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THE HABITAT OF KNOTHOLE MOSS *ANACAMPTODON SPLACHNOIDES* IN THE PRATS-DE-MOLLO-LA PRESTE PROTECTED AREA (PYRENÉES-ORIENTALES, FRANCE)

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Abstract. *Anacamptodon splachnoides* (Froel. *ex* Brid.) Brid. is a rare and endangered species throughout most parts of its known range. Its distribution and ecology are poorly known in France. To improve management of the Prats-de-Mollo La Preste Protected Area, better knowledge of the ecological requirements of this species was needed. A systematic survey of *A. splachnoides* colonies was undertaken in a 30 ha beech forest site of Prats-de-Mollo (Pyrénées-Orientales, France); 29 colonies were found on beech dendrotelms (microhabitats including a reservoir that retains water for periods varying in duration). Logistic regression based on recorded habitat characteristics showed that the species is linked to tortuous trees at the stand scale, and to gap formation. Conservation of the species requires a non-intervention reserve with a natural disturbance regime.

Key words: *Anacamptodon splachnoides*, ecology, dendrotelm, cavity, ancient wood, beech tree, conservation

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INTRODUCTION

Today the vast majority of European forests are used for commercial forestry (Vallauri 2005). Intensive silviculture management (e.g., clearcutting, plantations) is responsible for the loss of biological diversity in temperate forests (Schnitzler-Lenoble 2002; Gilg 2004; Paillet *et al*. 2010). Moribund and deformed veteran trees generally are eliminated to favor the growth of young, healthy ones (Vallauri 2005). Old stages, together with dead trees, are very important for many cryptogamic species such as lichens and bryophytes (Winter & Möller 2008; Bobiec *et al*. 2005; Fritz & Heilmann-Clausen 2010). Many forest bryophyte species are linked to a narrow ecological niche (Jonsson *et al*. 2005; Jansová & Soldán 2006; Frego 2007; Haeussler *et al*. 2007) and need old trees and trees with high diversity of natural morphological characteristics for survival (Hodgetts 1996).

The knothole moss, *Anacamptodon splachnoides* (Froel. *ex* Brid.) Brid., is a mostly epiphytic moss (Mohan 1981; Dierssen 2001) which grows in sheltered niches, knotholes, cavities where water stands, and fissures in tree bark (Britton 1898; Crum 1958; Mohan 1976; Bednarek-Ochyra *et al*. 1994). Exceptionally it has been reported growing on rock (Sharp & Anderson 1981). Most authors seem to agree that this plant needs a certain amount of moisture to live (Crum 1958; Mohan 1981; Sharp & Anderson 1981). Its occurrence is often linked to deep, shady, damp woods (Britton 1898). The highly specialized niche of the species prompted Mohan (1976) to recognize an original and paucispecific association, *Anacamptodontetum splachnoides* Mohan 1976 (Philippi 1998). On account of its rarity and the threat to it from commercial forestry, the species is red-listed with the IUCN status ‘Endangered’ (Anonymous 1995).

Anacamptodon splachnoides is a species of the Northern Hemisphere, where it has an amphiatlantic range (Bednarek-Ochyra *et al*. 1994). In Europe it shows a continental distribution and occurs at isolated localities in the Pyrenees (Mohan 1981). *Anacamptodon splachnoides* is a scarce species in France, collected in widely disjunct populations. It was reported from Alsace (Vosges) (Burckel 1891; Frahm 2002) and Allier (Montoncel and

Bois Noirs) (Héribaud 1899; Boulay 1884) where it has not been confirmed recently in spite of intensive field activity. In the past the bulk of localities were recorded in the Pyrenees (Haute-Garonne – Boulay 1884; Celle 2008; Ariège – Hébrard *et al.* 1988; Hautes-Pyrénées – Pierrot & Pierrot 1975). Recent mentions are from the southeastern Massif-Central (Ardèche) and Pyrenees. It is unclear whether the species is under-recorded or is suffering a genuine decline. The most important populations of *A. splachnoides* are found in the Pyrénées-Orientales, where it was only recently discovered (Hugonnot 2010). The Prats-de-Mollo La Preste Protected Area was found to harbor the most conspicuous populations of the species, with many colonies, allowing an in-depth study of its demographic and ecological characteristics.

To gain better knowledge of this species, its ecological requirements and its potential role as an indicator of old-growth forests, we studied the Prats-de-Mollo Protected Area at the request of its management, to characterize its habitat and understand the factors governing its establishment.

Material and methods

From preliminary field observations it appeared that *Anacamptodon splachnoides* grew mostly on beech within the study area, so the study concentrated on this phorophyte. The present work is part of a larger study involving several cavity-dwelling species: Tengmalm's owl and chiropterans (Sandron 2010). In that study the trees were numbered from 1 to 252; only a few of them, numbered as in the larger study, are considered in this paper.

