (for both epiphytes and ground species). This effect did not remain significant when used in
442 addition to stand composition effect, although it did enhance the DIC compared to the single “Stand
443 composition type” model (and even led to the best model DIC for global richness – See [Table SM12](#)).
444 Ground species richness at plot level remained best explained by stand composition alone.

445 Ground species abundance at the plot level was not influenced by interfering plant cover.

446 Discussion

447 Effects of tree species identity and composition on bryophyte diversity at the tree and stand levels

448 At both plot and tree levels, we found that pure oak and mixed stands tend to favour bryophyte
449 diversity compared to pure pine stands.

450 Our hypothesis H1a was confirmed, with higher bryophyte diversity (richness and abundance) on oak
451 than on pine trees. This confirms and extends previous findings ([Kiraly and Odor, 2010](#)) to other
452 climatic and edaphic conditions, since the stands in our data set are growing on acidic soils in poor
453 conditions. Bryophyte communities in our data set were relatively poor; even if we observed strong
454 differences between phorophyte species or stand composition types, these differences actually
455 represent a small number of species.

456 We found that, within similar climatic and edaphic conditions, some epiphytes or ground bryophytes
457 were more likely to be associated with pine than with oak, and vice versa (Hypothesis H1b). Our
458 results confirm Kiraly and Odor’s (2010) findings concerning the preference of *Hypnum cupressiforme*
459 and *Frullania dilatata* for oak and the preference of *Lophocolea heterophylla* for pine. More species
460 showed preferences for oak than for pine. This is similar to Cleavitt et al.’s (2009) and [Wallrup et al.’s](#)
461 (2006) findings in their studies on small-scale tree-level floristic diversity; they found more species
462 associated to the broadleaved trees than to conifers.

463 Mixed stands in our study enhanced bryophyte diversity on/under pine trees, confirming hypothesis
464 H2. This result contributes interesting new knowledge, since no previous published study strictly
465 compared pine (or oak) bryophyte diversity between pure and mixed stands. Cleavitt et al. (2009)
466 also found a positive effect of mixed *Acer rubrum-Picea rubens* stands on epiphytic (lichen and
467 bryophyte) richness on *Acer rubrum* trees, but did not study the effect on *Picea rubens* epiphytic
468 diversity.

469 In addition, we found that preference of bryophyte species for a given phorophyte species was also
470 influenced by stand composition (pure versus mixed), which confirms hypothesis H2: for example,
471 *Campylopus flexuosus* was more likely to be found in mixed stands, under pine trees. This may be

472 explained by less competition from interfering vascular plants, whose cover percentage was higher in
473 pure pine than in mixed stands. *Frullania dilatata* was more likely to be found on oak trees in pure
474 stands.

475 However, from a forest management point of view, results at the plot level (which is the
476 management scale) are of higher importance than those at the tree level:

477 **First**, mixed stands hosted significantly richer bryophyte communities and more abundant epiphytic
478 species than pure pine stands (confirming hypothesis H3 in this case), **but not more than** pure oak
479 stands, which indeed had even more abundant ground bryophyte communities. This result may be
480 due to the fact that we only took into account ground species within a radius of one meter around
481 the trunks: ground species dwelling between trees were not taken into account. Such data are
482 currently being collected on our Oak-Pine Tree Mixture (OPTMix) experimental design ([Korboulewsky
483 et al., 2015](#)) and should clarify our results at the plot level. Our results are consistent with results
484 obtained for soil fauna ([Korboulewsky et al., 2016](#)) and for floristic understory diversity ([Barbier et
485 al., 2008](#)): diversity was generally influenced by the mixture of deciduous and coniferous tree
486 species, but in almost all cases, maximum diversity was observed in one of the pure stands, not in the
487 mixed stands, and in some cases no differences was observed between mixed and pure stands
488 ([Barsoum et al., 2014](#) for spider and carabid beetle richness).

489 **Secondly**, we did not find any bryophyte species exclusively associated with any one stand
490 composition type, although we showed some trends – for example, *Campylopus flexuosus* was more
491 likely to be found in mixed stands under pine trees, and *Polytrichum formosum* was more likely to be
492 found under oak trees in pure than in mixed stands. As a consequence, bryophyte diversity at the
493 landscape level should benefit from the simultaneous presence of the three stand composition types:
494 pure oak, pure pine and mixed.

495

496 **Effects of the additional environmental variables on the bryophyte diversity**

497 Our exploratory models, **based on** an uncontrolled sampling design for the concerned variables, have
498 good explanatory potential for the mechanisms behind the observed effects of tree species identity
499 and stand composition type. **Their results are valid within the conditions of our study (see Table SM6
500 for the domain of variation of our exploratory variables).** They can be viewed as new hypotheses to
501 future studies and are discussed below.

502 *Substrate or water supply chemistry effects*

503 Among all the variables related to substrate or water supply chemistry (hypothesis H4), three
504 appeared to have strong effects on bryophyte diversity in our study, namely (i) October stemflow pH,
505 with a strong positive effect on epiphytic richness and abundance; (ii) February throughfall pH, with a
506 strong positive effect on ground species richness and abundance, whatever the distance from the
507 stem; and (iii) February throughfall conductivity, with a strong negative effect on ground species
508 richness and abundance at 75 cm from the stem.

509 We found that bryophyte communities associated **with** oak were richer and more abundant than the
510 communities associated **with** pine. **As far as epiphytic species richness is concerned, oak-pine**

511 bryophyte difference cannot be explained by competitive species cover according to Grime et al.'s
512 (1990) theory, since richer bryophyte communities on oak were also more covering (mean epiphytic
513 cover = 26.7% on oak, 1.95 % on pine, $p < 0.01$ for Student t-test). The oak-pine difference could be
514 rather explained by differences in bark structure and chemistry between the two tree species, or by
515 differences in water supply quantity and chemistry, as explained by previous authors, like [Barkman](#)
516 (1958) and several authors cited in [Kuusinen](#) (1996).

517 Concerning bark, Barkman (1958) identified pH values from 3.7 to 5 for oak. In our study, the values
518 were between 4.2 and 5.4 and differed significantly from pine bark pH values, which varied between
519 4 and 4.9. In comparison, Barkman (1958) and [Kuusinen](#) (1996) identified bark pH values well below
520 4 for pine. In our study, oak and pine bark also significantly differed in conductivity values, pine bark
521 conductivity being higher, and in stemflow and throughfall pH. Another frequently proposed
522 explanation is that pine bark is dry and exfoliates considerably, thus providing an unsuitable,
523 ephemeral habitat for bryophytes; whereas oak bark is rough, wrinkled and quite permanent and
524 thus offers shady, moist long-lasting microhabitats more adapted to bryophytes ([Barkman, 1958](#)).

525 We did not assess the effect of water supply quantity in our study, but this variable also varies
526 between tree species and may explain differences in bryophyte assemblages: in general, evergreen
527 species like pine intercept a higher quantity of rainfall than do broadleaved species, leading to lower
528 amounts of throughfall or stemflow in coniferous stands ([Barbier et al., 2009a](#)). According to [Levia](#)
529 [and Frost](#) (2003), the greater amount of stemflow under broadleaved trees could increase soil water
530 availability near the trunk and favor different flora than that found farther from the trunk.

531 We also chose to collect substrate and water supply data at 25 cm and at 75 cm from the trunk,
532 because stemflow characteristics may influence soil pH and nutrient content in the immediate
533 vicinity of the stem ([Chang and Matzner, 2000a](#)), but we did not find any significant effect of the
534 distance on soil and throughfall pH, contrary to the results of [Beniamino et al.](#) (1991) who observed
535 soil acidification near *Quercus robur* L. trunks. The distance from the trunk influenced only February
536 throughfall conductivity, which was significantly higher near the trunk (mean value $37 \mu\text{S cm}^{-1}$) than
537 further away ($33 \mu\text{S cm}^{-1}$). This could explain why this variable appeared in the best model explaining
538 ground bryophyte richness in addition to the tree species effect.

539 Our results lead us to believe that the phorophyte species effect on bryophyte richness and
540 abundance cannot be reduced to a simple linear effect of substrate or water supply characteristics;
541 first, because these variables were not strongly correlated with tree species (except for stemflow pH
542 values, strongly correlated to pine); secondly, because these variables, when individually taken as
543 simple explanation variables, gave models whose DIC were worse than the simple species model. It is
544 more likely that tree species effect reflected a combination of diverse substrate or water supply
545 characteristics. As far as epiphytic species are concerned, this is quite different with [Cleavitt et al.'s](#)
546 (2011) results, that showed that epiphytic diversity was determined first by stemflow pH and only
547 secondly by the tree species. However, [Cleavitt et al.'s](#) (2011) results were for epiphytic composition,
548 whereas we tested substrate or water supply variables only for epiphytic richness and abundance.
549 Our results show phorophyte species as the main explanatory factor for bryophyte diversity at tree
550 level under homogeneous climatic conditions; this is consistent with [Kiraly et al.](#) (2013) and [Odor et](#)
551 [al.](#) (2013).

552 *Stand density and interfering plant cover effects*

553 Hypotheses H5 and H6 **were not supported, as** the effect of basal area on epiphytic richness was
554 strongly quadratic, rather than linear decreasing. Furthermore, the effect was positive rather than
555 negative for global richness. Finally, basal area effect was positive on bryophyte abundance. The
556 quadratic effect of basal area on epiphytic richness may be due to a positive “substrate availability”
557 effect in the first part of the gradient of basal area values (18 to 40 $\text{m}^2 \text{ha}^{-1}$), and to a negative
558 “competition for light” effect in the second part of the gradient. The switch between the positive and
559 negative part of the basal area effect occurs between 25 and 30 $\text{m}^2 \text{ha}^{-1}$. Kiraly et al. (2013) found a
560 negative effect of stand density, expressed as number of trees per hectare. Their study dealt with
561 mixed broadleaved-coniferous stands in Hungary where basal area was between 24 and 34 $\text{m}^2 \text{ha}^{-1}$, a
562 gradient that is situated within the second part of our gradient.

563 Our exploratory results involving interfering vascular plant cover suggested a weakly significant
564 negative effect on the abundance of ground bryophyte species at tree level and on global richness at
565 the plot level. This trend is not consistent with Kiraly et al. (2013) and [Marialigeti et al. \(2009\)](#) who
566 showed a positive effect of the shrub **and understory herb**. Two different mechanisms may be at
567 work: competition for light between interfering plants and the bryophyte layer may explain the
568 negative effects observed in our study, whereas suitable shady conditions provided by the shrub
569 layer could explain the positive effects observed in Kiraly et al. (2013). These apparently inconsistent
570 results may also be explained by the fact that the shrub layer in Kiraly et al. (2013) and the
571 herbaceous layer in Marialigeti et al. (2009) belonged to other strata (either ligneous higher than 50
572 cm or herbaceous under 50 cm) than the interfering plants (mostly herbaceous or semi-ligneous over
573 50 cm) in our study.

574 **Conclusion**

575

576 Within the context of our study (mature stands, floodplain oak and pine temperate forests in acidic
577 conditions with variable humidity), mixed stands clearly enhanced the bryophyte diversity on pine at
578 tree level and hosted bryophyte communities of similar richness as pure oak stands at the stand
579 level. The bryophyte diversity in pure pine stands was clearly poorer than in oak or mixed stands.
580 However, since some species were found preferably on pines, either in pure stands (e.g. *Lophocolea*
581 *heterophylla*) or in mixed stands (e.g. *Campylopus flexuosus*), we conclude that bryophyte diversity at
582 the landscape level should benefit from the simultaneous presence of the three stand composition
583 types: pure oak, pure pine and mixed. Within the basal area gradient of the studied stands, an
584 increase in basal area appears to generally increase overall bryophyte diversity, but may diminish
585 epiphytic richness in the higher part of the gradient. Current forest management guidelines
586 encourage decreasing stand density in order to adapt the forest to climate change by reducing stand
587 water consumption, and this may be detrimental for bryophyte diversity. Exploratory models suggest
588 a strong effect of water supply chemistry which could partially, but not entirely, explain the
589 phorophyte species effect on bryophyte richness and abundance.

