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Do *Dialytrichia mucronata* and *D. saxicola* share the same ecological preferences? A case study in the Rhône Valley (France) and possible application for river incision biomonitoring

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ABSTRACT
Anthropization has led to severe river incision in several parts of Europe. Biomonitoring is of interest to characterize this incision or, conversely, the effectiveness of ecological restoration. Mosses of the upper flood zone are good candidates for such biomonitoring as they are small organisms with limited water-intake ability. Here we studied the *Dialytrichia mucronata* (Brid.) Broth. – *D. saxicola* (Lamy) M.J. Cano species pair, both mostly encountered in the upper flood zone; the latter was hypothesized to be more resistant to water stress. We analysed 179 bryosociological relevés in the French Rhône River watershed, distributed along a wide ecological interval. We performed Pearson's Chi-square test to determine whether the latitude, altitude, substrate, and phorophyte had an effect on *Dialytrichia* (Schimp.) Limpr. species distribution. Assemblages between *D. mucronata* and *D. saxicola* and other moss species were tested using a multivariate procedure. Also we compiled a preliminary French departmental scale distribution map for both species. The results showed that the two species differ ecologically and might be more stenoecious than suggested by their wide synecological spectrum. Eighty-three bryophyte species were documented to be associated with the studied species of *Dialytrichia*. The cumulative projected inertia for the first three axes of the factorial correspondence analysis was only 23.26%, with no clear structuration. It is concluded that neither the relative occurrence of *D mucronata* and *D. saxicola*, nor the communities with these species can be used to monitor incision driven changes in vegetation.

KEYWORDS
Bioindication,
Bryophyta,
hydrosystems,
Pottiaceae,
riparian forest,
watershed.

RÉSUMÉ
Dialytrichia mucronata *et* D. saxicola *ont-ils les mêmes préférences écologiques? L'exemple de la vallée du Rhône (France) et possibilité d'application à la bioindication de l'incision fluviale.*
L'anthropisation a conduit à une incision préoccupante des rivières partout en Europe. La bioindication peut caractériser cette incision, ou à l'inverse l'efficacité d'une renaturation. Les mousses de la partie supérieure de la zone inondable, en tant que petits organismes aux capacités de captage de l'eau limitées, sont de bonnes candidates pour cette bioindication. Ici nous testons la paire d'espèces *Dialytrichia mucronata* (Brid.) Broth. – *D. saxicola* (Lamy) M.J. Cano, toutes deux typiques de la partie supérieure de la zone d'inondation, mais la seconde ayant été supposée plus résistante au stress hydrique. Nous avons analysé 179 relevés bryosociologiques du bassin français du Rhône, sur un large éventail écologique. Des tests chi-deux de Pearson ont été conduits pour déterminer si la latitude, l'altitude, le substrat et le phorophyte ont un effet sur la distribution des espèces de *Dialytrichia* (Schimp.) Limpr. L'assemblage de *D. mucronata* et de *D. saxicola* avec d'autres bryophytes a été testé par une approche multivariée. Une carte préliminaire de répartition en France métropolitaine a été compilée pour chacune des espèces. Les résultats montrent que les deux espèces diffèrent écologiquement et pourraient être plus sténoèces que le suggère le large spectre synécologique. Pas moins de 83 espèces de bryophytes ont été rencontrées associées à l'une ou l'autre des espèces de *Dialytrichia*. L'inertie cumulée par les trois premiers axes de l'analyse factorielle des correspondances atteignait 23.26% seulement, et il n'y a pas de structuration claire des projections. Il est conclut que ni l'occurrence relative de *Dialytrichia mucronata* et *D. saxicola*, ni les communautés hébergeant ces espèces, ne peuvent être utilisées pour enregistrer les changements de végétation induits par l'incision.

MOTS CLÉS
Bioindication,
Bryophyta,
hydrosystèmes,
Pottiaceae,
ripisylve,
bassin versant.

INTRODUCTION

Most lowland streams in Western Europe are facing extensive changes (Higler 1993). Damming and other civil engineering, such as embankments, lowland agricultural intensification etc. are associated with a complex of ecological constraints that induce stream hydrologic disturbances (Freeman *et al.* 2007). Such watershed development often triggers channel incision and higher levels of turbidity (Shield *et al.* 2010), associated with extensive alteration of hydrosystem functionality and ecological services (Ioana-Toroima *et al.* 2015). In Western Europe, since the 1970s, many riverbeds have been incised by more than one meter (Piégay & Peiry 1997). The monitoring of these hydrologic perturbations represents a challenge (Newson & Large 2006; Vaughan *et al.* 2009; Boon *et al.* 2010; Shield *et al.* 2010).

The character of fluvial hydrosystems depends upon various fluxes, from headwaters to river mouth, from channel-to-floodplain and between surface waters and groundwater (Gurnell & Petts 2002). Fluvial ecosystems are highly sensitive to the temporal variations in these fluxes (Amoros & Petts 1993). Consequently, biomonitoring is often used to record fluvial hydrosystem changes over various time scales (Ziglio *et al.* 2008).

Mosses, having no roots and thus no ability to counter the decrease of water availability by modifying their root system, are highly sensitive to changes in the hydrology of hydrosystems (Philippi 1972; Glime & Vitt 1984; Puglisi *et al.* 2015). Although mosses have mostly been used to monitor trace metals and other contaminants in fluvial environments (Markert *et al.* 2003), riparian moss species could also be used as indicators of hydrological changes at the local scale (e.g. related to anthropization). Several literature data have highlighted that not only single species but also bryophyte communities can be considered useful environmental bioindicators, as some associations of the phytosociological classes *Psoretea decipientis* Mattick *ex* Follmann, 1974 (Puglisi *et al.* 2012, 2016) and *Ctenidītea mollusci* v. Hübschmann *ex* Grgić, 1980 (Puglisi *et al.* 2013, 2014).