Study site

The study site is in a national protected area where collection of plants is illegal. The Prats-de-Mollo Protected Area contains 200 ha of beech forests. We limited the study to a 30 ha area of beech forest located in a ravine at 1490 to 1790 m a.s.l. (Fig. 1).

Bryophyte assessment

For uniformity of tree observations, we chose to follow the contour lines at 10-meter intervals since the study zone was a steep ravine: we began at 1490 m a.s.l. and followed this contour line to the end of the study area; then we followed the 1500 m a.s.l. contour line, then 1510 m a.s.l., etc. All the cavities that could be seen from the ground were observed. All the cavities considered potential sites for moss species growth, that is, all the wet cavities, were described according to 16 parameters: altitude, ground slope (in degrees), distance to water (creek or pond), tree height, tree diameter at breast height (DBH), tree position (at forest edge or inside stand), origin of tree (coppice, bole), tree condition (1 – dominating, i.e., with an extended crown easily accessing light, 2 – subordinate, i.e., with a smaller crown and a more tortuous shape, accessing light with difficulty, 3 – growing, neither dominating nor

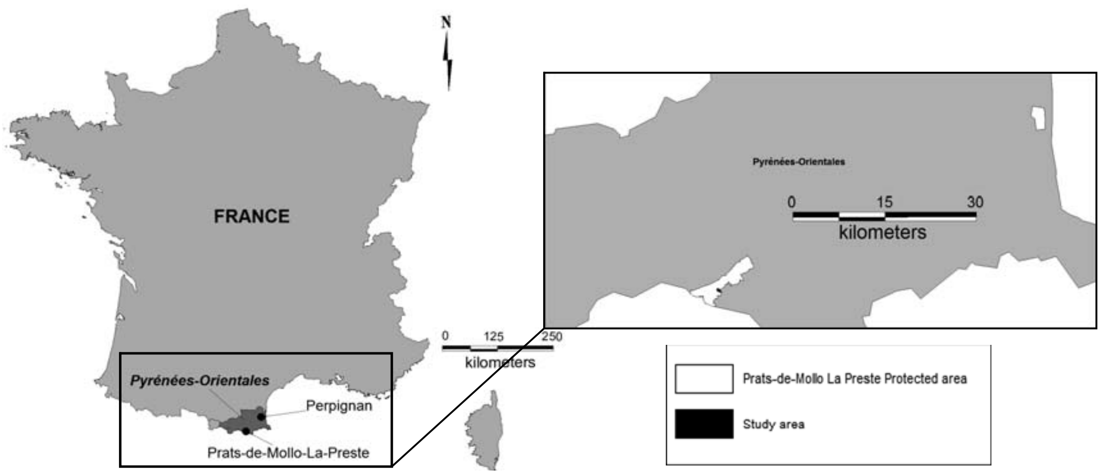

Fig. 1. Study area location.