590 **Acknowledgements**

591 This research was supported by the French Ministry of the Environment (ISCAR and DivClim Projects)
592 and carried out on a part of the OPTMix (Oak Pine Tree Mixture) experimental site

593 (<http://optmix.irstea.fr/>), managed by Irstea and supported by the Centre-Val de Loire region and the
594 French National Forest Office. This site belongs to the SOERE F-ORE-T which is supported annually by
595 Ecofor, Allenvi and the french national research infrastructure ANAEE-F
596 (<http://www.anaee-france.fr/fr/>).

597 We especially thank Catherine Menuet, Franck Stocchero and Sébastien Macé for their help with
598 field and laboratory work; Victoria Moore for her help in improving the English style; Peter Odor and
599 an anonymous reviewer for their useful comments on the manuscript.

600 **References**

601 AFNOR, 1996. Qualité du sol - Détermination du pH - Norme ISO 10390. AFNOR
602 (Association Française de Normalisation), Paris.

603 AFNOR, 2012. Qualité de l'eau - Détermination du pH - Norme ISO 10523. AFNOR
604 (Association Française de Normalisation), Paris.

605 Aude, E., Poulsen, R. S., 2000. Influence of management on the species composition of
606 epiphytic cryptogams in Danish Fagus forests. Applied Vegetation Science, 3 (1), 81-88.

607 Barbier, S., Balandier, P., Gosselin, F., 2009a. Influence of several tree traits on rainfall
608 partitioning in temperate and boreal forests: a review. Annals of Forest Science, 66 (602).

609 Barbier, S., Chevalier, R., Loussot, P., Bergès, L., Gosselin, F., 2009b. Improving biodiversity
610 indicators of sustainable forest management: tree genus abundance rather than tree genus
611 richness and dominance for understory vegetation in French lowland oak hornbeam forests.
612 Forest Ecology and Management, 258 (Supplement), S176-S186.

613 Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory
614 vegetation diversity and mechanisms involved - a critical review for temperate and boreal
615 forests. Forest Ecology and Management, 254 (1), 1-15.

616 Barkman, J.J., 1958. Phytosociology and ecology of cryptogamic epiphytes, including a
617 taxonomic survey and description of their vegetation units in Europe. Van Gorcum & Comp.
618 N.V., Assen, 628p.

619 Barsoum, N., Fuller, L., Ashwood, F., Reed, K., Bonnet-Lebrun, A.-S. et al., 2014. Ground-
620 dwelling spider (Araneae) and carabid beetle (Coleoptera: Carabidae) community
621 assemblages in mixed and monoculture stands of oak (*Quercus robur* L./*Quercus petraea*
622 (Matt.) Liebl.) and Scots pine (*Pinus sylvestris* L.). Forest Ecology and Management, 321, 29-
623 41.

624 Bates, J.W., 1992. Influence of chemical and physical factors on *Quercus* and *Fraxinus*
625 epiphytes at Loch Sunart, Western Scotland – A multivariate analysis. Journal of Ecology, 80
626 (1), 163-179.

627 Bates, J.W., Brown, D.H., 1981. Epiphyte differentiation between *Quercus petraea* and
628 *Fraxinus excelsior* trees in a maritime area of South West England. Vegetatio, 48, 61-70.

- 629 Beniamino, F., Ponge, J.F., Arpin, P., 1991. Soil acidification under the crown of oak trees: I.
630 Spatial distribution. *Forest Ecology and Management*, 40 (3-4), 221-232.
- 631 Brandtberg, P., Lundkvist, H., 2004. Does an admixture of *Betula* species in *Picea abies*
632 stands increase organic matter quality and nitrogen release? *Scandinavian Journal of Forest*
633 *Research*, 19 (2), 127-141.
- 634 Brandtberg, P.O., Lundkvist, H., Bengtsson, J., 2000. Changes in forest-floor chemistry
635 caused by a birch admixture in Norway spruce stands. *Forest Ecology and Management*, 130
636 (1-3), 253-264.
- 637 Camp, R.J., Seavy, N.E., Gorresen, P.M., Reynolds, M.H., 2008. A statistical test to show
638 negligible trend: Comment. *Ecology*, 89 (5), 1469-1472.
- 639 Cannell, M., Malcolm, D., Robertson, P. (Eds.), 1992. The ecology of mixed-species stands of
640 trees. Oxford Blackwell Scientific Pub., London, 312 p.
- 641 Cavard, X., Bergeron, Y., Chen, H.Y., Paré, D., 2011a. Effect of forest canopy composition
642 on soil nutrients and dynamics of the understory: Mixed canopies serve neither vascular nor
643 bryophyte strata. *Journal of Vegetation Science*, 22 (6), 1105-1119.
- 644 Cavard, X., Macdonald, S.E., Bergeron, Y., Chen, H., 2011b. Importance of mixedwoods for
645 biodiversity conservation: Evidence for understory plants, songbirds, soil fauna, and
646 ectomycorrhizae in northern forests. *Environmental Reviews*, 19, 141-161.
- 647 Chang, S.C., Matzner, E., 2000a. Soil nitrogen turnover in proximal and distal stem areas of
648 European beech trees. *Plant and Soil*, 218 (1-2), 117-125.
- 649 Chang, S.C., Matzner, E., 2000b. The effect of beech stemflow on spatial patterns of soil
650 solution chemistry and seepage fluxes in a mixed beech/oak stand. *Hydrological Processes*, 14
651 (1), 135-144.
- 652 Chen, J., Shiyomi, M., Hori, Y., Yamamura, Y., 2008. Frequency distribution models for
653 spatial patterns of vegetation abundance. *Ecological Modelling*, 211 (3-4), 403-410.
- 654 Cleavitt, N., Ewing, H., Weathers, K., Lindsey, A., 2011. Acidic atmospheric deposition
655 interacts with tree type and impacts the cryptogamic epiphytes in Acadia National Park,
656 Maine, USA. *Bryologist*, 114 (3), 570-582.
- 657 Cleavitt, N.L., Dibble, A.C., Werier, D.A., 2009. Influence of tree composition upon
658 epiphytic macrolichens and bryophytes in old forests of Acadia National Park, Maine.
659 *Bryologist*, 112 (3), 467-487.
- 660 del Rio, M., Sterba, H., 2009. Comparing volume growth in pure and mixed stands of *Pinus*
661 *sylvestris* and *Quercus pyrenaica*. *Annals of Forest Science*, 66 (5), 502 (p1)-502 (p11).
- 662 Dumas, Y., 2006. Espèces interférentes. In: Gama, A. (Ed.), *Guide Pratique - Utilisation des*
663 *herbicides en forêt et gestion durable*. Ministère de l'Agriculture et de la Pêche - Office
664 National des Forêts, pp. 181-221.

- 665 Farmer, A., Bates, J., Bell, J., 1991. Seasonal variations in acidic pollutant inputs and their
666 effects on the chemistry of stemflow, bark and epiphyte tissues in three oak woodlands in
667 N.W. Britain. *New Phytologist*, 118 (441), 451.
- 668 Felton, A., Lindbladh, M., Brunet, J., Fritz, Ö., 2010. Replacing coniferous monocultures with
669 mixed-species production stands: An assessment of the potential benefits for forest
670 biodiversity in northern Europe. *Forest Ecology and Management*, 260 (6), 939-947.
- 671 Fritz, Ö., Heilmann-Clausen, J., 2010. Rot holes create key microhabitats for epiphytic lichens
672 and bryophytes on beech (*Fagus sylvatica*). *Biological Conservation*, 143 (4), 1008-1016.
- 673 Gargominy, O., Terceirie, S., Régnier, C., Ramage, T., Schoelinck, C. et al., 2015. TAXREF
674 v9.0, référentiel taxonomique pour la France : méthodologie, mise en œuvre et diffusion.
675 SPN-2015-64, Museum National d'Histoire Naturelle, Service du Patrimoine Naturel, Paris.
- 676 Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences.
677 *Statistical Science*, 7, 457-511.
- 678 Gonzalez-Mancebo, J., Losada-Lima, A., McAlister, S., 2003. Host specificity of epiphytic
679 bryophyte communities of a laurel forest on Tenerife (Canary Islands, Spain). *The Bryologist*,
680 106 (3), 383-394.
- 681 Gosselin, F., 2011. Propositions pour améliorer l'équipement biométrique du détective
682 écologique. Application à la modélisation de la relation entre gestion forestière et biodiversité.
683 HDR Thesis, Université Pierre et Marie Curie, Paris.
- 684 Gosselin, F., 2015. Reevaluating Europe's other debt with improved statistical tools.
685 *Biodiversity and Conservation*, 24(1), 205-211.
- 686 Grime, J.P., Rincon, E., Wickerson, B., 1990. Bryophytes and plant strategy theory. *Botanical
687 journal of Linnean Society*, 104, 175-186.
- 688 Gustafsson, L., Eriksson, I., 1995. Factors of importance for the epiphytic vegetation of aspen
689 *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *Journal of
690 Applied Ecology*, 32 (2), 412-424.
- 691 Herpigny, B., Gosselin, F., 2015. Analyzing plant cover class data quantitatively: customized
692 cumulative zero-inflated beta distributions show promising results. *Ecological Informatics*, 26
693 (3), 18-26.
- 694 Jactel, H., Brockerhoff, E., Duelli, P., 2005. A test of the biodiversity-stability theory: Meta-
695 analysis of tree species diversity effects on insect pest infestations, and re-examination of
696 responsible factors. In: Scherer-Lorenzen, M., Körner, C. and Schulze, E. (Eds.), *Forest
697 Diversity and Function*. Ecological Studies Series.. Springer-Verlag, pp. 235-254.
- 698 Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects.
699 *Ecology Letters*, 10 (9), 835-848.

- 700 Kiraly, I., Nascimbene, J., Tinya, F., Odor, P., 2013. Factors influencing epiphytic bryophyte
701 and lichen species richness at different spatial scales in managed temperate forests.
702 *Biodiversity and Conservation*, 22 (1), 209-223.
- 703 Kiraly, I., Odor, P., 2010. The effect of stand structure and tree species composition on
704 epiphytic bryophytes in mixed deciduous-coniferous forests of Western Hungary. *Biological*
705 *Conservation*, 143 (9), 2063-2069.
- 706 Korboulewsky, N., Perez, G., Chauvat, M., 2016. How tree diversity affects soil fauna
707 diversity: A review. *Soil Biology and Biochemistry*, 94, 94-106.
- 708 Korboulewsky, N., Perot, T., Balandier, P., Ballon, P., Barrier, R. et al., 2015. OPTMix –
709 Dispositif expérimental de suivi à long terme du fonctionnement de la forêt mélangée.
710 *Rendez-Vous Techniques de l'ONF*, 47, 60-70.
- 711 Koricheva, J., Vehvilainen, H., Riihimäki, J., Ruohomäki, K., Kaitaniemi, P. et al., 2006.
712 Diversification of tree stands as a mean to manage pests and diseases in boreal forests: myth
713 or reality? *Canadian Journal of Forest Research*, 36 (2), 324-336.
- 714 Kriebitzsch, W.U., Bültmann, H., von Oheimb, G., Schmidt, M., Thiel, H. et al., 2013. Forest-
715 specific diversity of vascular plants, bryophytes and lichens. In: Kraus, D. and Krumm, F.
716 (Eds.), *Integrative approaches as an opportunity for the conservation of forest biodiversity*. In
717 *Focus - Managing Forest in Europe*. European Forest Institute, pp. 158-169.
- 718 Kuusinen, M., 1996. Epiphyte flora and diversity on basal trunks of six old-growth forest tree
719 species in southern and middle boreal Finland. *Lichenologist*, 28, 443-463.
- 720 Leith, I., Mitchell, R.J., Truscott, A.M., Cape, J.N., van Dijk, .. et al., 2008. The influence of
721 nitrogen in stemflow and precipitation on epiphytic bryophytes, *Isoetecium myosuroides*
722 *Brid.*, *Dicranum scoparium* *Hewd.* and *Thuidium tamariscinum* (*Hewd.*) *Schimp* of Atlantic
723 oakwoods. *Environmental Pollution*, 155 (2), 237-246.
- 724 Levia, D.F., Frost, E.E., 2003. A review and evaluation of stemflow literature in the
725 hydrologic and biogeochemical cycles of forested and agricultural ecosystems. *Journal of*
726 *Hydrology*, 274 (1-4), 1-29.
- 727 Lubbe, T., Schuldt, B., Coners, H., Leuschner, C., 2016. Species diversity and identity effects
728 on the water consumption of tree sapling assemblages under ample and limited water supply.
729 *Oikos*, 125 (1), 86-97.
- 730 Lunn, D.J., Thomas, A., Best, N., Spiegelhalter, D., 2000. WinBUGS - A Bayesian modelling
731 framework: Concepts, structure, and extensibility. *Statistics and Computing*, 10 (4), 325-337.
- 732 Lygis, V., Vasiliauskas, R., Stenlid, J., Vasiliauskas, A., 2004. Silvicultural and pathological
733 evaluation of Scots pine afforestations mixed with deciduous trees to reduce the infections by
734 *Heterobasidion annosum* s.s. *Forest Ecology and Management*, 201 (2-3), 275-285.
- 735 Lynch, H.J., Thorson, J.T., Shelton, A.O., 2014. Dealing with under- and over-dispersed
736 count data in life history, spatial, and community ecology. *Ecology*, 95 (11), 3173-3180.