Of special interest is a pair of upper flood-zone moss species for which one putatively replaces the other when the hydrosystems begin to experience incision-induced decrease in humidity. Found on various substrates, *Dialytrichia mucronata* (Brid.) Broth. and *D. saxicola* (Lamy) M.J. Cano could be good candidates. Bizot & Roux (1968) hypothesized that *D. saxicola* may replace *D. mucronata* when hydrosystems become drier overall. *Dialytrichia saxicola* was recently shown to be more widely distributed in Western Europe than originally thought (Oesau 2007; Tinguy 2007; Bailly 2008; Hodgetts 2011; Philippe & Hugonnot 2011). In the literature, diverse and somewhat contrary statements have been made about the two species and their water requirements (Sérgio & Sim-Sim 1984; Bates *et al.* 2007; Bailly 2008; Vieira *et al.* 2012). Nevertheless, the ecological exigencies of both species have never been compared on a large scale.

Dialytrichia mucronata and *D. saxicola*, the only two species in the genus (Pottiaceae), are closely related and largely sympatric (Lara 2006). At the end of the last century, most bryophyte records for Europe included only one species (*D. mucronata*) within the moss genus *Dialytrichia* (Schimp.) Limpr. (Frey *et al.* 1995). Indeed, until recently most authors did not consider leaf fragility as a taxonomically significant feature but rather as a morphological anomaly. Later, Lara (2006) elevated the fragile-leaved taxon *D. mucronata* var. *fragilifolia* Bizot & Roux to the species rank as *Dialytrichia fragilifolia* (Bizot & Roux) F. Lara. Subsequently, Cano (2007) evidenced that the correct name of this taxon is *D. saxicola* (Lamy) M.J. Cano.

Dialytrichia saxicola was actively searched for and discovered in several European countries, including Belgium, France, Germany, Italy, Netherlands, Portugal (including Madeira, based on old collections, see Sérgio & Sim-Sim 1984), Spain and United Kingdom (Sérgio & Carvalho 2003; Draper *et al.* 2004; Preston & Blockeel 2006; Oesau 2007; Bailly 2008; Vieira *et al.* 2012; Ros *et al.* 2013; Hodgetts 2015). The *D. mucronata* distribution range is wider, including Mediterranean and Western Europe, reaching southward to Northern Africa and Turkey (Erdağ & Kürschner 2011; Ros *et al.* 2013) and extending north to Austria, Germany, Netherlands and Southern United Kingdom (Smith 2004).

It has long been observed that *Dialytrichia* species sometimes occur far away from water (Bridel 1819, 1826; Corbière 1889; Bizot & Roux 1968; Philippi 1968; Manzke & Wentzel 2003). Later, in Portugal, Sérgio & Sim-Sim (1984) characterized *D. mucronata* var. *mucronata* as hygrophilous, rheophilous and neutrophilous, *Dyalitrichia mucronata* var. *conferta* (Corb.) Corb. as xerophilous and *D. fragilifolia* as sciaphilous and mesophilous. This issue has attracted much attention after Lara's revision (2006), which confirmed that *D. mucronata* has a wide ecological spectrum, including water-availability as well as pH or substrate requirements, while the ecological range of *D. saxicola* seems narrower. Bates *et al.* (2007) concluded that the two species have similar ecological requirements, even though their few observations agreed with the view that *D. saxicola* presumably prefers more shaded sites higher above the normal water level than *D. mucronata*. From our field experience in the Rhône watershed both species colonize riparian trees as well as artificial settings such as channels, locks, masonry docks, iron devices (Hugonnot *et al.* 2018; pers. obs.).

The aims of this study were: 1) to determine whether *D. mucronata* and *D. saxicola* share the same ecological preferences; 2) to assess the relevance of using this species pair as bioindicators of water level changes; and 3) to know the preliminary distribution of both species in France. We tested whether *D. saxicola* is associated with bryophyte communities and ecological factors characteristic of drier ecological conditions more so than *D. mucronata*.

MATERIAL AND METHODS

Study area (Fig. 1)

We studied the French Rhône River watershed, i.e., the Rhône from the Camargue delta up to the Swiss border. After crossing the Swiss border the Rhône traverses the folded southern Jura Mountains towards the west until Lyon, where it curves and flows southward to the Mediterranean Sea in a graben bordered to the west by the Massif Central and to the east by perialpine range. The Rhône River main tributaries are, from the Swiss border seaward: Ain, Saône, Isère, Drôme, Ardèche, Durance, Gard. We studied the Rhône River itself, as well as all main tributaries (except the Isère), as well as some smaller tributaries (Cèze, Doubs, Loue, Ognon), including small streams (Aiguillon, Azergues, Longevent, Mezayon, Pollon, Reyssouze, Salon) (see Supplementary material for locations). The study area was distributed from 43.807°N to 47.332°N (decimal degrees, Lambert II extended). We further considered 45°N as the limit between northern and southern populations, as this latitude fit with the northern border of the Mediterranean flora extension within the Rhône Valley (Braun-Blanquet *et al.* 1952). Five of the relevés were prepared in the type locality for *D. fragilifolia* (forêt de Malmont, Rochefort-du-Gard), a meso-Mediterranean forest (*Quercion ilicis* Br.-Bl. *ex* Molinier, 1934), which is ecologically atypical for the genus *Dialytrichia* as it thrives there far away from streams (Bizot & Roux 1968).

Field sampling

Riparian ecosystems were prospected, geographically distributing the observation effort as much systematically as possible. Urbanization, accessibility and other factors limited the prospection. Riparian forests, riparian isolated trees and river embankments were particularly targeted. At each site all hard substrates were searched for the species, as *Dialytrichia* can grow on roots, trunks, concrete, stone, etc.