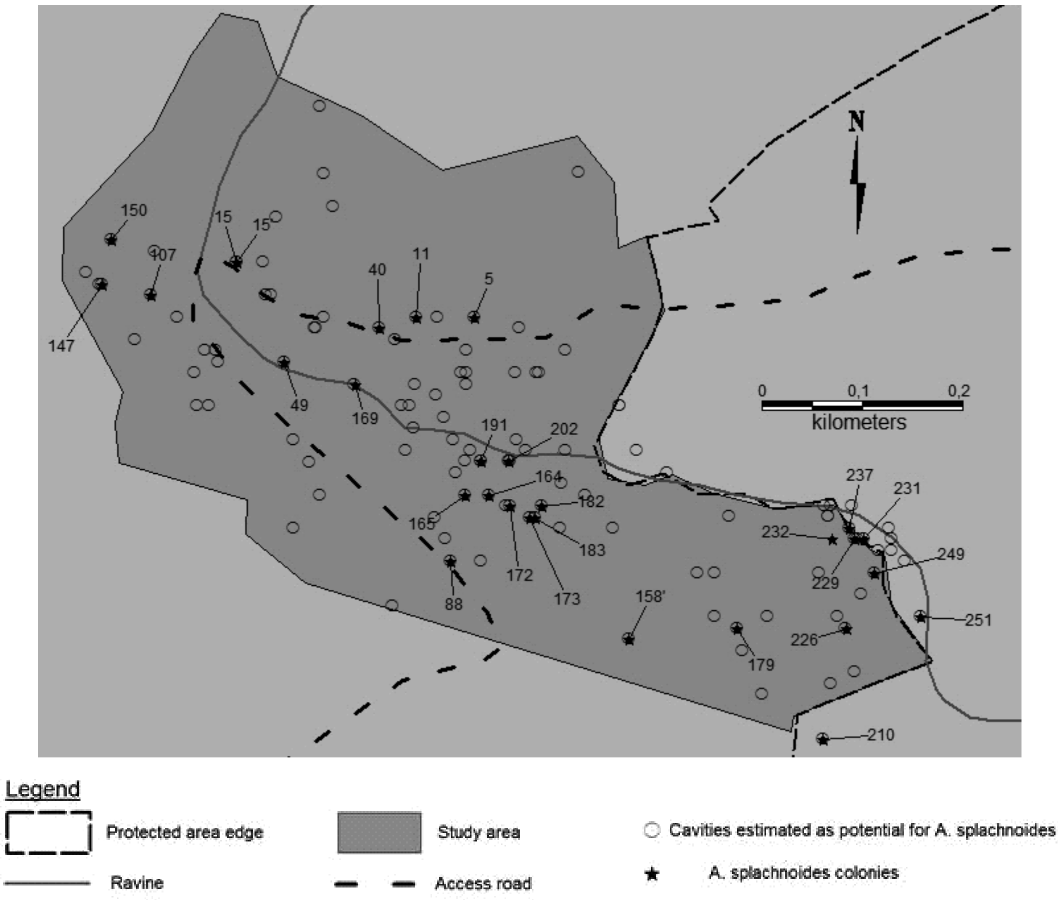

Fig. 2. Distribution of *Anacamptodon splachnoides* (Froel. *ex* Brid.) Brid among potential cavities.

subordinate but generally younger and thinner), direction of cavity opening (in degrees), cavity height from the ground, cavity origin (injury, woodpecker activity, falling or fusion of branches, etc), cavity shape (bowl, other), opening diameter, cavity volume, dampness, and water retention (yes or no). The moss colonies were also described precisely. For each colony, we noted the number of sporophytes, colony area, colony health status [dry, poor (partly dry and with a few sporophytes), good (some sporophytes on a homogeneous green colony, with a few very dry parts), excellent (no dry parts, several sporophytes and extensive area)], and the colony position (dry place inside cavity, water inside cavity, outside cavity, edge of cavity). The location of each surveyed tree was recorded with a GPS and then mapped with MapInfo software. This work was done on 16 days between May and July 2010.

STATISTICAL ANALYSIS

To determine the factors that favor the establishment of the moss species, we performed a logistic regression to explain the binary variable 'presence or lack of moss' on the basis of environmental data in a three-stage assessment: (*i*) Selection of the variables linked to the binary response, using χ^2 tests for the qualitative variables) and Student's *t* or Mann-Whitney tests (depending on the normality of the data) for the quantitative ones. For each quantitative variable we divided our plot into two subplots, the first containing trees with moss, the second containing trees without moss. With Student's *t* and Mann-Whitney tests we determined the differences in position between these two sub-plots for each variable. In this step the significance level was taken as $\alpha = 0.25$, in order to retain variables that might acquire significance when combined with other variables, as Remm *et al.* (2005) did in a similar study, following Hosmer and Lemeshow (1989). (*ii*) Checking the independence of the variables retained from the first stage. Logistic regression admits only independent explanatory variables. Correlation tests and χ^2 tests were performed for all pairs of selected variables. To study the potential link between qualitative variables and quantitative ones, we organized the latter by classes. (*iii*) Logistic regression from the selected variables.

In view of the insufficiency of knowledge about *Anacamptodon splachnoides*, and consequently the lack of a hypothesis about the main factors promoting the establishment of this moss, we used three methods for selecting the best model: AIC minimization, upward stepwise according to Wald criteria, and backward stepwise according to likelihood criteria.

RESULTS

POTENTIAL CAVITIES FOR *ANACAMPTODON SPLACHNOIDES* AND DISTRIBUTION OF MOSS COLONIES

In the study area we found 119 potential cavities on 115 individual trees. The potential cavities are spread quite homogeneously on the site except for the north part, where they are absent. Among these cavities we found 29 colonies of *Anacamptodon splachnoides*. The colonies were highly aggregated spatially (Fig. 2).