- 737 Marialigeti, S., Nemeth, B., Tinya, F., Odor, P., 2009. The effects of stand structure on
738 ground-floor bryophyte assemblages in temperate mixed forests. *Biodiversity and*
739 *Conservation*, 18 (8), 2223-2241.
- 740 McGee, G., Kimmerer, R., 2002. Forest age and management effects on epiphytic bryophyte
741 communities in Adirondack northern hardwood forests, New York, U.S.A. *Canadian Journal*
742 *of Forest Research*, 32 (9), 1562-1576.
- 743 Migge, S., Maraun, M., Scheu, S., Schaefer, M., 1998. The oribatid mite community
744 (Acarina) of pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*) of
745 different age. *Applied Soil Ecology*, 9 (1-3), 115-121.
- 746 Millar, R.B., 2009. Comparison of hierarchical bayesian models for overdispersed count data
747 using DIC and Bayes' factors. *Biometrics*, 65 (3), 962-969.
- 748 Nagano, I., 1972. On the relations of the chemical composition of some mosses to their
749 substrate rocks. *Journal of the Hattori Botanical Laboratory*, 35, 391-398.
- 750 Neite, H., Wittig, R., 1985. Correlation of chemical soil pattern with the floristic pattern in the
751 trunk base area of the beech. *Acta Oecologica*, 6 (4), 375-385.
- 752 Odor, P., Kiraly, I., Tinya, F., Bortignon, F., Nascimbene, J., 2013. Patterns and drivers of
753 species composition of epiphytic bryophytes and lichens in managed temperate forests. *Forest*
754 *Ecology and Management*, 306, 256-265.
- 755 Oxbrough, A., French, V., Irwin, S., Kelly, T.C., Smiddy, P. et al., 2012. Can mixed species
756 stands enhance arthropod diversity in plantation forests? *Forest Ecology and Management*,
757 270, 11-18.
- 758 Parrotta, J.A., 1999. Productivity, nutrient cycling, and succession in single- and mixed-
759 species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala*
760 in Puerto Rico. *Forest Ecology and Management*, 124 (1), 45-77.
- 761 Pérot, T., Picard, N., 2012. Mixture enhances productivity in a two-species forest: evidence
762 from a modeling approach. *Ecological Research*, 27 (1), 83-94.
- 763 Perot, T., Vallet, P., Archaux, F., 2013. Growth compensation in an oak–pine mixed forest
764 following an outbreak of pine sawfly (*Diprion pini*). *Forest Ecology and Management*, 295
765 (0), 155-161.
- 766 Pretzsch, H., 2003. Diversity and productivity of forests. *Allgemeine Forst Und Jagdzeitung*,
767 174 (5-6), 88-98.
- 768 Raabe, S., Müller, J., Manthey, M., Dürhammer, O., Teuber, U. et al., 2010. Drivers of
769 bryophyte diversity allow implications for forest management with a focus on climate change.
770 *Forest Ecology and Management*, 260 (11), 1956-1964.
- 771 Saas, Y., Gosselin, F., 2014. Simulation-based comparative analysis of spatial count
772 regression methods on regularly and irregularly-spaced locations. *Ecography*, 37 (5), 476-489.

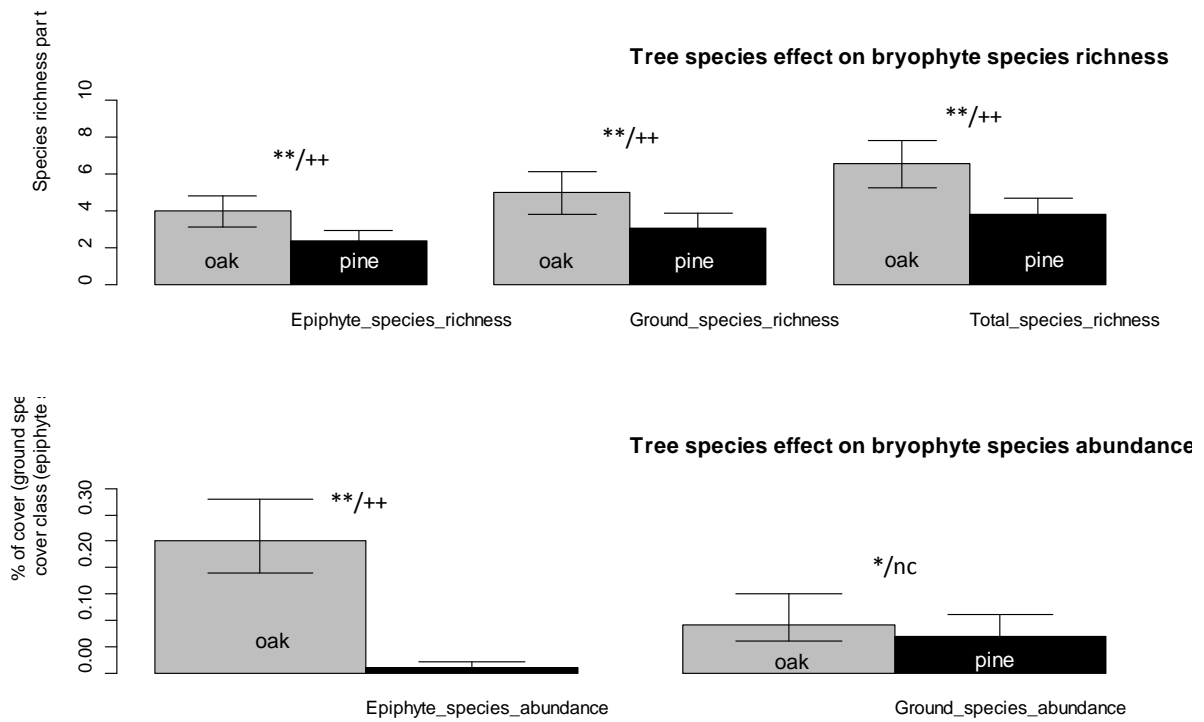
- 773 Scheu, S., Albers, D., Alpei, J., Bury, R., Klages, U., Migge, S. et al., 2003. The soil fauna
774 community in pure and mixed stands of beech and spruce of different age: trophic structure
775 and structuring forces. *Oikos*, 101 (2), 225-238.
- 776 Simmons, E.A., Buckley, G.P., 1992. Ground vegetation under planted mixtures of trees. In:
777 Cannell, M.G.R., Malcolm, D.C. and Robertson, P.A. (Eds.), *The ecology of mixed-species*
778 *stands of trees*. Blackwell Scientific Publications, Oxford, pp. 211-231.
- 779 Smith, K.W., 1992. Birds populations: effects of tree species mixtures. In: Cannell, M.G.R.,
780 Malcolm, D.C. and Robertson, P.A. (Eds.), *The ecology of mixed-species stands of trees*.
781 Blackwell Scientific Pub., Oxford, pp. 233-242.
- 782 Sobek, S., Gossner, M., Scherber, C., Steffan-Dewenter, I., Tschardtke, T., 2010. Tree
783 diversity drives abundance and spatiotemporal beta-diversity of true bugs (Heteroptera).
784 *Ecological Entomology*, 34 (6), 772-782.
- 785 Sutinen, R., Teirila, A., Panttaja, M., Sutinen, M.L., 2002. Distribution and diversity of tree
786 species with respect to soil electrical characteristics in Finnish Lapland. *Canadian Journal of*
787 *Forest Research*, 32 (7), 1158-1170.
- 788 Tinya, F., Márialigeti, S., Király, I., Németh, B., Ódor, P., 2009. The effect of light conditions
789 on herbs, bryophytes and seedlings of temperate mixed forests in Orség, Western Hungary.
790 *Plant Ecology*, 204 (1), 69-81.
- 791 Toigo, M., Vallet, P., Perot, T., Bontemps, J., Piedallu, C. et al., 2015. Overyielding in mixed
792 forests decreases with site productivity. *Journal of Ecology*, 103 (2), 505-512.
- 793 Vallet, P., Pérot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway
794 spruce: evidence based on large-scale inventory data and a generic modelling approach.
795 *Journal of Vegetation Science*, 22, 932-942.
- 796 Vaychis, M., Danusyavichus, Y.u., 1978. Effect of birch on soil properties in a pine
797 plantation. *Pochvovedenie* (1), 113-123.
- 798 Vellak, K., Paal, J., Liira, J., 2003. Diversity and distribution pattern of bryophytes and
799 vascular plants in a boreal spruce forest. *Silva Fennica*, 37 (1), 3-13.
- 800 Virtanen, R., Johnston, A.E., Crawley, M.J., Edwards, G.R., 2000. Bryophyte biomass and
801 species richness on the Park Grass Experiment, Rothamsted, UK. *Plant Ecology*, 151 (2), 129-
802 141.
- 803 Wallrup, E., Saetre, P., Rydin, H., 2006. Deciduous trees affect small-scale floristic diversity
804 and tree regeneration in conifer forests. *Scandinavian Journal of Forest Research*, 21 (5), 399-
805 404.
- 806 Watt, A.D., 1992. Insect pest population dynamics: effects of tree species diversity. In:
807 Cannell, M.G.R., Malcolm, D.C. and Robertson, P.A. (Eds.), *The ecology of mixed-species*
808 *stands of trees*. Blackwell Scientific Pub., Oxford, pp. 267-275.

809 Wittig, R., Neite, H., 1985. Acid indicators around the trunk base of *Fagus sylvatica* in
810 limestone and loess beechwoods: distribution pattern and phytosociological problems.
811 *Vegetatio*, 64 (2-3), 113-119.

812 Zilliox, C., Gosselin, F., 2014. Tree species diversity and abundance as indicators of
813 understory diversity in French mountain forests: Variations of the relationship in geographical
814 and ecological space. *Forest Ecology and Management*, 321, 105-116.