When a substrate colonized by *Dialytrichia* was found, a relevé area was designated around the target species patch(es). The relevé area was maximized to include the largest visually and floristically homogenous surface and it ranged from 100 to 900 cm². Such small surfaces are hypothesized to encompass minimal ecological variation. The standard method described by Braun-Blanquet (1964) was used, as applied by Barkman (1959) or Baisheva (2000). We performed 175 bryosociological relevés, assigning every occurring species a Braun-Blanquet's abundance coefficient. In addition, ecological factors such as substrate, inclination, altitude, geographical coordinates and vegetation cover were also noted.

Our field sampling was complemented with four relevés from the literature (Bailly 2008) as they originated from the same watershed.

Specimens study

Dialytrichia samples (usually 2-3 tufts) were microscopically examined and identified to the species level on the basis of the morphological and anatomical features listed by Bates *et al.* (2007) and Vadam & Philippe (2008). The nomenclature of tracheophytes follows Tison & de Foucault (2014), that of bryophytes follows Ros *et al.* (2007) for liverworts and Ros *et al.* (2013) for mosses (except for genus *Ulota*, for which we follow Caparrós *et al.* 2016).

Species distribution in France

From various literature sources (Lambinon & Empain 1973; Wattez 2016; Tinguy & Bick 2017; Durfort & Le Bail 2018; Hugonnot *et al.* 2018), the data obtained for this study and unpublished data kindly communicated by several bryologists (Pascal Amblard, Gilles Bailly, Ariel Bergamini, Manuel Bibas, Denis Cartier, Isabelle Chabissou, Leica Chavoutier, Yann Dumas, Marta Infante Sánchez, Aurélien Labroche,

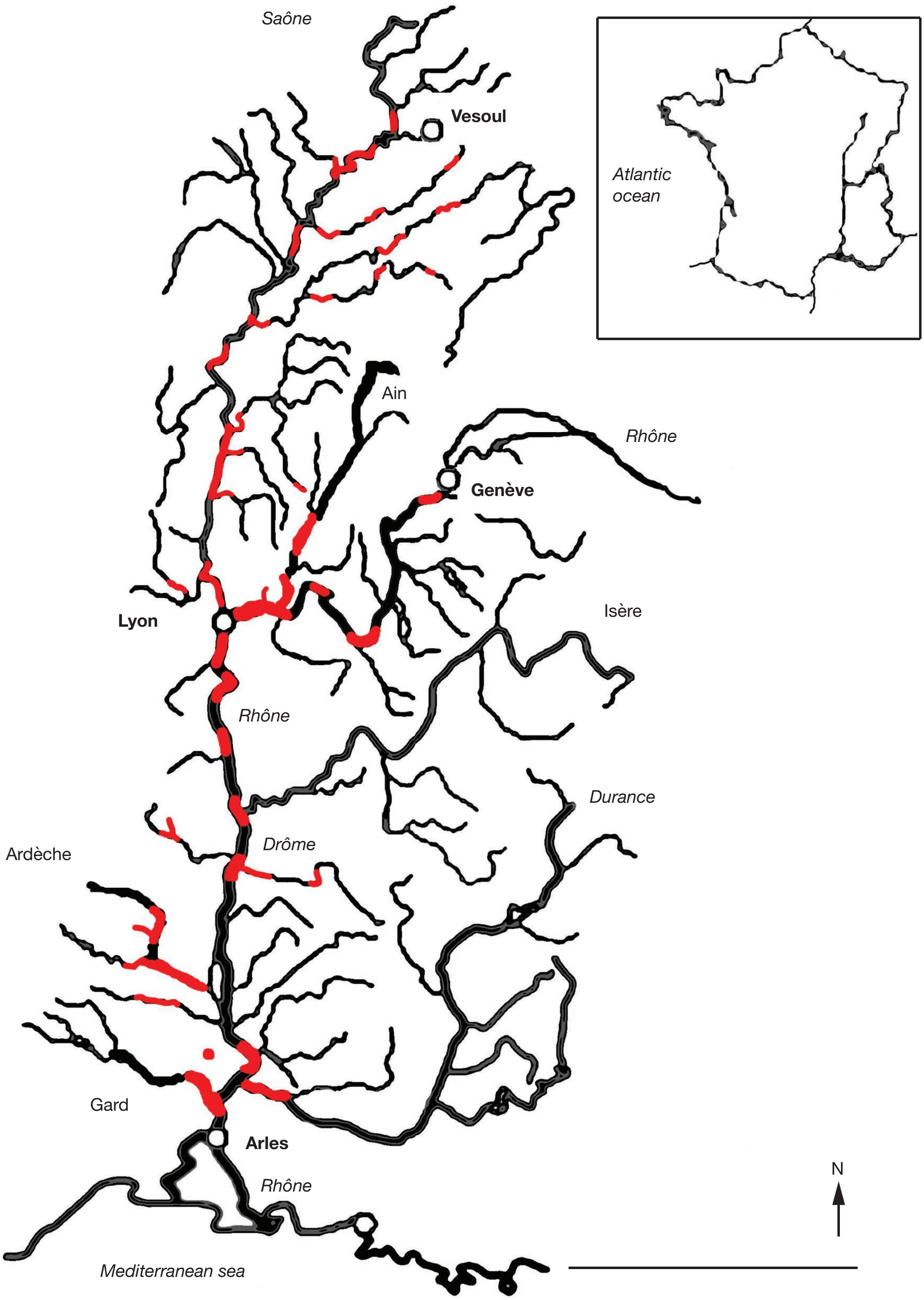
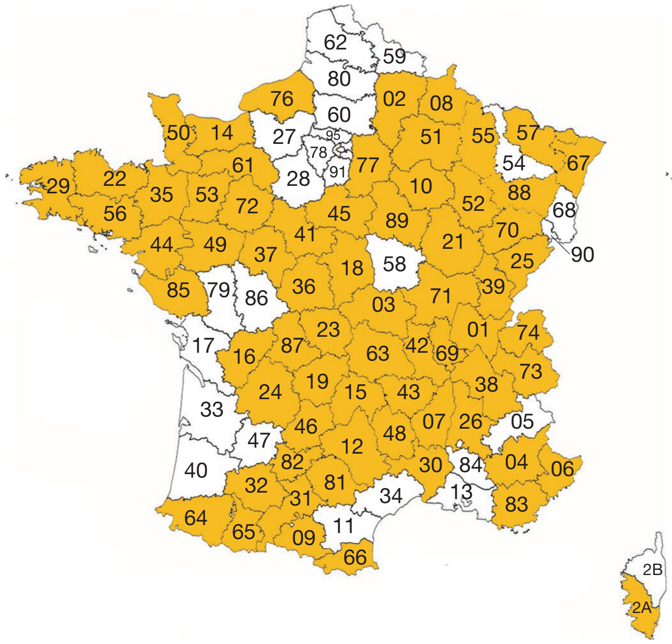


FIG. 1. — French Rhône River watershed. Stream sections that were searched for *Dialytrichia* (Schimp.) Limpr. are in **red**.