COLONY CHARACTERISTICS

Except for colony 232 (growing in a dry fissure of bark), all the observed *Anacamptodon splachnoides* patches were growing in cavities. Twenty-two of the 29 observed colonies bore sporophytes. The number of recorded sporophytes was highly variable ($\mu = 28 \pm 22$, sd = 58), with the maximum number (300) found in colony 182. Colony area also varied greatly, from 5 to 200 cm^2 ($\mu = 58 \pm 18$ cm^2, sd = 48). Fifteen colonies were in good condition, 6 were in a poor condition, 5 were completely dry and 3 were in excellent condition (Table 1). The topographic position of the moss varied: 11 colonies were partly in a dry place at the bottom of the cavity and partly on the edge of it, 7 were only in a dry place at the bottom of the cavity, 4 were only on the edge of the cavity, 3 were outside the cavity, one was in a moist place at the bottom of the cavity, one was partly in a moist place at the bottom of the cavity and partly on the edge, and one was in a dry place and a moist place on the bottom of the cavity and also on the edge.

DESCRIPTIVE CHARACTERISTICS OF CAVITIES OCCUPIED BY THE MOSS SPECIES

Tables 2 and 3 give the main results for cavity characteristics, which were highly heterogeneous as shown by the standard deviations of the quantitative parameters and the proportions of the different terms of the qualitative ones. The χ^2 tests done to identify any links between qualitative characteristics and the presence/absence of moss indicated that only the edge position of the tree and tree height were significantly linked to the occurrence of the moss.

Similarly, t-tests and Mann-Whitney tests of the quantitative parameters done to identify differences between the two subplots (cavities bearing moss and cavities without moss), indicated that cavity height from the ground differed significantly between the two subplots: cavities bearing moss were higher ($\mu = 153 \pm 37$ cm) than those without it ($\mu = 119 \pm 16$ cm).

MAIN FACTORS IMPLICATED IN THE ESTABLISHMENT OF A*NACAMPTODON SPLACHNOIDES*

RESULTS OF LOGISTIC REGRESSION

The three methods for selecting the best model (AIC minimization, upward stepwise according to Wald criteria, and backward stepwise according to likelihood criteria) led to the same model, including two explanatory parameters: tree height and edge position of the tree. Table 4 presents the regression results: the first part compares the independent (or trivial) model (which does not include the explanatory variables) with the complete model. The second part presents the significance of the model (based on the likelihood ratio

Table 1. Colony descriptions. IDP – Inside cavity in a dry place; IW – Inside cavity in water; O – Outside cavity; EH – On edge of cavity (numbers with apostrophes indicate trees having two cavities. For tree number 158, only one of them had an *A. splachnoides* colony).

Tree	Number of sporophytes	Colony area (cm^2)	Health status	Colony position
t 5	20	50	Poor	IDP
t 11	100	75	Excellent	IDP + EH
t 15	5	80	Poor	IW + O
t 15’	0	30	Good	IW
t 40	60	100	Excellent	IDP +IW + EH
t 49	0	98	Dry	IDP + EH
t 88	6	30	Good	O
t 107	10	25	Dry	IDP
t 147	4	80	Good	EH
t 150	4	30	Good	IDP + EH
t 158’	20	124	Poor	IDP + EH
t 164	4	35	Dry	IDP + EH
t 165	0	5	Good	IDP
t 169	100	20	Good	O
t 172	20	12	Good	IDP + EH
t 173	40	200	Poor	IDP + EH
t 179	0	15	Good	EH
t 182	300	180	Excellent	IDP + EH
t 183	21	20	Good	IDP + EH
t 191	20	20	Good	IDP
t 202	16	10	Good	IDP
t 210	7	35	Good	IDP + EH
t 226	0	80	Good	IDP
t 229	13	70	Poor	IDP
t 231	40	40	Good	IDP + EH
t 232	20	100	Poor	In depression on branch
t 237	0	40	Dry	EH
t 249	5	30	Dry	EH
t 251	0	60	Good	O

and the Wald test), and the last part presents the parameters of the model (the explanatory power of the variables). The results shown in the first two parts of the Table 4 confirm the significance of the model: the AIC criteria and deviance are minimized, McFadden and Nagelkerke’s R^2 are greater than 0, and the null hypothesis (no influence of the explanatory variables) is excluded by the p-values.

The only factor significantly ($\alpha = 0.05$) and positively linked to the presence of moss is edge position (term ‘Yes’: coefficient = 0.254, p = 0.026). We also note a very slight tendency of tree height to influence the establishment of the species, positively for the smallest trees (term ‘0_10’ m) and negatively for the highest ones (term ‘10_20’), but this effect is not significant. Interestingly, the influence of this factor is shown by the χ^2 test but not confirmed by logistic regression. Perhaps there was interference between this factor and another factor implicated in the logistic regression (e.g., tree height), which suppressed the link. Although the height of the cavity on the phorophyte tree does not appear to be linked with the presence of moss according to our model, it seems linked to this species as shown by the t-test.

Table 2. Description of cavities bearing moss. Qualitative data characteristics and χ^2 test results (* – significant at $\alpha = 0.25$).