815 **Figures**

816



818

819

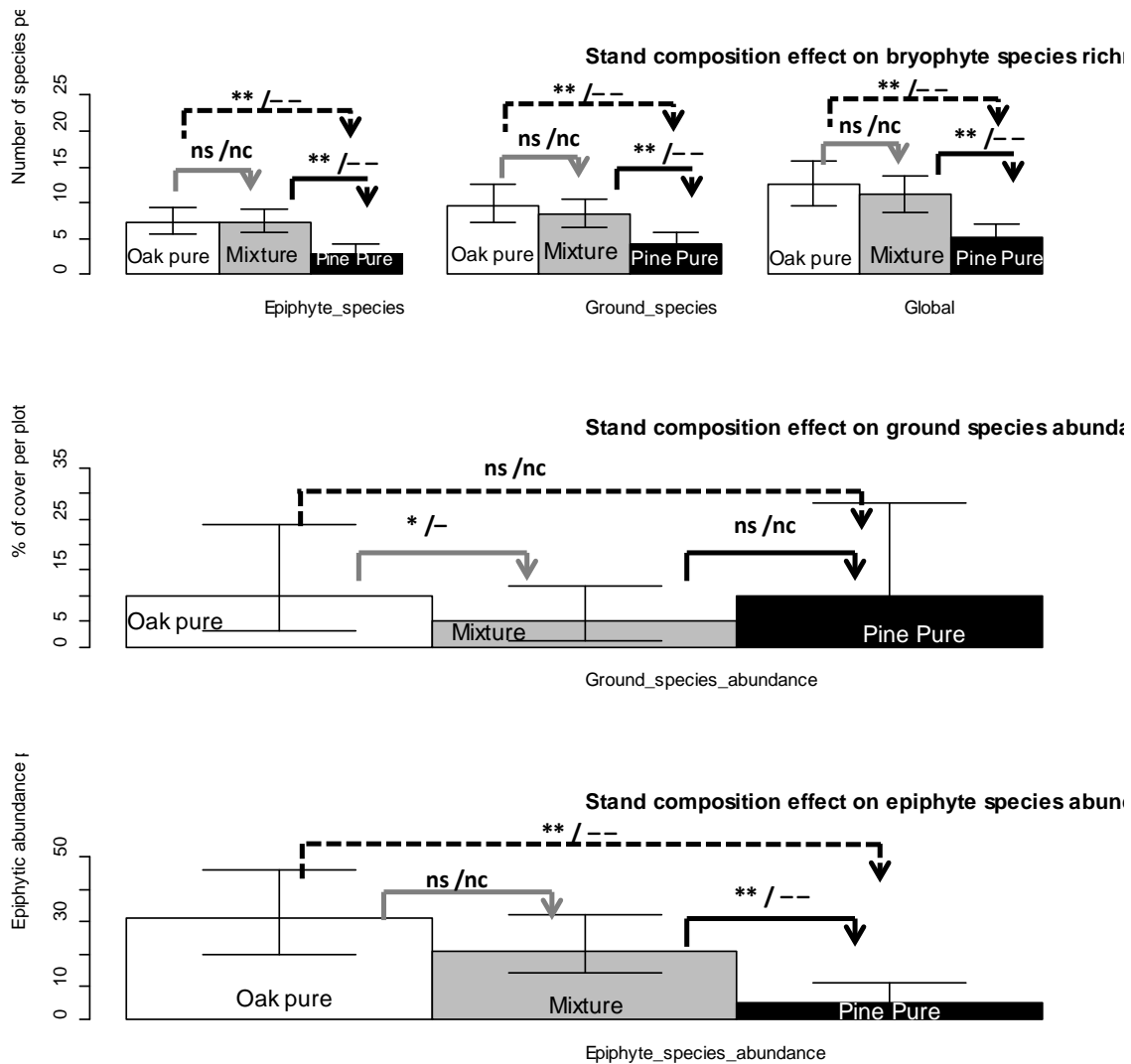
820

821

822

Figure 1. Tree species effect on bryophyte diversity at tree level: oak-pine difference for epiphyte, ground and total bryophyte species richness, for epiphyte species abundance and for ground-species abundance. **=significant (p<0.01), *=significant (p<0.05), ++: very strong effect (more than 20% species (or cover) more on oak), nc: non conclusive magnitude of the effect.

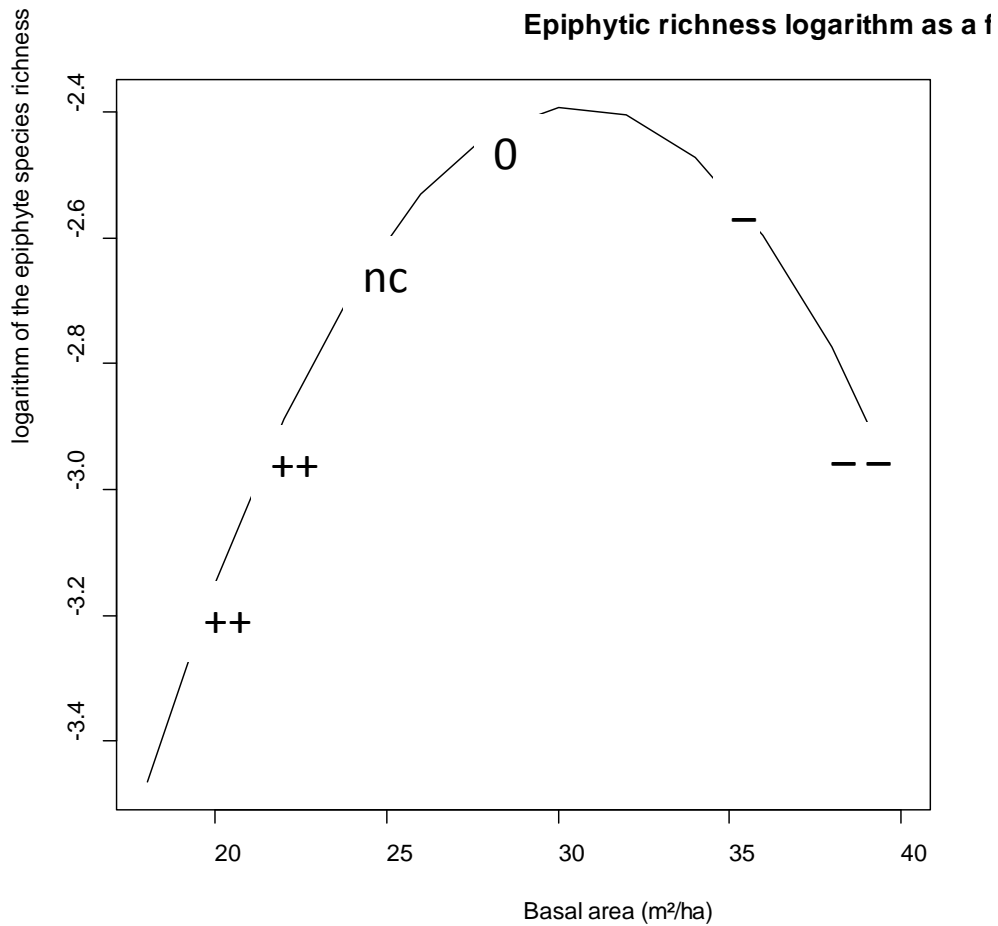
823



824

825 **Figure 2.** Stand composition effect on bryophyte diversity at “plot” level (group of three trees): differences between pure
 826 oak, pure pine and mixed stands are given for epiphytes, ground species and global species richness (top graph), for
 827 ground species abundance within 1m around the trunks, assessed as a percentage of cover (middle) and for epiphyte
 828 species abundance, assessed in mean percentage of cover. Grey line: differences between pure oak and mixed stands.
 829 Black line: differences between pure pine and mixed stands. Dotted line: differences between pure oak and pure pine
 830 stands. **=significant (p<0.01), *=significant (p<0.05), ns=non-significant, - -: very strong difference (magnitude more
 831 than 20%), -: strong difference (magnitude more than 10%), nc: non conclusive magnitude of the effect.

832



833

834 **Figure 3. Quadratic effect of basal area on epiphyte richness at plot level!** The values here illustrate the case of pure oak
 835 stands and do not include the inter-plot variability (random effects). **=significant (p<0.01), *=significant (p<0.05),
 836 ns=non-significant, --: very strong difference (magnitude more than 20%), -: strong difference (magnitude more than
 837 10%), nc: non conclusive magnitude of the effect.

Tables

Table 1. Tree level presence probabilities of bryophyte species on (or under) oak and pine, regardless of stand composition type, and magnitude analysis of the oak-pine difference (**Hypothesis H1**). Presence probabilities were estimated through logistic regression for the most frequent species (at least nine occurrences). **The values here do not include the inter-plot variability (random effects)**

SPECIES	Number of occurrences	Presence probability on oak (O)	Presence probability on pine (P)	Difference (analyzed ratio: O/P)	
				significance	Magnitude
<i>Hypnum jutlandicum</i> Holmen & E.Warncke	54	0.36 [0.18 ; 0.55]	0.92 [0.8 ; 0.99]	*	--
<i>Hypnum cupressiforme</i> Hedw.	63	1.00 [1.00 ; 1.00]	0.49 [0.13 ; 0.86]	*	++
<i>Lophocolea heterophylla</i> (Schrad.) Dumort.	24	0.12 [0.04 ; 0.26]	0.43 [0.26 ; 0.61]	*	--
<i>Campylopus flexuosus</i> (Hedw.) Brid.	10	0.02 [0.001 ; 0.11]	0.09 [0.01 ; 0.31]	*	--
<i>Lophocolea bidentata</i> (L.) Dumort., 1835	9	0.12 [0.02 ; 0.37]	0.00 [0.00 ; 0.00]	*	++
<i>Dicranum scoparium</i> Hedw.	62	0.89 [0.59 ; 0.98]	0.68 [0.36 ; 0.92]	ns	nc
<i>Frullania dilatata</i> (L.) Dumort.	24	0.59 [0.38 ; 0.79]	0.00 [0.00 ; 0.00]	*	++
<i>Frullania tamarisci</i> (L.) Dumort.	12	0.2 [0.05 ; 0.48]	0.00 [0.00 ; 0.00]	*	++
<i>Leucobryum glaucum</i> (Hedw.) Angstr.	16	0.20 [0.05 ; 0.39]	0.1 [0.03 ; 0.25]	ns	nc
<i>Orthotrichum lyellii</i> Hook. & Taylor	9	0.13 [0.03 ; 0.37]	0.00 [0.00 ; 0.00]	*	++
<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.	15	0.13 [0.03 ; 0.34]	0.1 [0.02 ; 0.28]	ns	nc
<i>Polytrichum formosum</i> Hedw.	37	0.85 [0.6 ; 0.97]	0.05 [0.006 ; 0.2]	*	++
<i>Pseudoscleropodium purum</i> (Hedw.) M.Fleisch.	57	0.83 [0.52 ; 0.97]	0.8 [0.45 ; 0.96]	ns	nc
<i>Thuidium tamariscinum</i> (Hedw.) Schimp.	26	0.49 [0.29 ; 0.68]	0.09 [0.03 ; 0.22]	*	++

ns = non-significant, nc = no possible conclusion about the effect magnitude, *=significant (p<0.05), **=significant (p<0.01), --=very strong negative effect (probability higher by more than 20% on pine), ++= very strong positive effect (probability higher by more than 20% on oak). **The values (means and 95% confidence intervals) are rounded to two decimal places.**

Table 2. Mean estimated bryophyte species richness and abundance values on oak and on pine, in pure compared to mixed stands (**Hypothesis H2**), with their 95% confidence intervals, and analysis of the pure-mixed difference: the stand composition effect depends on tree species identity. **The values here do not include the inter-plot variability (random effects).**

Tree level		SRglob (n=84)	SRepiph (n=84)	SRground (n=84)	ABground/N (n=84)	ABepiph (n=84)	
	Composition	Pure	7.23 [5.44 ; 9.41]	3.99 [2.88 ; 5.49]	5.73 [4.2 ; 7.6]	0.11 [0.02 ; 0.47]	0.19 [0.09 ; 0.33]
		Mixed	6.74 [6.53 ; 6.89]	4.51 [4.37 ; 4.66]	4.69 [4.47 ; 4.83]	0.06 [0.02 ; 0.2]	0.28 [0.23 ; 0.32]
On oak	Difference (analyzed ratio: Mixed/Pure):	significance	ns	ns	ns	*	ns
	Magnitude	nc	nc	nc	-	nc	
	Composition	Pure	3.08 [1.9 ; 4.88]	1.78 [0.98 ; 3.15]	2.38 [1.65 ; 3.33]	0.12 [0.01 ; 0.66]	0.02 [0.004 ; 0.08]
		Mixed	4.42 [3.7 ; 5.21]	2.93 [2.36 ; 3.63]	3.66 [3.56 ; 3.7]	0.04 [0.01 ; 0.19]	0.01 [0.008 ; 0.02]
On pine	Difference (analyzed ratio: Mixed/Pure):	significance	*	**	*	*	ns
	Magnitude	+	++	+	--	nc	

ns = non-significant, nc = no possible conclusion about effect magnitude, *=significant (p<0.05), **=significant (p<0.01), += strong positive effect (more than 10% more species in mixed stands), ++= very strong positive effect (more than 20% more species in mixed stands).