Julien Lagrandie, Thomas Legland, Hugues Tinguy, Jean-Marc Tison), we compiled a departmental scale distribution map for France for each of the species, as no recent synthesis was available. As they did not result from systematical prospection and as observation pressure was uneven, these maps were just tentative.



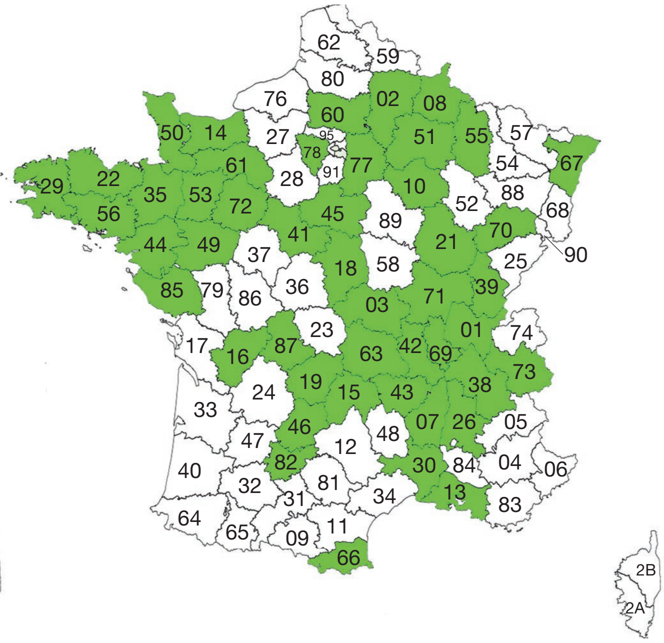


Fig. 2. — Preliminary distribution maps for *Dialytrichia mucronata* (Brid.) Broth. (left - **orange**) and *D. saxicola* (Lamy) M.J. Cano (right - **green**) in France based on literature sources (Lambinon & Empain 1973; Wattez 2016; Tinguy & Bick 2017; Durfort & Le Bail 2018; Hugonnot *et al*. 2018), data obtained for this study and unpublished data kindly communicated by several bryologists. Unshaded departments may or may not host the species. The numbers on the map are those of the departments, and correspondences can be found at https://fr.wikipedia.org/wiki/Liste_des_départements_français.

Data analyses

We first performed Pearson's Chi-square test (X^2) to determine whether the latitude, substrate, and phorophyte had an effect on *Dialytrichia* species distribution (p-value = probability value; df = degrees of freedom). The influence of the altitude on *D. mucronata* and *D. saxicola* distribution was tested through a linear regression procedure. We then compared the observed *Dialytrichia* species distributions in the north vs. the south, on woody vs. mineral substrates, and on varying woody species (phorophytes) (i.e., the observed contingency tables) with *Dialytrichia* species expected distributions (expected contingency table) under the null hypothesis, i.e., row and column variables of the contingency tables were independent (no effect of the latitude, substrate, and phorophyte). These expected *Dialytrichia* species distributions (expected contingency table) were automatically generated by the test. Each cell value of the expected contingency table was calculated as the product of the row and column marginals. The relationship between the altitude and *Dialytrichia* species abundance was tested through a linear regression based on a linear model (LM) procedure (Wilkinson & Rogers 1973; Chambers 1992) after confirming the normal distribution of model residuals based on quantile-quantile plots (QQplots, Becker *et al.* 1988). Assemblages between *D. mucronata* and *D. saxicola* and other moss species were tested using a multivariate procedure based on the 179 relevés comprising all species abundances (contingency table), with R^2 the percentage of variations in the *Dialytrichia* species abundance accounted by the regression. We considered moss species occurring in less than 3% of the relevés as artefacts and did not include them in the subsequent analysis. Indeed, they were too infrequent to be considered as representative of the moss community since their presence could result from random process (chance) instead of actual ecological filters. A factorial correspondence analysis was performed based on the contingency table using the ADE4 package (Chessel *et al.* 2007; Dray & Dufour 2007), and the inertias explained by the projected axes were calculated. In addition, species richness between assemblages including *D. mucronata* or *D. saxicola* only and both species were compared using an ANOVA procedure.

All statistical analyses were performed using R 3.2.3 (R Development Core Team 2008).

RESULTS

Preliminary species distribution in France (Figs 1 and 2)

During our study none of the studied species were found along the Drôme and Durance, two main tributaries with rapid and highly variable flow.

The compilation at departmental scale does not evidence any clear pattern. The two *Dialytrichia* species occur together in at least 43 departments, covering about half of metropolitan France surface, and are therefore widely distributed. The apparent lack of data for *D. saxicola* in south-westernmost France could result from uneven observation pressure, but *D. mucronata* is widely recorded there.

Dialytrichia species ecological requirements

The moss *D. saxicola* prevailed in the relevés, occurring alone in 96 relevés (54%). Seventy-six relevés (42%) had *D. mucro-*

Table 1. — Comparisons of *Dialytrichia* (Schimp.) Limpr. species distributions depending on various environmental factors. The total number of relevés was 179 and only seven included both *Dialytrichia* species. Values indicate the observed distributions of the two species, while values in brackets indicate the expected values under the null hypothesis (see the Material and Methods section for calculations).