Characteristic	Terms	Abundance	DF	p-value
Tree height (m)	0_10	17	2	0.010*
	10_20	11		
	20_30	1		
Tree position at the edge of the forest	Yes	7	1	0.029*
	No	22		
Origin	Coppice	20	1	0.300
	Bole	9		
Condition	Dominating	12	2	0.849
	Subordinate	6		
	Growing	11		
Bowl shape	Yes	12	1	0.976
	No	17		
Cavity origin	Branch	20	3	0.581
	Branch fusion	4		
	Injury	1		
	Unknown	3		
Dampness	Wet	27	1	0.434
	Very wet	1		
Water retention	Yes	8	1	0.746
	No	20		

Table 3. Mann-Whitney and t-test results. * – significant by t-test and Mann-Whitney test ($\alpha = 0.25$).

Data	Lack of *Anacamptodon*		Presence of *Anacamptodon*		Parametric (p) or non parametric test (np)	p-value *t*-test or Mann-Whitney test
	mean (± C.I. 95%)	SD	mean (± C.I. 95%)	SD		
Cavity volume (L)	3 ± 1	6	2 ± 0,8	2	np	0.434981359
Opening diameter (cm)	12 ± 2	9	12 ± 3	7	np	0.848941626
Cavity height from ground (cm)	119 ± 16	78	153 ± 37	98	p	0.066* 114DF
Cavity orientation (degrees)	203 ± 20	101	186 ± 30	88	np	0.518144843
DBH (cm)	38 ± 3	15	36 ± 6	16	np	0.310219588
Distance to water (m)	64 ± 12	56	60 ± 19	50	np	0.803371662
Slope exposure (degrees)	111 ± 20	87	89 ± 30	76	np	0.259828659
Altitude (m)	1622 ± 12	59	1615 ± 22	57	p	0.602 114DF

DISCUSSION

Locally, *Anacamptodon splachnoides* depends most on *Fagus sylvatica* phorophytes for growth and production of spores. The observation of *A. splachnoides* only on *F. sylvatica* phorophytes may be not conclusive, as we did not actively search for this species on other phorophytes during the course of the study. It was nevertheless apparent that *Anacamptodon splachnoides* was most abundant on beech, in accordance with reports in the literature. In Europe, *F. sylvatica* is certainly

Table 4. Logistic regression results after three selection methods.

	Independent	Complete
AIC	130.218	122.522
–2 Log(Likelihood)	128.218	114.522
R^2(McFadden)	0.000	**0.107**
R^2(Nagelkerke)	0.000	**0.166**

Null hypothesis test H0 : Y=0.241 (Data *A. splachnoides*)

Statistic	DF	Khi²	Pr > χ^2 (p-value)
–2 Log(Likelihood)	3	13.696	0.003*
Wald	3	12.067	0.007*

Standardized coefficients (Variable *A. splachnoides*):

Source	Coefficient	Sd	χ^2 Wald	Pr > χ^2 (p-value)
Cavity height from ground	0.000	0.000		
Tree height (20-30 m)	0.000	0.000		
Tree height (10-20 m)	–0.160	0.315	0.259	0.611
Tree height (0-10 m)	0.220	0.305	0.523	0.469
Forest edge position-N	0.000	0.000		
Forest edge position-Y	**0.254**	0.114	4.950	0.026*

the most frequently cited phorophyte (Amann 1919; Bednarek-Ochyra *et al*. 1994), although other phorophytes including conifers are also reported (Pierrot & Pierrot 1975; Schröder & Meinunger 1994, 2000; Ahrens 2001). The absence of *A. splachnoides* in the northern part of the study site could be due to the total absence of beech in this part of the site, which contains only pines, *Pinus uncinata*, which do not form cavities here. It would be useful to make a systematic survey of colonies on other trees in order to identify the affinities of *A. splachnoides* more precisely.

Only 29 colonies of *A. splachnoides* were found among the 119 potential cavities, possibly indicating that the species is a weak colonizer of new trees, a suggestion supported by the spatial aggregation of phorophytes. However, *A. splachnoides* is a monoicous species that produces sporophytes in abundance (in 75% of the known colonies on the study site). Its spores are *ca* 10 µm in diameter and therefore are considered to be easily wind-dispersed over long distances (Van Zanten 1977, 1983; Van Zanten & Pócs 1981; Van Zanten & Gradstein 1988). Hence the limitation is likely to be ecological, involving, for example, spore adherence in the cavity, or the spore germination phase. Wind dissemination is likely inhibited by the structural characteristics of the forest stands, which are located in deep ravines well protected from wind currents. Also, several cavities considered to have potential might in fact be suboptimal for reasons unknown to us.