SRepiph= epiphytic richness; SRground= ground bryophyte richness within 1 m of the trunk; SRglob=epiphytic and ground richness per tree; ABground= ground bryophyte abundance within 1 m of the trunk; N= maximum measured ground bryophyte abundance within 1m of the trunk (15,000 cm²); ABepiph=mean epiphyte cover (in percentage of cover)

Table 3. Presence probabilities of the most frequent bryophyte species on oak and pine trees in interaction with stand composition type, estimated through logistic regression (Hypothesis H2). The values here do not include the inter-plot variability (random effects).

	Number of occurrences	Presence probability on oak			Presence probability on pine		
		in pure stands	in mixed stands	Pure/mixed difference	in pure stands	in mixed stands	Pure/mixed difference
<i>Campylopus flexuosus</i> (Hedw.) Brid.	10	0.04 [0.0004 ; 0.15]	0.01 [0.003 ; 0.25]	ns/nc	0.00 [0.00 ; 0.00]	0.26 [0.05 ; 0.63]	ns(lim*)/--
<i>Lophocolea bidentata</i> (L.) Dumort., 1835	9	0.07 [0.005 ; 0.34]	0.19 [0.02 ; 0.57]	ns/nc	0.00 [0.00 ; 0.00]	0.00 [0.00 ; 0.00]	ns/nc
<i>Lophocolea heterophylla</i> (Schrad.) Dumort.	24	0.16 [0.04 ; 0.39]	0.07 [0.01 ; 0.25]	ns/nc	0.42 [0.19 ; 0.67]	0.42 [0.21 ; 0.68]	ns/nc
<i>Dicranum scoparium</i> Hedw.	62	1.00 [1.00 ; 1.00]	0.85 [0.6 ; 0.97]	ns/nc	0.21 [0.05 ; 0.48]	0.94 [0.74 ; 0.99]	** / --
<i>Frullania dilatata</i> (L.) Dumort.	24	0.64 [0.36 ; 0.88]	0.54 [0.26 ; 0.8]	ns/nc	0.00 [0.00 ; 0.00]	0.00 [0.00 ; 0.00]	ns/nc
<i>Frullania tamarisci</i> (L.) Dumort.	12	0.11 [0.01 ; 0.43]	0.31 [0.06 ; 0.72]	ns/nc	0.00 [0.00 ; 0.00]	0.00 [0.00 ; 0.00]	ns/nc
<i>Hypnum cupressiforme</i> Hedw.	63	1.00 [1.00 ; 1.00]	1.00 [1.00 ; 1.00]	ns/[00]	0.1 [0.01 ; 0.54]	0.84 [0.35 ; 0.98]	ns(lim*)/--
<i>Hypnum jutlandicum</i> Holmen & E.Warncke	54	0.31 [0.11 ; 0.58]	0.42 [0.18 ; 0.68]	ns/nc	0.89 [0.67 ; 0.98]	0.97 [0.83 ; 1]	ns/nc
<i>Leucobryum glaucum</i> (Hedw.) Angstr.	16	0.35 [0.12 ; 0.63]	0.11 [0.02 ; 0.33]	ns/nc	0.00 [0.00 ; 0.00]	0.2 [0.06 ; 0.46]	ns(lim*)/--
<i>Orthotrichum lyellii</i> Hook. & Taylor	9	0.13 [0.01 ; 0.49]	0.11 [0.01 ; 0.44]	ns/nc	0.00 [0.00 ; 0.00]	0.00 [0.00 ; 0.00]	ns/nc
<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.	15	0.15 [0.02 ; 0.5]	0.08 [0.01 ; 0.35]	ns/nc	0.15 [0.02 ; 0.52]	0.04 [0.003 ; 0.26]	ns/nc
<i>Polytrichum formosum</i> Hedw.	37	1.00 [1.00 ; 1.00]	0.65 [0.32 ; 0.89]	** / +	0.02 [0 ; 0.17]	0.06 [0.006 ; 0.26]	ns/nc
<i>Pseudoscleropodium purum</i> (Hedw.) M.Fleisch.	57	0.62 [0.24 ; 0.91]	0.73 [0.32 ; 0.95]	ns/nc	1.00 [1.00 ; 1.00]	0.46 [0.13 ; 0.82]	** / ++
<i>Thuidium tamariscinum</i> (Hedw.) Schimp.	26	0.47 [0.19 ; 0.75]	0.53 [0.25 ; 0.8]	ns/nc	0.06 [0.006 ; 0.25]	0.11 [0.02 ; 0.34]	ns/nc

Pure/Mixed difference: ratio between the presence probability of the species in pure stands and its presence probability in mixed stands.

+ (resp. ++): non negligible difference in presence probability, with ratio >1, negligibility threshold = 10% (resp. 20%) ;

– (resp. – –): non negligible difference in presence probability, with ratio <1, negligibility threshold = 10% (resp. 20%) ;

00: very negligible difference (threshold = 10%); 0: negligible difference (threshold = 20%); nc: no possible conclusion about the magnitude of the difference; ns: non-significant ($p < 0.05$)

*: significant ($p < 0.005$) **: significant ($p < 0.001$).

The values (means and 95% confidence intervals) are rounded to two decimal places.

Table 4. Plot level. Presence probabilities of the most frequent bryophyte species in mixed and pure stands, estimated through logistic regression (Hypothesis H3). The values here do not include the inter-plot variability (random effects)

Species	Nb occurr.	Species presence probability			Difference between stands		
		Pure oak stands	Mixed stands	Pure pine stands	Analyzed Ratio	significance	magnitude
<i>Hypnum jutlandicum</i> Holmen & E. Warncke	26	0.8 [0.29 ; 0.99]	1.00 [1.00 ; 1.00]	1.00 [1.00 ; 1.00]	M/O	ns	nc
					M/P	ns	00
					O/P	ns	nc
<i>Hypnum cupressiforme</i> Hedw.	23	1.00 [1.00 ; 1.00]	1.00 [1.00 ; 1.00]	0.2 [0.01 ; 0.7]	M/O	ns	00
					M/P	*	++
					O/P	*	++
<i>Lophocolea heterophylla</i> (Schrad.) Dumort.	17	0.41 [0.08 ; 0.82]	0.59 [0.26 ; 0.87]	0.93 [0.53 ; 1]	M/O	ns	nc
					M/P	ns	nc
					O/P	ns	-
<i>Campylopus flexuosus</i> (Hedw.) Brid.	9	0.16 [0.01 ; 0.74]	0.49 [0.09 ; 0.9]	0.00 [0.00 ; 0.00]	M/O	ns	nc
					M/P	ns (lim)	++
					O/P	*	++
<i>Dicranum scoparium</i> Hedw.	25	1.00 [1.00 ; 1.00]	1.00 [1.00 ; 1.00]	0.6 [0.14 ; 0.95]	M/O	ns	00
					M/P	ns	Nc(+)
					O/P	*	Nc(+)
<i>Frullania dilatata</i> (L.) Dumort.	16	1.00 [1.00 ; 1.00]	0.67 [0.31 ; 0.91]	0.00 [0.00 ; 0.00]	M/O	*	-
					M/P	*	++
					O/P	*	++
<i>Frullania tamarisci</i> (L.) Dumort.	9	0.39 [0.05 ; 0.87]	0.38 [0.07 ; 0.8]	0.00 [0.00 ; 0.00]	M/O	ns	nc
					M/P	ns	++
					O/P	*	++
<i>Leucobryum glaucum</i> (Hedw.) Angstr.	12	0.94 [0.53 ; 1]	0.39 [0.09 ; 0.78]	0.00 [0.00 ; 0.00]	M/O	*	-
					M/P	ns	00
					O/P	*	00

<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.	11	0.38 [0.05 ; 0.86]	0.28 [0.04 ; 0.71]	0.4 [0.05 ; 0.89]	M/O	ns	nc
					M/P	ns	nc
					O/P	ns	nc
<i>Polytrichum formosum</i> Hedw.	19	1.00 [1.00 ; 1.00]	0.85 [0.49 ; 0.98]	0.06 [0.001 ; 0.5]	M/O	*	nc
					M/P	ns	++
					O/P	*	++
<i>Pseudoscleropodium purum</i> (Hedw.) M.Fleisch.	24	0.95 [0.56 ; 1]	0.86 [0.47 ; 0.98]	1.00 [1.00 ; 1.00]	M/O	ns	nc
					M/P	*	nc
					O/P	ns	nc
<i>Thuidium tamariscinum</i> (Hedw.) Schimp.	19	0.94 [0.51 ; 1]	0.86 [0.5 ; 0.98]	0.2 [0.02 ; 0.71]	M/O	ns	nc
					M/P	ns	++
					O/P	*	++

M/O: ratio between the presence probability in mixed stands and in pure oak stands. M/P: ratio between the presence probability in mixed stands and in pure pine stands. O/P: ratio between the presence probability in pure oak stands and in pure pine stands.

+ (resp. ++): non negligible difference in presence probability, with ratio >1, negligibility threshold = 10% (resp. 20%);

- (resp. --): non negligible difference in presence probability, with ratio <1, negligibility threshold = 10% (resp. 20%);

00: very negligible difference (threshold = 10%); 0: negligible difference (threshold = 20%); nc: no possible conclusion about the magnitude of the difference. ns: non-significant (p<0.05) *: significant (p<.005).

The values (means and 95% confidence intervals) are rounded to two decimal places.

Supplementary material

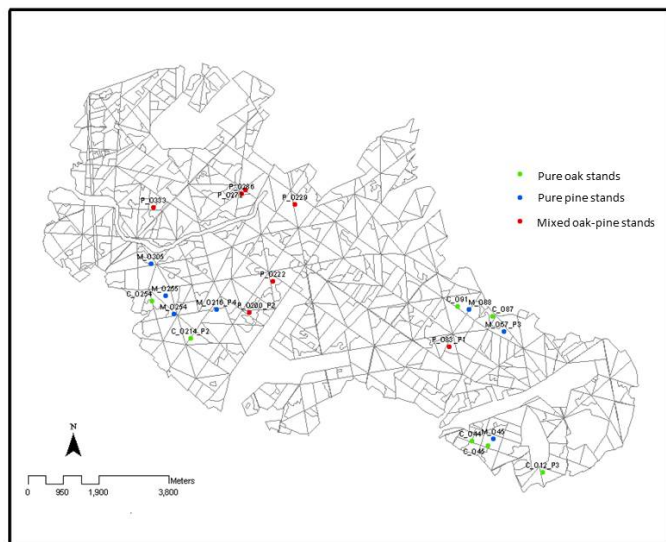


Figure SM1. The study design consisted in seven repetitions for three stand types: pure oak, pure pine and mixed oak-pine stands, leading to a total of 21 plots.