	Dialytrichia mucronata	***Dialytrichia saxicola***
Number of relevés including the species	83	103
Altitude range of species presence (m a.s.l.)	57-385	6-237
Number of relevés north of 45°N	60 (67)	91 (80)
Number of relevés south of 45°N	23 (16)	12 (19)
Number of relevés on mineral substrate	29 (18)	10 (21)
Number of relevés on bark substrate	54 (62)	90 (75)

Table 2. — Observed vs. expected number of corticolous relevés for *Dialytrichia mucronata* (Brid.) Broth. and *D. saxicola* (Lamy) M.J. Cano, distributed in the different phorophytes sampled, which are ranked according to the expected difference (theoretical – observed) for *D. mucronata.*

	Dialytrichia mucronata	***Dialytrichia saxicola***
Fraxinus excelsior L.	12 (7.4)	9 (12.6)
Acer campestre L.	3 (1.1)	0 (1.9)
Alnus glutinosa (L.) Gaertn.	9 (7.8)	12 (13.2)
Acer negundo L.	3 (1.9)	2 (3.1)
Populus alba L.	8 (7.1)	10 (11.9)
Populus nigra L.	7 (6)	11 (10)
Acer monspessulanum L.	1 (0.4)	0 (0.6)
Buxus sempervirens L.	1 (0.4)	0 (0.6)
Corylus avellana L.	1 (0.4)	0 (0.6)
Platanus ×hispanica Münchh.	1 (0.4)	0 (0.6)
Juglans regia L.	1 (1.1)	1 (1.9)
Acer platanoides L.	0 (0.4)	1 (0.6)
Crataegus monogyna Jacq.	0 (0.4)	1 (0.6)
Populus ×canadensis Moench	0 (0.4)	1 (0.6)
Prunus spinosa L.	0 (0.4)	1 (0.6)
Rhamnus cathartica L.	0 (0.4)	1 (0.6)
Robinia pseudoacacia L.	0 (0.4)	1 (0.6)
Tilia cordata Mill.	0 (0.7)	2 (1.2)
Ulmus minor Mill.	0 (1.5)	4 (2.5)
Salix alba L.	7 (8.6)	22 (14.4)
Quercus pubescens Willd.	0 (1.9)	5 (3.1)
Quercus robur L.	0 (2.2)	6 (3.8)

nata only, and seven relevés (4%) included both species. See Table 1 and Supplementary material.

Both species were more frequently observed north of 45°N, with 151 of the relevés (81%) made north of this latitude. It was indeed quite difficult to find the genus south of 45°N (35 relevés, 39%), and populations there were smaller. *Dialytrichia saxicola* was more frequent than expected under the null hypothesis north of 45°N, and symmetrically *D. mucronata* was more frequent than expected under the null hypothesis south of 45°N (Table 1, Chi-square test $X^2 = 6.1$, p-value = 0.01, df = 1).

On average, *D. saxicola* was apparently found at lower altitudes (167.02 m a.s.l.) than *D. mucronata* (186.34 m a.s.l.). The same is true if maximum altitude is considered (Table 1). However, linear regression did not show any significant relationship between the abundances of each species and altitude ($R^2 < 0.01$, p-value > 0.05 for the two species).

Various substrates were associated with *Dialytrichia* species, including the bark of 22 woody species (Table 2) and five types of mineral substrates: migmatite (4 relevés), limestone (20), dolomitic sandstone (1), iron (1) and concrete (13).

Dialytrichia mucronata was more frequently observed on mineral substrate than expected under the null hypothesis, while *D. saxicola* was more frequent on trees (Table 1, Chi-square test, $X^2 = 15.4$, p-value < 0.001, df = 1).

Occurrences on the types of mineral substrates were too infrequent to be compared statistically (29 and 10 relevés for *D. mucronata* and *D. saxicola*, respectively, on total on mineral substrates, Table 1). Although the two species had almost the same number of occurrences on concrete, *D. saxicola* was observed only once on limestone (vs 20 times for *D. mucronata*), and *D. mucronata* only once on migmatite (vs.three times for *D saxicola*).

Dialytrichia mucronata was found on 12 different tree species and *D. saxicola* on 17 (Table 2). The two species were not randomly distributed on the different phorophyte species, *D. mucronata* being less frequent than expected under the null hypothesis on bark, and symmetrically *D. saxicola* being more frequent than expected (Tables 1 and 2; Chi-square test, $X^2 = 33.9$, p-value = 0.04, df = 21; phorophyte species in Table 2 are ranked according to the difference theoretical – observed for *D. mucronata*). It can be noted that tree species that rarely occur in riparian forests (*Acer monspessulanum* L., *Buxus sempervirens* L. and *Juglans regia* L.), as they do not withstand long-term soil water logging, were found in the middle part of the Table 2 only. They are thus phorophytes for which the number of observed trees bearing *D. mucronata* was more or less equal to the theoretically expected number. This suggests that outside riparian forests the two *Dialytrichia* species do not differ much in phorophyte choice. The three tree species (i.e. *Quercus pubescens* Willd., *Q. robur* L. and *Salix alba* L.) with the lowest *D. mucronata* frequencies are all known to be particularly rich in tannic acid (Kraus *et al.* 2003). Strictly riparian tree species were encountered at both ends of the Table 2 (e.g. *Alnus glutinosa* (L.) Gaertner and *Salix alba*), thus being phorophytes for which the number of observed trees bearing *D. mucronata* differs much from the theoretically expected number.