The vast majority of colonies were found growing in the bottom of water-retaining cavities in trees, which are called dendrotelms. A dendrotelm is a peculiar type of microhabitat which includes a reservoir that retains water for periods varying in duration. Rainwater or percolating water accumulates in the cavity, eventually overflowing (rain tracks are often visible just below the dendrotelm). *Anacamptodon splachnoides* may then be considered a temporary hygrophilic species. Most likely, submergence varies greatly in duration and usually is brief, because a great number of observed colonies were dry during our fieldwork. Probably the species requires the presence of water for part of its life but also has high tolerance to occasional drought. A requirement for humic components dissolved in water cannot be ruled out. Competitive effects may also be implicated, as the trickling of humic infusions excludes almost all nonspecialized epiphytes. Among the bryophytes, only *Zygodon forsteri* shows a similar highly specialized epiphyte niche, with an apparent requirement for submergence in standing or running water rich in humic components (Doignon 1953; Heras-Pérez *et al*. 1997; Adams & Rumsey 2005).

Two factors seem to favor establishment of this moss: the low height of the tree (< 10 m) and above all the edge position of the tree. Besides these two factors another one can be noted: the high position of the cavity. This finding is in accord with observations by Britton (1898) and Bednarek-Ochyra *et al*. (1994), who noted the moss in very high cavities. For this we can suggest two hypotheses: establishment in high cavities could be due to its need for a great amount of light, or to easier accessibility for the moss spores. The link between the presence of the moss and edge position of the tree is rather easy to explain. It is likely that edge position is favorable to the moss because of the greater amount of light (hemiheliophily) in this position. This explanation also accounts for the apparent preference of the moss for high cavities. Gaps created by disturbances (e.g., violent storms, loss of branches brought down by snow) are a common feature of natural woodlands (Peterken 1996) and are partly responsible for the edge effect. Gaps may also be more efficient spore-trapping areas than homogeneous, dense forest stands.

Anacamptodon splachnoides can be considered a powerful indicator species, because it thrives in old-growth forests which are subjected to internal disturbances operating at different spatial scales, from the tree scale (leading to the formation of cavities) to the stand scale (gap formation).

It is difficult to understand the link between tree height and the presence of the moss: it is probably an induced effect, better explained by the shape of the tree. Because most of the trees holding the moss were tortuous and with very short trunks, the low height can be seen as a consequence of depleted vigor which prevented healthy growth and produced tortuous trunks. Mohan (1976, 1981) and Schröder and Meinunger (2000) reported that the trees on which they found *A. splachnoides* were small, deformed and tortuous. This suggestion needs to be studied in detail and on a wider scale.

Although *A. splachnoides* is widespread in the Northern Hemisphere it is nowhere common or abundant (Bednarek-Ochyra *et al*. 1994; Meinunger & Schröder 2007). In many European countries, most authors have noted a marked decline of the species, so that it is included in regional red lists (Schmidt & Heinrichs 2000; Kučera & Váňa 2003; Schnyder *et al*. 2004). In France it was reported from very isolated localities, with low numbers of phorophytes (Héribaud 1899; Hébrard *et al.* 1988; Pierrot & Pierrot 1975), making it highly vulnerable to any modification of the habitat. With its dozens of colonies, the Prats-de-Mollo Protected Area bears a heavy responsibility to conserve the species.

All woodlands with *A. splachnoides* should be protected from commercial forestry activities in order to maintain the natural evolution of the stands, which produces a high number of dendrotelms and edge effects. *A. splachnoides* dendrotelms should surveyed over the whole Prats-de-Mollo Protected Area in order to improve conservation of the extant populations. The known colonies should be monitored to identify demographic tendencies.

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REFERENCES

ADAMS K. J. & RUMSEY F. J. 2005. Notes on Essex Specialities. 9: the distribution of the Red-Data moss *Zygodon forsteri* (Dicks. ex With.) Mitt. Knothole Moss (Forster's Yoke-moss) in Epping Forest. *Essex Naturalist* **22**: 93–102.

AHRENS M. 2001. *Anacamptodon* Brid. In: M. NEBEL & G. PHILIPPI (eds), *Die Moose Baden-Württembergs*. **2**: 242–245. Verlag Eugen Ulmer, Stuttgart.

AMANN J. 1919. Flore des mousses de la Suisse. Deuxième partie. Bryogéographie de la Suisse. Imprimeries Réunies S.A., Lausanne.

ANONYMOUS 1995. Red Data Book of European Bryophytes. European Committee for Conservation of Bryophytes (ECCB), Trondheim.