Table SM1. Tree- and plot-level main and exploratory hypotheses.

Hypothesis Type	Level	Tested effects	Bryophyte diversity component	Hypothesis
Main	Tree	Tree species (H1)	Richness and abundance	H1a) Bryophyte species diversity (both epiphyte and ground) is higher on oak than on pine
			Composition	H1b) Presence probability of bryophyte species (both epiphyte and ground) on and under a tree differs between oak and pine.
		Interaction between tree species identity and stand composition (H2)	Richness, abundance and composition	H2) For a given tree-species, both epiphyte and ground bryophyte diversity differs between pure and mixed stands.
	Plot	Stand composition (H3)	Richness and abundance	H3a) The plot species diversity (both epiphyte and ground species) is higher in mixed stands than in pure ones; this is related to higher habitat heterogeneity.
Composition			H3b) Presence probability of bryophyte species at the plot level depends on the composition of the stand (pure pine, pure oak, mixture).	
Exploratory	Tree	Substrate and water supply characteristics (H4)	Epiphytic bryophyte diversity	H4a) Epiphytic bryophyte diversity increases with trunk diameter, with inclination and with bark and stemflow pH or conductivity.
			Ground bryophyte diversity	H4b) Ground bryophyte diversity under the tree varies with trunk diameter and increases with soil and throughfall pH and conductivity.
	Plot	Basal area and interfering plants (H5)	Richness and abundance	H5) Species diversity (both epiphyte and ground) decreases with stand density or interfering understory plant cover.
	Plot	Basal area and interfering plants (H6)	Richness and abundance	H6) Plot species diversity (both epiphyte and ground) decreases with tree density or interfering understory plant cover; this is related to less light.

Table SM2. Models used at tree or plot level and corresponding response variables. The main models are those for which the sampling design was balanced. Other models are based on other environmental data used as single explanatory variables or additional covariates.

Scale	Hypothesis	Response variable	Models	Variable content of the model in R syntax	Covariable	Model type			
Tree	H1a	SRepiph SRground SRglob ABground SRground25 SRground75 ABground25 ABground75 ABepiph	Tree species	~ Tree_Species - 1		Main			
			Tree	H1b	Sp.Occurence	Tree_Species	~ Tree_Species - 1		Main
			Tree	H2	SRepiph SRground SRglob ABground SRground25 SRground75 ABground25 ABground75 ABepiph Sp.Occurence	Tree_Species:Stand_composition	~ ifelse(Compo_MP=="Pure",1,-1); Tree_Species+ Tree_Species		Main
			Tree	H4a	SRepiph ABepiph	Tree_Species + Covariable	~ Tree_Species + Covariable	Bark pH	Exploratory
						Covariable	~ Covariable	Bark conductivity	Exploratory
						Tree_Species:Stand_composition + Covariable	~ ifelse(Compo_MP=="Pure",1,-1); Tree_Species+ Tree_Species + Covariable	Trunk diameter Trunk Inclination October stemflow pH February stemflow conductivity	Exploratory
			Tree	H4b	SRground ABground (SRglob) SRground25 SRground75 ABground25 ABground75 SRground25 ABground25 SRground75 ABground75	Tree_Species + Covariable	~ Tree_Species + Covariable		Exploratory
						Covariable	~ Covariable		Exploratory
						Tree_Species:Stand_composition + Covariable	~ ifelse(Compo_MP=="Pure",1,-1); Tree_Species+ Tree_Species + Covariable	Tree diameter	Exploratory
SRground25	Tree_Species + Covariable	~ Species + Covariable				pH.TF25.Oct	Exploratory		
ABground25	Covariable	~ Covariable				pH.TF25.Feb	Exploratory		
	Tree_Species:Stand_composition + Covariable	~ ifelse(Compo_MP=="Pure",1,-1); Tree_Species+ Tree_Species + Covariable				pH.OM.25 pH.Surf25 conduc.TF25	Exploratory		
SRground75	Tree_Species + Covariable	~ Tree_Species + Covariable				pH.TF75.Oct	Exploratory		
ABground75	Covariable	~ Covariable				pH.TF75.Feb	Exploratory		
	Tree_Species:Stand_composition + Covariable	~ ifelse(Compo_MP=="Pure",1,-1); Tree_Species+ Tree_Species + Covariable	pH.OM.75 pH.Surf75	Exploratory					

				Covariable	conduc.TF75	
Tree	H5	SRepiph	Tree_Species + Covariable	~ Tree_Species + Covariable		Exploratory
		ABepiph	Covariable	~ Covariable		Exploratory
		SRground	Tree_Species:Stand_composition +	~ ifelse(Compo_MP=="Pure",1,-1):		Exploratory
		ABground	Covariable	Tree_Species+ Tree_Species +	G	
		SRglob		Covariable	G+G^2	
	SRground25				Rec_Interf_Glob	
	SRground75					
	ABground25					
	ABground75					
	SRepiph	Tree_Species : Covariable	~ Tree_Species + Tree_Species :			Exploratory
	ABepiph		Covariable - 1			
	SRground	Tree_Species : Stand_composition :	~Stand_sp_type +			Exploratory
	ABground	Covariable	Covariable:Stand_sp_type - 1	G		
	SRglob			G+G^2		
	SRground25					
SRground75						
ABground25						
ABground75						
SRground25	Tree_Species + Covariable	~ Tree_Species + Covariable			Exploratory	
ABground25	Covariable	~ Covariable			Exploratory	
				Rec_Interf_25		
		Tree_Species:Stand_composition +	~ ifelse(Compo_MP=="Pure",1,-1):		Exploratory	
		Covariable	Tree_Species+ Tree_Species +			
			Covariable			
	SRground75	Tree_Species + Covariable	~ Tree_Species + Covariable		Exploratory	
	ABground75	Covariable	~ Covariable		Exploratory	
		Tree_Species:Stand_composition +	~ ifelse(Compo_MP=="Pure",1,-1):		Exploratory	
		Covariable	Tree_Species+ Tree_Species +	Rec_Interf_75		
			Covariable			
Plot	H3a	SRepiph	Stand composition	~Stand_composition	G	Main
		SRground			G+G^2	
		SRglob			Rec_Interf_Glob	
	ABground					
	H3b	Sp.Occurence	Stand_Composition	~ Stand_Composition - 1		Main
	H6	SRepiph	Covariable	~Covariable		Exploratory
	SRground	Stand_Composition + Covariable	~ Stand_Composition + Covariable - 1	G	Exploratory	
	SRglob	Stand_Composition:Covariable	~ Stand_composition + Covariable:	G+G^2	Exploratory	
	ABground		Stand_composition -1	Rec_Interf_Glob		

SRepiph = species richness resulting from data collected on trunks. SRground = species richness resulting from data collected on the forest floor within a distance of 1 meter around the trunk. SRglob = species richness resulting from data collected both on the trunk and on the forest floor within a distance of 1 meter around the trunk. ABground: abundance of species collected on the forest floor within a distance of 1 meter around the trunk. SRground25 (resp.ABground25) = species richness (resp. abundance) resulting from data collected on the forest floor at 25 cm from the trunk. SRground75 (resp.ABground75) = species richness (resp. abundance) resulting from data collected on the forest floor at 75 cm from the trunk. ABepiph: total abundance of species collected on trunks. Sp.Occurence: presence probability of a bryophyte species.

Tree_Species: 2-level factor (pine or oak). Compo_MP: 2-level factor (pure or mixed). Stand_composition: 3-level factor (oak pure, pine pure, mixture). Stand_sp_type : 4-level factor (oak in pure stands, oak in mixed stands, pine in pure stands, pine in mixed stands). Diameter: mean quadratic diameter at 1.3m height. Inclination: trunk inclination (angle from the vertical, in degrees). Bark.pH: measured bark pH. Bark.conduc: measured bark conductivity. pH.TF25.Oct (resp. pH.TF75.Oct): measured pH of throughfall samplings collected in October at 25 cm (resp. 75 cm) from the trunk. pH.TF25.Feb (resp. pH.TF75.Feb): measured pH of throughfall samplings collected in February at 25 cm (resp. 75 cm) from the trunk. Conduc.TF25 (resp. conduc.TF75): measured conductivity of throughfall samplings collected in February at 25 cm (resp. 75 cm) from the trunk. pH.OM.25 (resp. pH.OM.75): measured pH of the organo-mineral horizon samples collected at 25 cm (resp. 75 cm) from the trunk. pH.Surf25 (resp. pH.Surf75): measured pH of the surface soil samples

collected at 25 cm (resp. 75 cm) from the trunk. G: basal area of the plot ($\text{m}^2 \text{ha}^{-1}$). Rec_Interf_25 (resp. Rec_Interf_75): Cover percentage of interfering vegetation within a 50cm-width ring centered 25 cm (resp. 75 cm) from the trunk. Rec_Interf_Glob : cover percentage of interfering vegetation inside a ring 1 meter in width traced around the trunk.

Table SM3. Notations for the magnitude of the effect. A strong effect leads to a variation of more than 10% in the response variable, a very strong effect leads to a variation of more than 20%. Note that $\beta \Delta X$ is equal to $\log(\text{mean}(Y_{\text{new}}) / \text{mean}(Y_{\text{init}}))$, where Y_{new} is the modeled response random variable after the simulated variation ΔX of the explanatory variable, and Y_{init} is the response random variable for the initial value of X .

Version	Case (In this example, the response random variable Y is count data, modelled by $\text{mean}(Y) = \exp(\alpha + \beta X)$. X is the explanatory variable and ΔX the simulated variation in X).	Notation	Meaning
weak	$P(\log(0.9) < \beta \Delta X < \log(1.1)) \geq 95\%$	00	Very negligible effect
	$P(\beta \Delta X > \log(1.1)) \geq 95\%$	+	Strong positive effect
	$P(\beta \Delta X < \log(0.9)) \geq 95\%$	-	Strong negative effect
	Other cases	nc	No possible conclusion
strong	$P(\log(0.8) < \beta \Delta X < \log(1.2)) \geq 95\%$	0	Negligible effect
	$P(\beta \Delta X > \log(1.2)) \geq 95\%$	++	Very strong positive effect
	$P(\beta \Delta X < \log(0.8)) \geq 95\%$	--	Very strong negative effect
	Other cases	nc	No possible conclusion

Table SM4. List of bryophyte species recorded during the study (21 bryophytes, 8 liverworts in bold). Code = abbreviated name. Nb occur. = number of occurrences in our dataset at tree level. Species = scientific names following Gargominy et al.'s (2015) nomenclature.