Dialytrichia species grouping with other bryophytes

Dialytrichia species were found to grow in association with 83 bryophyte species (See Appendix 1 and Supplementary material). Some were ecologically very different, as *Fontinalis antipyretica* Hedw. and *Grimmia dissimulata* E. Maier. The average species richness of the relevés with *Dialytrichia* was 5.43, despite the large number of species with which both were associated. In our research the assemblages with *D. mucronata*

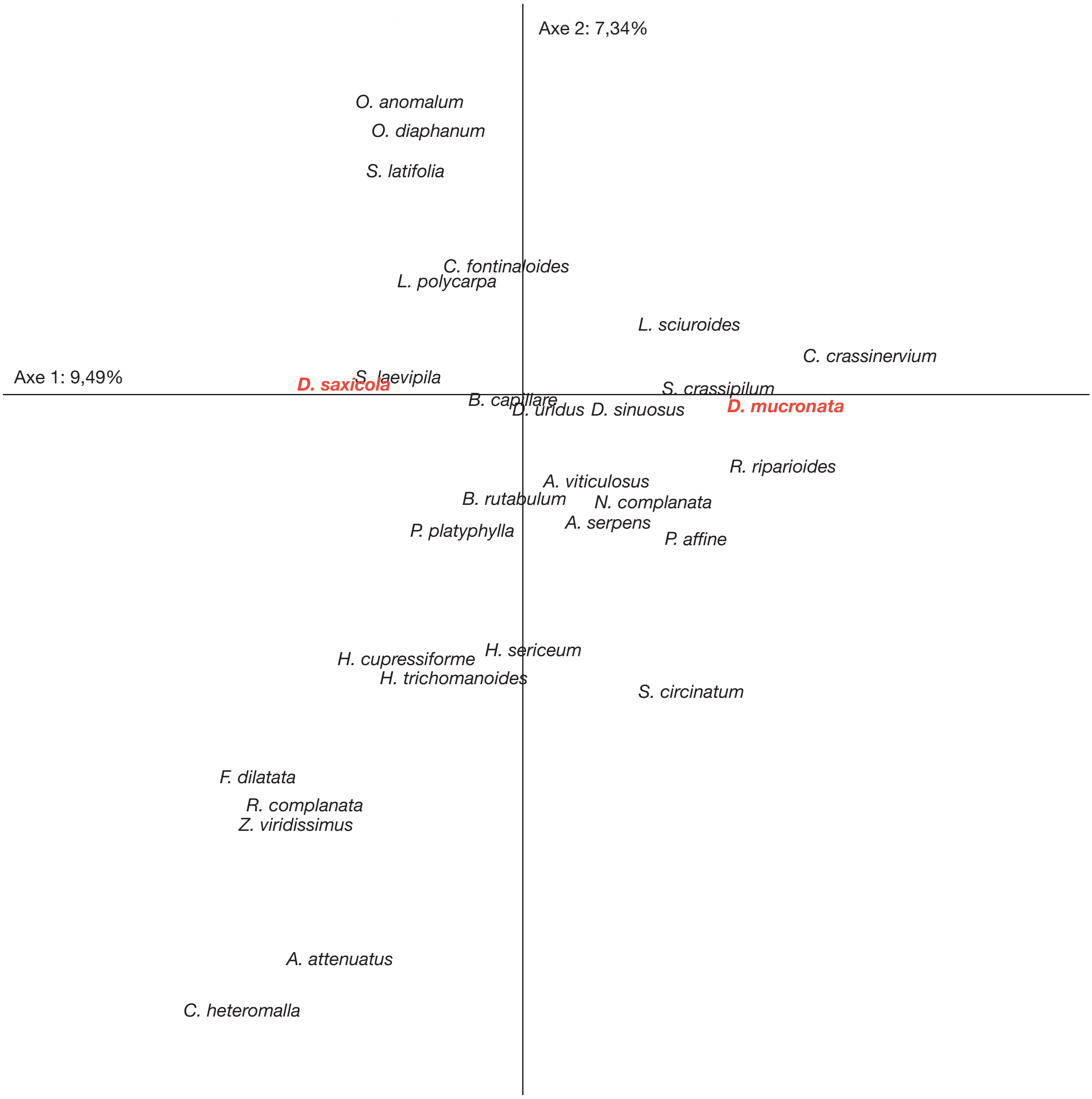


Fig. 3. — *Dialytrichia* (Schimp.) Limpr. species grouping with other bryophyte species obtained with a factorial correspondence analysis. The figure presents the species positions in the factorial plan. The percentage of inertia is indicated for the first two axes of the analysis. See Annexe 1 for full species names. Only the bryophyte species occurring in more than 3% of all relevés were included in this analysis.

only were not significantly more species rich (average 5.14) than those with *D. saxicola* only (average 4.83). Assemblages with both species were more species rich than those with only one of the species (average 5.43).

The cumulative projected inertia for the first three axes of the multivariate analysis (correspondence analysis) was 23.26%. For the first two axes (Fig. 3) the inertia was only 16.82%. It is thus clear that the set of relevés was not strongly structured by a dominant factor. The two *Dialytrichia* species were mainly separated on the first axis and much less on the second axis.

Along axis 1, *D. saxicola* is close to *Syntrichia laevipila* Brid., a mesophytic to slightly xerophytic species (Dierßen 2001). At the opposite end of the same axis, *D. mucronata* is associated, though less strongly, with *Cirriphyllum crassinervium* (Taylor) Loeske & M. Fleisch., *Rhynchostegium riparioides* (Hedw.) Cardot and *Schistidium crassipilum* H.H. Blom. While the last species has a large ecological spectrum, the two other species are hygroclinous (Dierßen 2001). Hygrophytic species, such as *Cinclidotus fontinaloides* (Hedw.) P. Beauv., had a median position along axis 1.

A set of three species (*Orthotrichum anomalum* Hedw., *O. diaphanum* Schrad. *ex* Brid. and *Syntrichia latifolia* (Bruch *ex* Hartm.) Huebener) can be found at the extreme positions along axis 2. *Orthotrichum anomalum* is a saxicolous species, while *O. diaphanum* is nitrophilous, and *S. latifolia* develops on heavily silted substrates of flooded zones; the three species are related to mineral-rich conditions (Dierßen 2001). At the negative end, although both hygrophilous, *Anomodon attenuatus* (Hedw.) Huebener and *Cryphaea heteromalla* (Hedw.) D. Mohr are typical for unsilted substrates outside of the flood zone. However, a species typical of frequently flooded and silted substrates, *Didymodon sinuosus* (Mitt.) Delogne (Dierßen 2001; Hugonnot & Celle 2013) is found at the median position along axis 2.