BEDNAREK-OCHYRA H., OCHYRA R. & SZMAJDA P. 1994. *Anacamptodon splachnoides* (Brid.) Brid. In: R. OCHYRA & P. SZMAJDA (eds), *Atlas of the geographical distribution of spore plants in Poland*, 9: 37–40. W. Szafer Institute of Botany, Polish Academy of Sciences & Adam Mickiewicz University, Kraków – Poznań.

BOBIEC A., GUTOWSKI J. M., LAUDENSLAYER W. F., PAWLACZYK P. & ZUB K. 2005. The afterlife of a tree. WWF Poland, Warszawa – Hajnówka.

BOULAY M. 1884. Muscinées de la France. Première Partie – Mousses., F. Savy, Libraire-Editeur, Paris.

BRITTON E.G. 1898. New or rare mosses – I. *Anacamptodon splachnoides* (Froehl.) Brid. *Bryologist* **1**: 41–42.

BURCKEL G. 1891. Catalogue des hépatiques et des mousses d'Alsace. *Mitteilungen der naturhistorische Gesellschaft in Colmar, N.F.* **1**: 3–58.

CELLE J. 2008. Atlas préliminaire des Bryophytes de la Haute-Garonne. *Isatis, Revue botanique de la Haute-Garonne et du midi Toulousain* **8**: 1–153.

CRUM H. 1958. *Anacamptodon* in north America. *Bryologist* **61**: 136–140.

DIERSSEN K. 2001. Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophyt. Biblioth.* **56**: 1–289.

DOIGNON P. 1953. Observations écologiques sur le *Zygodon forsteri* Dicks. *Rev. Bryol. Lichenol.* **22**: 202–205.

FRAHM J. P. 2002. La bryoflore des Vosges et des zones limitrophes. *Limprichtia* **19**: 1–132.

FREGO K. A. 2007. Bryophytes as potential indicators of forest integrity. *Forest Ecology and Management* **242**: 65–75.

FRITZ O. & HEILMAN-CLAUSEN J. 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). *Biol. Conservation* **10**: 1–9.

GILG O. 2004. Forêts à caractère naturel. Caractéristiques, conservation et suivi. Cahiers Techniques de l'ATEN: 74. ATEN, Montpellier.

HAEUSSLER S., BERGERON Y., BRAIS S. & HARVEY B. D. 2007. Natural dynamics-based silviculture for maintaining plant biodiversity in Populus tremuloides-dominated boreal forests of eastern Canada. *Canad. J. Bot.* **85**: 1158–1170.

HÉBRARD J.-P., PIERROT R. B., QUÉTU G. & ROGEON M. A. 1988. Contribution à la bryoflore de la Haute Cerdagne et du Capcir. *Bull. Soc. Bot. Centre-Ouest, Nouvelle série* **19**: 401–414.

HERAS-PÉREZ P., INFANTE-SÁNCHEZ M. & UGARTE SAN VICENTE I. 1997. Datos sobre la presencia de *Zygodon forsteri* (WIth.) Mitt. (Bryophyta, Musci) en Alava (Norte de España). Propuestas para la conservación de este musgo singular de la brioflora Vasca. *Estudios del Museo Ciencias Naturales de Alavá* **12**: 43–50.

HÉRIBAUD J. 1899. Les Muscinées d'Auvergne. *Mém. Acad. Sci. Clermont-Ferrand* **14**: 1–544.

HODGETTS N. G. 1996. The conservation of lower plants in woodland. Joint Nature Conservation Committee (Great Britain).

HOSMER D. W. & LEMESHOW S. 1989. Applied logistic regression. John Wiley and Sons, New York.

HUGONNOT V. 2010. RN de Prats-de-Mollo (Pyrénées-Orientales) – Inventaire des Bryophytes. Rapport d'étude, Association Loisirs Botaniques, Varennes-Saint-Honorat, France.

JONSSON B. G., KRUYS N. & THOMAS R. 2005. Ecology of species living on dead wood – Lessons for dead wood management. *Silva Fenn.* **39**: 289–309.

JANSOVÁ I. & SOLDÁN Z. 2006. The habitat factors that affect the composition of bryophyte and lichen communities on fallen logs. *Preslia* **78**: 67–86.

KUČERA J. & VÁŇA J. 2003. Check- and Red List of bryophytes of the Czech Republic (2003). *Preslia* **75**: 193–222.

MEINUNGER L. & SCHRÖDER W. 2007. Verbreitungsatlas der Mosse Deutschlands. **3**. Herausgegeben von O. Dürhammer für die Regensburgische Botanische Gesellschaft, Regensburg.

MOHAN G. 1976. Contributii la studiul asociatiilor de briofite epifite din România (I). *Peuce, Muzeul Deltei Dunării Tulcea* **5**: 417–486.