Code	Name	Nb occur.	Oak only	Pine only	Oak and pine
BRARUT	<i>Brachythecium rutabulum</i> (Hedw.) Schimp.	3	x		
BRYCAP	<i>Ptychostomum capillare</i> (Hedw.) Holyoak & N. Pedersen	1	x		
CAMFLE	<i>Campylopus flexuosus</i> (Hedw.) Brid.	24			x
CAMINT	<i>Campylopus introflexus</i> (Hedw.) Brid.	1	x		
DICHET	<i>Dicranella heteromalla</i> (Hedw.) Schimp.	7			x
DICMON	<i>Dicranum montanum</i> Hedw.	3		x	
DICSCOP	<i>Dicranum scoparium</i> Hedw.	223			x
EURSTR	<i>Eurhynchium striatum</i> (Hedw.) Schimp.	12	x		
FRUDIL	<i>Frullania dilatata</i> (L.) Dumort.	24	x		
FRUTAM	<i>Frullania tamarisci</i> (L.) Dumort.	16	x		
HYPAND	<i>Hypnum andoi</i> A.J.E.Sm.	1	x		
HYPCUP	<i>Hypnum cupressiforme</i> Hedw.	213			x
HYPJUT	<i>Hypnum jutlandicum</i> Holmen & E.Warncke	185			x
ISOALO	<i>Isothecium alopecuroides</i> (Lam. ex Dubois) Isov.	9	x		
ISOMYO	<i>Isothecium myosuroides</i> Brid., 1827	5	x		
LEUGLA	<i>Leucobryum glaucum</i> (Hedw.) Angstr.	26			x
LOPBID	<i>Lophocolea bidentata</i> (L.) Dumort., 1835	18	x		
LOPHET	<i>Lophocolea heterophylla</i> (Schrader.) Dumort.	26			x
METFUR	<i>Metzgeria furcata</i> (L.) Dumort.	1	x		
ORTLYE	<i>Orthotrichum lyellii</i> Hook. & Taylor	9	x		
ORTSTRIA	<i>Orthotrichum striatum</i> Hedw.	1	x		
PLASUC	<i>Plagiothecium succulentum</i> (Wilson) Lindb.	1		x	
PLESCH	<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.	28			x
POLFOR	<i>Polytrichum formosum</i> Hedw.	93			x
RADCOM	<i>Radula complanata</i> (L.) Dumort.	3	x		

RHYTRI	<i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst.	1	x	
SCLPUR	<i>Pseudoscleropodium purum</i> (Hedw.) M.Fleisch.	222		x
THUTAM	<i>Thuidium tamariscinum</i> (Hedw.) Schimp.	72		x
ULOBRU	<i>Ulota bruchii</i> Hornsch. Ex Brid.	6	x	
ULosp	<i>Ulota</i> sp.	2		

Table SM 5. Descriptive statistics of mean species richness per tree, on trunks and on the soil within a distance of 1m from the trunk: mean species richness, standard deviation, minimum and maximum values.

	Tree species	Mixture type	Mean	sd	min	max
Number of species on trunk per tree	pine	pure	1.81	0.87	1	4
		mixed	3.05	1.07	1	5
	oak	pure	4.28	1.58	2	7
		mixed	4.28	1.58	2	7
Number of species on ground per tree	pine	pure	2.42	1.07	1	5
		mixed	3.76	1.3	1	7
	oak	pure	5.85	1.74	4	10
		mixed	4.76	2.38	1	12
Abundance of ground species (cover in cm²)	pine	pure	1761	2068	128	6975
		mixed	602	396	2	1464
	oak	pure	1639	872	410	3823
		mixed	990	671	160	2169

Table SM 6. Descriptive statistics of exploratory variables (mean values, standard deviation, minimum and maximum values).

Tree level	Variable	Unit	Phorophyte	Mixture type	Mean	sd	min	max	
	Trunk diameter	cm	pine	pure	41.6	5	35	51	
				mixed	41.5	8.5	27.6	60	
				oak	pure	33.9	5.5	27	46
					mixed	29.5	5.9	20	41.5
	Trunk inclination	degrees	pine	pure	3.5	2.9	0	8	
				mixed	2.8	3.5	0	12	
				oak	pure	1.7	2.4	0	7
					mixed	3.3	4.1	0	14
	Bark pH	pH unit	pine	pure	4.48	0.25	4.08	4.88	
				mixed	4.39	0.18	3.96	4.65	
				oak	pure	4.85	0.27	4.38	5.47
					mixed	4.86	0.32	4.16	5.33
	Bark conductivity	$\mu\text{S cm}^{-1}$	pine	pure	7.6	3	3.4	15.4	
				mixed	10.3	6.7	4.4	36	
				oak	pure	24.4	9.8	11.6	56.2
					mixed	23	9.2	12.5	39.6
	October stemflow pH	pH unit	pine	pure	4.09	0.15	3.73	4.36	
				mixed	4.19	0.34	3.72	5.28	
				oak	pure	5.33	0.41	4.66	6.07
					mixed	5.53	0.26	5	5.96
	February stemflow conductivity	$\mu\text{S cm}^{-1}$	pine	pure	150.6	48.5	84.2	291	
				mixed	153.2	33.5	103.4	229	
				oak	pure	158.9	50.4	104.5	272
					mixed	149.3	51.9	78.2	279
	February throughfall pH – 25 cm from the trunk	pH unit	pine	pure	4.6	0.1	4.24	4.71	
				mixed	4.46	0.23	4.1	4.95	
				oak	pure	4.99	0.27	4.52	5.48
					mixed	4.98	0.46	4.31	6.59
	February throughfall pH – 75 cm from the trunk	pH unit	pine	pure	4.58	0.27	4.16	5.49	
				mixed	4.52	0.26	4.1	5.34	
				oak	pure	5	0.23	4.49	5.36
					mixed	4.7	0.27	4.14	5.27
	February throughfall conductivity – 25 cm from the trunk	$\mu\text{S cm}^{-1}$	pine	pure	35.6	8.6	15.7	48.6	
				mixed	40.9	12.9	19.6	62.5	
				oak	pure	29.5	8.5	19.5	52.6
					mixed	40	21	18.5	106.9

February throughfall conductivity – 75 cm from the trunk	$\mu\text{S cm}^{-1}$	pine	pure	33.5	8.9	16.8	50.2
			mixed	40	12	17.9	61.8
		oak	pure	25.9	6.7	17.4	46.7
			mixed	33.1	13.7	18.3	66.5
October throughfall pH – 25 cm from the trunk	pH unit	pine	pure	5.17	0.41	4.61	5.98
			mixed	5.06	0.33	4.45	6.05
		oak	pure	5.45	0.24	4.95	5.89
			mixed	5.47	0.48	4.81	7.04
October throughfall pH – 75 cm from the trunk	pH unit	pine	pure	5.04	0.25	4.51	5.53
			mixed	5.19	0.44	4.1	6.15
		oak	pure	5.54	0.32	5.16	6.27
			mixed	5.37	0.33	4.72	5.98
Soil surface pH – 25 cm from the trunk	pH unit	pine	pure	4.31	0.45	3.41	5.45
			mixed	4.33	0.55	3.86	6.34
		oak	pure	4.55	0.42	4.17	6
			mixed	4.38	0.29	3.92	5.3
Soil surface pH – 75 cm from the trunk	pH unit	pine	pure	4.53	0.52	3.95	5.79
			mixed	4.24	0.17	3.99	4.59
		oak	pure	4.68	0.65	4.15	6.68
			mixed	4.27	0.26	3.85	4.78
Soil OM pH – 25 cm from the trunk	pH unit	pine	pure	4.09	0.5	3.48	6.09
			mixed	4.01	0.18	3.85	4.65
		oak	pure	4.36	0.33	3.81	5.17
			mixed	4.24	0.57	3.87	6.25
Soil OM pH – 75 cm from the trunk	pH unit	pine	pure	4.04	0.16	3.77	4.35
			mixed	4.05	0.12	3.88	4.26
		oak	pure	4.31	0.33	3.76	5.03
			mixed	4.02	0.17	3.74	4.41
Interfering plant cover – 25 cm from the trunk	%	pine	pure	54	22	2	95
			mixed	16	17	0	54
		oak	pure	14	16	0	62
			mixed	15	14	0	59
Interfering plant cover – 75 cm from the trunk	%	pine	pure	64	14	34	89
			mixed	23	21	0	59.5

			oak	pure	12	15	0	47
				mixed	19	13	0	38
Stand level	Stand basal area	$\text{m}^2 \text{ha}^{-1}$	Pure oak stands		22.3	2.17	18.3	25.1
			Pure pine stands		29	6.9	19.4	40.3
			Mixed stands		31.5	5.7	23.9	38.4
	Interfering plant cover	%	Pure oak stands		17	14	4	43
			Pure pine stands		60	10	45	76
			Mixed stands		19	13	0	40

Table SM 7. Mean estimated species richness and abundance values on oak and pine, with their 95% confidence intervals, and analysis of the oak-pine difference (**Hypothesis H1**). The values here do not include the inter-plot variability (random effects)

Tree level		SRglob (n=84)	SRepiph (n=84)	SRground (n=84)	ABground/N (n=84)	ABepiph (n=84)
Tree species	Pine	3.84 [3.15 ; 4.71]	2.38 [1.89 ; 2.97]	3.09 [2.46 ; 3.91]	0.07 [0.04; 0.11]	0.01 [0.009; 0.02]
	Oak	6.55 [5.27 ; 7.85]	3.99 [3.12 ; 4.85]	4.98 [3.84 ; 6.15]	0.09 [0.06 ; 0.15]	0.25 [0.19 ; 0.33]
Difference	Significance	**	**	**	*	**
(analyzed ratio: SRpine/SRoak)	Magnitude	--	--	--	nc	--

**=significant (p<0.01), *=significant (p<0.05), --=very strong negative effect (decrease of more than 20% in species or cm² on pine), nc: no conclusion.

Table SM 8. Marginalized DIC values for models at tree level. The two first rows give the marginalized DIC for the two main models. Following rows concern exploratory models. For each response variable in the column, the best model corresponds to the lowest DIC value (greyed cells). The sign “-“ means “irrelevant”.

	SRepiph (n=71)	SRground (n=84)	SRground25 (n=78)	SRground75 (n=81)	SRglob (n=84)	ABground (n=84)	ABground25 (n=78)	ABground75 (n=81)	ABepiph (n=71)
Tree species	246.6128	329.5329	285.9509	307.6195	348.6007	1382.033	1203.622	1084.623	135.6862
Tree species: Stand_composition	241.1881	320.8182	275.037	311.1888	343.0812	1375.811	1203.072	1080.115	137.9688
Tree species + diameter	247.462	329.3704	282.4924	309.2575	348.8818	1374.875	1206.741	1083.84	138.7513
Tree species : Stand_composition + diameter	240.4589	319.2333	274.4461	312.8724	341.88	1374.316	1208.817	1079.027	142.8075
<i>Diameter</i>	273.7516	361.415	308.4155	315.4372	394.7232	1375.058	1207.218	1083.489	217.9436
Tree species + Inclination	248.6265	-	-	-	-	-	-	-	136.5563
Tree species : Stand_composition + Inclination	240.8859	-	-	-	-	-	-	-	141.2402
<i>Inclination</i>	273.2961	-	-	-	-	-	-	-	236.1879
Tree species + bark pH	245.9701	-	-	-	-	-	-	-	139.5103
Tree species : Stand_composition + bark pH	236.527	-	-	-	-	-	-	-	142.38
Bark pH	253.0802	-	-	-	-	-	-	-	213.7892
Tree species + bark conductivity	250.6488	-	-	-	-	-	-	-	137.3931
Tree species : Stand_composition + bark conductivity	241.1134	-	-	-	-	-	-	-	140.4444
Bark conductivity	266.6219	-	-	-	-	-	-	-	202.675
G	290.488	365.7751	310.611	319.1584	405.2095	1393.525	1221.3	1084.73	235.4274
G + G^2	281.7078	370.275	311.0587	320.1454	405.0296	1376.229	1207.141	1088.959	237.9216
Tree species + G	242.83	330.6584	289.0151	309.0797	350.9077	1377.168	1205.519	1089.478	133.2547
Tree species + G + G^2	234.7218	333.2187	290.1662	309.2801	355.0115	1381.548	1198.805	1091.329	136.1485
Tree species : Stand_composition + G	242.8979	325.2636	277.6279	313.2523	349.1779	1376.837	1204.88	1080.014	139.6016
Tree species : Stand_composition + G + G^2	231.6277	325.31	279.1284	314.0015	342.7478	1379.299	1203.973	1083.228	140.9286
Tree species: G	243.9205	327.6824	284.795	311.141	347.7326	1374.371	1197.892	1083.67	135.4038
Tree species : (G + G^2)	234.8344	326.833	287.6842	310.3945	343.7358	1398.013	1201.381	1090.281	139.869
Tree species:Compo :G	238.3853	324.3939	282.4791	314.7519	340.762	1369.954	1205.06	1064.625	148.9925
Tree species:Compo :(G+ G^2)	232.7007	329.7672	287.5461	321.8711	347.864	1373, 347	1212.891	1067.121	158.1981
Tree species + October stemflow pH	244.7375	-	-	-	-	-	-	-	140.6675
Tree species : Stand_composition + October stemflow pH	240.4682	-	-	-	-	-	-	-	141.0112
October stemflow pH	244.5123	-	-	-	-	-	-	-	170.4704
February stemflow pH	257.6953	-	-	-	-	-	-	-	175.1187
Tree species + February stemflow conductivity	-	-	-	-	-	-	-	-	137.7916