Analyses of various sub-sets of the database were not performed. Based on field evidence, no clearer partitioning of the relevés was noted.

DISCUSSION

Chorology

The moss *Dialytrichia saxicola* is now recognized as widely distributed in Western Europe. It can no longer be considered a Mediterranean xero-thermophilous vicariant of *D. mucronata* (Bates *et al.* 2007; Siebel 2008), although the range of the latter remains notably larger. Our preliminary distribution maps also supports that *D. saxicola* is not a more southern species than *D. mucronata* in France. Formerly considered to have a strongly Atlantic distribution pattern (Sérgio & Carvalho 2003; Lara 2006), at least in the Iberian Peninsula, *D. saxicola* also thrives in a sub-continental climate in the French Rhône watershed, from the Mediterranean area to the northern Franche-Comté, and further north-eastward to Alsace. Although it is difficult to quantify, we noted that both species were more difficult to find in the riparian forests south of Valence, i.e., in the area under Mediterranean climatic influence.

Comparing the autecology of the two species

In the studied area *D. saxicola* is statistically not more of a lowland plant than *D. mucronata*, which contradicts the generally accepted characteristics (Bailly 2008). Both species were found on a wide range of substrates, and *D. saxicola* is not exclusive to riparian trees (willows, poplars and alders) as frequently suggested. Colonizing 17 different phorophyte species *D. saxicola* seems to be more generalist than *D. mucronata*. This statement is limited by the fact that the distribution of the different phorophyte species along the Rhône River and its tributaries is not random. Additionally, the distribution of the different rock types along the Rhône River and its tributaries is also not random, which might bias the results.

Although reported from limestone in Belgium, in the Rhône Valley *D. saxicola* possibly avoids this substrate. This is questionable because the two species have almost the same number of occurrences on concrete, a carbonate-rich substrate. The relative avoidance of limestone rocks by *D. saxicola* suggested by the literature is thus not driven by intolerance to high pH or calcium carbonate, but probably rather by physical factors.

Bryosociological approach

The species pair has never been compared using a bryosociological approach. Bryological assemblages from North-Western France featuring *D. mucronata* were assigned by Lecointe (1976) to *Syntrichio latifoliae-Leskeetum polycarpae* v. Hübschmann 1952 subassociation *dialytrichietosum mucronatae* Barkman 1958, but the two *Dialytrichia* species were usually not distinguished at that time (Augier 1966).

Sérgio & Sim-Sim (1984) compared the assemblages with *D. mucronata* and those with *D. saxicola* (under *D. mucronata* var. *fragilifolia*) in Portugal. Their approach, however, was not based on bryosociological relevés and their taxonomic concepts are not in full accordance with modern ones. While Rogeon & Pierrot (1980) indicated that *D. mucronata* formed part of *Cinclidoto fontinaloidis–Dialytrichetum mucronatae* Giacomini, 1951 or *Cinclidodetum fontinaloides* Gams *ex* v. Hübschmann, 1971, Bailly (2008) assigned four relevés with *D. saxicola* to the *Syntrichio latifoliae-Leskeetum polycarpae*. This would confirm that *Dialytrichia saxicola* is found in more mesophilous habitats than *D. mucronata* (Bates *et al.* 2007).

However, our dataset does not allow the characterization of discrete sets of relevés, nor the clear-cut recognition of bryophyte associations. Both *Dialytrichia* species are distributed along a gradient, from species groups including several strongly hygrophilous species, such as *Cinclidotus fontinaloides* and *Fontinalis antipyretica*, to more dessication-tolerant species such as *Frullania dilatata* (L.) Dumort. and *Zygodon rupestris* Schimp. *ex* Lorentz. This compositional variability of the riparian bryoassociations in the best functionally-preserved sections of lowland streams is well known (Hugonnot & Celle 2013, 2015). Indeed, the *Syntrichio latifoliae-Leskeetum polycarpae* association is relatively typical for riparian trees in sections of the lowland rivers with little human impact (*Salicion albae* Soó, 1930), where the water regime can vary strongly (Philippi 1972, 1974, 1984; Marstaller 2006; Anishchenko 2011; Hugonnot 2011). In this variable setting, the associations range from truly alluvial assemblages to more mesophilous ones, where species such as *Hypnum cupressiforme* Hedw., *Orthotrichum diaphanum*, *Syntrichia laevipila*, etc. can be found. Towards the main channel, where flooding is longer and deeper, both *Dialytrichia* species were frequently observed associated with *C. fontinaloides*, within assemblages that were usually less species rich. As already noted (Lecointe 1976; Hugonnot & Celle 2013), although the best characteristic species of the *Syntrichio latifoliae-Leskeetum polycarpae* association, *Syntrichia latifolia* is not constant, and it was observed here associated with *Dialytrichia* in a small portion of the relevés only. *Leskea polycarpa* was much more frequently associated with one or the other species of *Dialytrichia*, but was absent in half of the cases.

The composition of the corticolous association *Syntrichio latifoliae-Leskeetum polycarpae* is more variable, while that of the *Cinclidoto fontinaloidis-Dialytrichetum mucronatae* is more constant, often limited to the two characteristic species. This species poor grouping could be determined by more intense silting, which makes the mosses less dependent on the nature of substrate (Devantery 1995).