MOHAN G. 1981. Ecological and bryosociological researches in the species *Anacamptodon splachnoides* from Rumania. *Bull. Soc. Hist. Nat. Afrique N.* **69**: 173–187.

PAILLET Y., BERGÈS L., HJÄLTÉN J., ÓDOR P., AVON C., BERNHARDT-RÖMERMANN M., BIJLSMA R. J., DE BRUYN L., FUHR M., GRANDIN U., KANKA R., LUNDIN L., LUQUE S., MAGURA T., MATESANZ S., MÉSZÁROS I., SEBASTIÀ M. T., SCHMIDT W., STANDOVÁR T., TÓTHMÉRÉSZ B., UOTILA A., VALLADARES F., VELLAK K. & VIRTANEN R. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology* **24**(1): 101–112.

PETERKEN G. G. 1996. Natural woodlans. Ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge.

PHILIPPI G. 1998. Bemerkenswerte Moosfunde aus dem Scharzwald und dem angrenzenden Oberheingebiet. *Carolinea* **56**: 63–78.

PIERROT L. & PIERROT R. B. 1975. Muscinées des Pyrénées centrales. *Monde Pl.* **383**: 4–7.

REMM J., LÖHMUS A. & REMM K. 2005. Tree cavities in riverine forests: What determines their occurrence and use by hole-nesting passerines? *Forest Ecology and Management* **221**: 267–277.

SANDRON L. 2010. Inventaire et étude des cavités des hêtres de la Réserve Naturelle de Prats-de-Mollo La Preste: élaboration d'un protocole et expérimentation dans une zone-test. Study report available in the Prats-de-Mollo Protected area, France.

SCHMIDT C. & HEINRICHS J. 2000. Rote Liste der gefährdeten Moose (Anthocerohyta et Bryophyta) in Nordrhein-Westfalen. 2. Fassung. In: LANDESANSTALT FÜR ÖKOLOGIE, BODENORDNUNG UND FORSTEN/LANDESAMT FÜR AGRARORDNUNG NORDRHEIN-WESTFALEN (ed.), *Rote Liste der gefährdeten Pflanzen und Tiere in Nordrhein-Westfalen. 3. Fassung*. *Schriftenreihe der Landesanstalt für Ökologie, Bodenordnung und Forsten Nordrhein-Westfalen* **17**(1999): 173–224.

SCHNITZLER-LENOBLE A. 2002. Ecologie des forêts naturelles d'Europe. Biodiversité, sylvigénèse, valeur patrimoniale des forêts primaires. Editions Tec & Doc, Londres, Paris, New York.

SCHNYDER N., BERGAMINI A., HOFMANN H., MÜLLER N., SCHUBIGER-BOSSARD C. & URMI E. 2004. Liste rouge des bryophytes menacées en Suisse. OFEFP, FUB & NISM, série OFEFP: l'Environnement Pratique, Berne.

SCHRÖDER W. & MEINUNGER L. 1994. Über Neufunde von *Anacamptodon splachnoides* (Brid.) Brid. in Bayern. *Herzogia* **10**: 133–136.

SCHRÖDER W. & MEINUNGER L. 2000. Weitere Neufunde von *Anacamptodon splachnoides* (Brid.) Brid. in Bayern. *Limprichtia* **14**: 11–12.

SHARP A. J. & ANDERSON L. E. 1981. An unusual substrate for Knothole moss, *Anacamptodon splachnoides*. *Bryologist* **84**: 539–542.

VALLAURI D. 2005. Le bois dit mort, une lacune des forêts en France et en Europe. In: D. VALLAURI, J. ANDRE, B. DODELIN, R. EYNARD-MACHET & D. RAMBAUD (eds), *Bois mort et à cavités – Une clé pour des forêts vivantes*, pp. 9–17. Tec & Doc, Paris.

WINTER S. & MÖLLER G. C. 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management* **255**: 1251–1261.

ZANTEN VAN B. O. & GRADSTEIN S.R. 1988. Experimental dispersal geography of neotropical liverworts. *Nova Hedwigia Beih.* **90**: 41–94.

ZANTEN VAN B. O. & PÓCS T. 1981. Distribution and dispersal of bryophytes. *Advances Bryol*. **1**: 479–562.

ZANTEN VAN B. O. 1977. Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern Hemisphere. Congrès International de Bryologie, Bordeaux. *Bryophyt. Bilbioth.* **13**: 715–733.

ZANTEN VAN B. O. 1983. Possibilities of long-range dispersal in bryophytes with special reference to the Southern Hemisphere. *Sonderb. Naturwiss. Vereins Hamburg* **7**: 49–64.

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