Tree species : Stand_composition + February stemflow conductivity	-	-	-	-	-	-	-	-	137.9571
February stemflow conductivity	-	-	-	-	-	-	-	-	234.5286
Tree species + Rec_Interf_Glob (or 25 or 75)	246.9127	328.8958	282.9757	309.8029	348.7878	1380.924	1206.838	1088.29	137.0244
Tree species : Stand_composition + Rec_Interf_Glob(or 25 or 75)	238.5542	270.4887	278.1338	313.9323	341.7483	1376.635	1206.519	1078.95	139.6359
Rec_Interf_Glob(or 25 or 75)	264.1685	346.0743	292.9108	314.4641	386.6704	1383.865	1208.267	1089.428	228.9618
Tree species + October throughfall pH at 25/75 cm	-	-	288.7395	309.4676	-	-	1205.979	1084.967	
Tree species : Stand_composition + October throughfall pH at 25/75 cm	-	-	278.7437	312.7931	-	-	1206.459	1077.787	
October throughfall pH at 25/75 cm	-	-	315.5185	319.8461	-	-	1210.012	1082.211	
Tree species + February throughfall pH at 25/75 cm	-	-	287.5883	303.4898	-	-	1200.228	1069.704	
Tree species : Stand_composition + February throughfall pH at 25/75 cm	-	-	276.605	304.8738	-	-	1203.304	1053.174	
February throughfall pH at 25/75 cm	-	-	301.4618	305.8914	-	-	1200.757	1070.64	
Tree species + organomineral horizon pH at 25/75 cm	-	-	284.7572	309.3773	-	-	1204.571	1086.317	
Tree species : Stand_composition + organo-mineral horizon pH at 25 cm	-	-	272.8443	312.7839	-	-	1202.727	1080.393	
Organo-mineral horizon pH at 25/75 cm	-	-	319.0061	317.6215	-	-	1207.859	1083.853	
Tree species + soil surface pH at 25/75 cm	-	-	288.7372	309.3372	-	-	1204.283	1086.29	
Tree species: Stand_composition + soil surface pH at 25/75 cm	-	-	277.1499	313.7613	-	-	1203.496	1079.117	
soil surface pH at 25/75 cm	-	-	312.5959	319.3124	-	-	1209.666	1083.751	
Tree species + February throughfall conductivity at 25/75 cm	-	-	287.1121	301.4843	-	-	1202.216	1077.073	
Tree species: Stand_composition + February throughfall conductivity at 25/75 cm	-	-	276.7498	302.3266	-	-	1208.678	1075.363	
February throughfall conductivity at 25/75 cm	-	-	317.4102	305.9008	-	-	1212.285	1079.034	

Table SM 9. Effects of stand composition type on bryophyte diversity at plot level (group of three trees) – Hypothesis H3.

Plot level – Composition effect		SRepiph (n=28)	SRground (n=28)	SRglob (n=28)	ABground/N (n=28)	ABepiph (n=28)
Composition	Pure Pine (P)	2.91 [1.99 ; 4.18]	4.22 [2.94 ; 5.93]	5.18 [3.71 ; 7.02]	0.1 [0.04 ; 0.28]	0.05 [0.02 ; 0.11]
	Pure Oak (O)	7.23 [5.52 ; 9.31]	9.67 [7.29 ; 12.51]	12.51 [9.58 ; 15.82]	0.1 [0.03 ; 0.24]	0.31 [0.2 ; 0.46]
	Mixture (M)	7.28 [5.8 ; 9.03]	8.37 [6.44 ; 10.48]	11.13 [8.72 ; 13.65]	0.05 [0.01 ; 0.12]	0.21 [0.14 ; 0.32]
Oak-Pine difference (analyzed ratio : O/P)	Significance	**	**	**	ns	**
	Magnitude	++	++	++	nc	++
Mixture-Pine difference (analyzed ratio : M/P)	Significance	**	**	**	ns	**
	Magnitude	++	++	++	nc	++
Mixture-Oak difference (analyzed ratio : M/O)	Significance	ns	ns	ns	*	ns
	Magnitude	nc	nc	nc	--	nc

SRepiph: mean epiphytic species richness per plot; SRground: mean ground species richness within 1m of the trunk per plot; SRglob: mean epiphytic and ground species richness per plot. ABground= total ground bryophyte abundance at plot level, i.e. within 1m of the trunks of three trees par plot; N= maximum measured ground bryophyte abundance at plot level (45,000 cm²)

Table SM 10. Best model for epiphytic and ground bryophyte species richness response variable at tree level.

Tree level – Best models for richness		log(SRglob)			log(SRepiph)			log(SRground)			log(SRground25)			log(SRground75)		
		(n=84)			(n=84)			(n=84)			(n=78)			(n=81)		
Model	Effects	Parameter estimated	P-val.	Magnitude	Parameter estimated	P-val.	Magnitude	Parameter estimated	P-val.	Magnitude	Parameter estimated	P-val.	Magnitude	Parameter estimated	P-val.	Magnitude
				G +4.39 +6.39			G +4.39 +6.39			cover +17.98 +24.23			pH +0.44 +0.55			cond. +9.94 +11.6
Species : Compo : G	G on oak in mixed stands	-0.014 [-0.04 ; 0.02]	ns	0 nc												
	G on oak in pure stands	0.07 [-0.01 ; 0.15]	ns	nc nc												
	G on pine in mixed stands	0.03 [-0.007 ; 0.06]	ns	nc nc												
	G on pine in pure stands	0.004 [-0.03 ; 0.04]	ns	0 nc												
Species : Compo+ Gquadratic	Scaled G component				0.176 [0.013; 0.335]	*										
	(Scaled G) ² component				- 0.212 [-0.35 ; -0.074]	**										
	Position on the G gradient															
	18 m ² ha ⁻¹						++	++								
	20 m ² ha ⁻¹						++	++								
	25 m ² ha ⁻¹						nc	nc								
	30 m ² ha ⁻¹						0	nc								
35 m ² ha ⁻¹						-	--									
40 m ² ha ⁻¹						--	--									

Species :Compo+ RecInterfGlob	Interfering plant cover					-3.4.10 ⁻⁵ [- 0.006 ; 0.006]	ns	0	0							
Species :Compo+ OM_pH	Organo- mineral horizon pH									-0.22 [-0.46 ; 0.017]	ns	0	0			
Species + Throughfall conductivity	Throughfall conductivity												-0.022 [- 0.04 ; - 0.008)	**	nc	-

*=significant (p<0.05), **=significant (p<0.01), += strong positive effect (more than 10% additional species after simulated variation of the explanatory variable), += very strong positive effect (increase more than 20%), -= strong negative effect (fall of more than 10%), -- = very strong negative effect (fall of more than 20% in species). G= basal area (m² ha⁻¹), throughfall conductivity in μS cm⁻¹, Interfering plant cover in %.

Table SM 11. Best model for ground and epiphytic species abundance at tree level.

Tree level – Best models for abundance		logit(ABground/Nmax)				logit(ABground25/Nmax)				logit(ABground75/Nmax)				logit(ABepiph)			
		(n=84)				(n=84)				(n=84)				(n=84)			
Model	Effects	Parameter estimated	P-val.	Magnitude		Parameter estimated	P-val.	Magnitude		Parameter estimated	P-val.	Magnitude		Parameter estimated	P-val.	Magnitude	
				G	G			G	G			pH	pH			G	G
				+4.39	+6.39			+4.39	+6.39			+0.278	+0.311			+4.39	+6.39
Species : Compo : G	G on oak in mixed stands	-0.09 [-0.69 ; 0.49]	ns	nc	nc												
	G on oak in pure stands	-0.06 [-1.21 ; 1.16]	ns	nc	nc												
	G on pine in mixed stands	0.15 [-0.42 ; 0.74]	ns	nc	nc												
	G on pine in pure stands	0.59 [0.07 ; 1.12]	*	++	++												
Species + G	scaled G													0.26 [0.01 ; 0.52]	*	nc	nc (+)
Species : G	scaled G on oak					-0.28 [-0.62 ; 0.07]	ns	nc	nc								
	scaled G on pine					0.2 [-0.2 ; 0.58]	ns	nc	nc								
Species: Compo + February throughfall pH	centered Feb. throughfall pH									2.2 [1.4 ; 3.1]	**	++	++				

*=significant ($p < 0.05$), **= significant ($p < 0.01$), += very strong positive effect (increase of more than 20% after simulated variation of the explanatory variable), nc: no possible conclusion about the magnitude, Nmax= maximum value for one abundance record per tree, G = basal area ($m^2 ha^{-1}$).

Table SM 12. Best models for bryophyte richness and abundance at plot level

Plot level – Best models		log(SRglob)				log(SRrepiph)				log(SRground)			Logit(ABground/N)				Logit(ABepiph/3)			
		(n=28)				(n=28)				(n=28)			(n=28)				(n=28)			
Model	Effects	Parameter estimated	P-val.	Magnitude		Parameter estimated	P-val.	Magnitude		Parameter estimated	P-val.	Magnitude	Parameter estimated	P-val.	Magnitude		Parameter estimated	P-val.	Magnitude	
				cover +17.98	cover +24.23			G +4.39	G +6.39						G +4.39	G +6.39			G +4.39	G +6.39
Compo+ Interfering plant cover	Interfering plant cover	0.008 [-0.001; 0.017]	ns	nc	nc															
Compo+ G quadratic	Scaled G component					0.174 [-0.024 ; 0.37]	ns													
	(Scaled G) ² component					- 0.287 [-0.47 ; -0.1]	**													
	Position on the G gradient 18 m ² ha ⁻¹							++	++											
	20 m ² ha ⁻¹							++	++											
	25 m ² ha ⁻¹							nc	nc											
	30 m ² ha ⁻¹							0	nc											
	35 m ² ha ⁻¹							-	--											
	40 m ² ha ⁻¹							--	--											
Compo										See Table SM9										
G	G												-0.03 [-0.07; 0.002]	ns	nc	nc	-0.03 [-0.097 ; 0.03]	ns	nc	nc

*=significant (p<0.05), **=significant (p<0.01), +++ very strong positive effect (increase of more than 20% after simulated variation of the explanatory variable), -- = strong negative effect (decrease of more than 10%), --- = very strong negative effect (decrease of more than 20%), nc: no possible conclusion about the magnitude, N= maximum value for one abundance record per plot, G = basal area (m² ha⁻¹), Interfering plant cover in %.

Table SM 13. Marginalized DIC values for models at plot level. The first row gives the marginalized DIC for the main stand composition model. Following rows concern exploratory models. For each response variable in a column, the best model corresponds to the lowest DIC value (grayed cells)

	SRglob (n=28)	SRepiph (n=28)	SRground (n=28)	ABground (n=28)	ABepiph (n=28)
Stand_composition	136.0504	117.2316	128.595	515.9012	211.3317
G	167.6226	143.0606	153.2769	514.3386	149.3234
G + G ²	170.5247	142.3934	153.7258	516.5306	154.835
Stand Composition : G	139.2621	122.8585	133.8167	522.9837	212.3769
Stand Composition : (G + G ²)	141.4208	116.3089	137.1419	515.6355	221.2377
Stand_composition + G	138.7728	120.0632	132.8068	516.3748	231.1198
Stand_composition + G+ G ²	137.0047	109.3212	132.2244	517.3257	233.0303
Stand_composition + Rec_Interf_Glob	133.1976	116.6574	130.3806	517.9365	157.8678
Rec_Interf_Glob	154.0383	132.7376	139.401	518.2489	228.7067