CONCLUSIONS

Our bryosociological relevés were distributed along a wide ecological interval, as characterized by the large number of associated bryophyte species. Our results suggest that within this interval, no clear-cut meaningful associations could be recognized. Multivariate analysis could not distinguish exclusive groups, and thus it is concluded that within the French Rhône watershed *Dialytrichia mucronata* and *D. saxicola* communities cannot truly be used to monitor incision-driven (conversely, ecological restoration-driven) changes in vegetation. The two species, however, do differ ecologically and might be more stenoecious than suggested by their wide synecological spectrum. The observed differences might possibly be explained by several unconsidered factors, e.g., local mean monthly temperature or precipitation curves. Regardless, the two species of *Dialytrichia* are good bioindicators, relatively characteristic for sections of the rivers where the hydrological regime is relatively unaltered.

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Appendix 1. — List of the 83 bryophyte species encountered with *Dialytrichia* in studied relevés. An unidentified *Fissidens* and an unidentified *Bryum* were also encountered. The nomenclature of the taxa follows Ros *et al.* (2007) for liverworts and Ros *et al.* (2013) for mosses, except for genus *Ulota* for which we followed Caparrós *et al.* (2016).

Alleniella complanata (Hedw.) S. Olsson, Enroth & D. Quandt
Amblystegium serpens (Hedw.) Schimp.
Anomodon attenuatus (Hedw.) Huebener
A. viticulosus (Hedw.) Hook. & Taylor
Barbula unguiculata Hedw.
Brachythecium rivulare Schimp.
Brachythecium rutabulum (Hedw.) Schimp.
Bryoerythrophyllum recurvirostrum (Hedw.) P.C. Chen
Bryum argenteum Hedw.
Bryum dichotomum Hedw.
Calliergonella cuspidata (Hedw.) Loeske
Cinclidotus fontinaloides (Hedw.) P. Beauv.
Cinclidotus riparius (Host *ex* Brid.) Arn.
Cirriphyllum crassinervium (Taylor) Loeske & M. Fleisch.
Cryphaea heteromalla (Hedw.) D. Mohr
Dialytrichia mucronata (Brid.) Broth.
D. saxicola (Lamy) M.J. Cano
Dicranella varia (Hedw.) Schimp.
Didymodon fallax (Hedw.) R.H. Zander
D. luridus Hornsch.
D. sinuosus (Mitt.) Delogne
D. spadiceus (Mitt.) Limpr.
D. tophaceus (Brid.) Lisa
D. vinealis (Brid.) R.H. Zander
Encalypta streptocarpa Hedw.
Exsertotheca crispa (Hedw.) S. Olsson, Enroth & D. Quandt
Fissidens dubius P. Beauv.
F. viridulus (Sw. *ex* anon.) Wahlenb.
Fontinalis antipyretica Hedw.
Frullania dilatata (L.) Dumort.
Grimmia dissimulata E. Maier
G. pulvinata (Hedw.) Sm.
Gymnostomum calcareum Nees & Hornsch.
Homalia trichomanoides (Hedw.) Brid.
Homalothecium sericeum (Hedw.) Schimp.
Hygroamblystegium varium (Hedw.) Mönk.
Hypnum cupressiforme Hedw.
Isothecium alopecuroides (Lam. *ex* Dubois) Isov.
Kindbergia praelonga (Hedw.) Ochyra
Leptodictyum riparium (Hedw.) Warnst.
Leptodon smithii (Hedw.) F. Weber & D. Mohr
Leskea polycarpa Hedw.
Leucodon sciuroides (Hedw.) Schwägr.
Metzgeria furcata (L.) Dumort.
Microeurhynchium pumilum (Wilson) Ignatov & Vanderp.
Nyholmiella obtusifolia (Brid.) Holmen & Warncke
Orthotrichum affine Schrad. *ex* Brid.
O. anomalum Hedw.
O. cupulatum Hoffm. *ex* Brid.
O. diaphanum Schrad. *ex* Brid.
O. lyellii Hook. & Taylor
Oxyrhynchium hians (Hedw.) Loeske
Plagiomnium affine (Blandow *ex* Funck) T.J. Kop.
Plasteurhynchium striatulum (Spruce) M. Fleisch.
Pohlia melanodon (Brid.) A.J. Shaw
Porella platyphylla (L.) Pfeiff.
Ptychostomum capillare (Hedw.) Holyoak & N. Pedersen
P. moravicum (Podp.) Ros & Mazimpaka
Pylaisia polyantha (Hedw.) Schimp.
Radula complanata (L.) Dumort.
Rhynchostegiella curviseta (Brid.) Lindb.
R. tenella (Dicks.) Limpr.
Rhynchostegium riparioides (Hedw.) Cardot
Schistidium crassipilum H.H. Blom
S. elegantulum H.H. Blom
S. helveticum (Schkuhr) Deguchi
Sciuro-hypnum populeum (Hedw.) Ignatov & Huttunen
Scorpiurum circinatum (Bruch) M. Fleisch. & Loeske
Syntrichia laevipila Brid.
S. latifolia (Bruch *ex* Hartm.) Huebener
S. montana Nees
S. papillosa (Wilson) Jur.
S. ruralis (Hedw.) F. Weber & D. Mohr
S. virescens (De Not.) Ochyra
Thamnobryum alopecurum (Hedw.) Gangulee
Tortula inermis (Brid.) Mont.
T. muralis Hedw.
Trichostomum brachydontium Bruch
T. crispulum Bruch
Ulota crispa (Hedw.) Brid.
U. crispula Bruch
Zygodon rupestris Schimp. *ex* Lorentz
Z. viridissimus (Dicks.) Brid.

Appendix 2. — Supplementary material. French Rhône River watershed bryosociological relevés analyzed. A total of 175 were carried out in the sampling of the present work and four were taken from Bailly (2008). The standard method described by Braun-Blanquet (1964) was used, as applied by Barkman (1959) and Baisheva (2000), assigning an abundance coefficient. The symbol "&" is used in substitution of the "+" proposed by Braun-Blanquet to the very low abundances. Download the Appendix 2 from this link: http://sciencepress.mnhn.fr/sites/default/files/documents/en/bryologie2019v40a13-supp.mat_.xls