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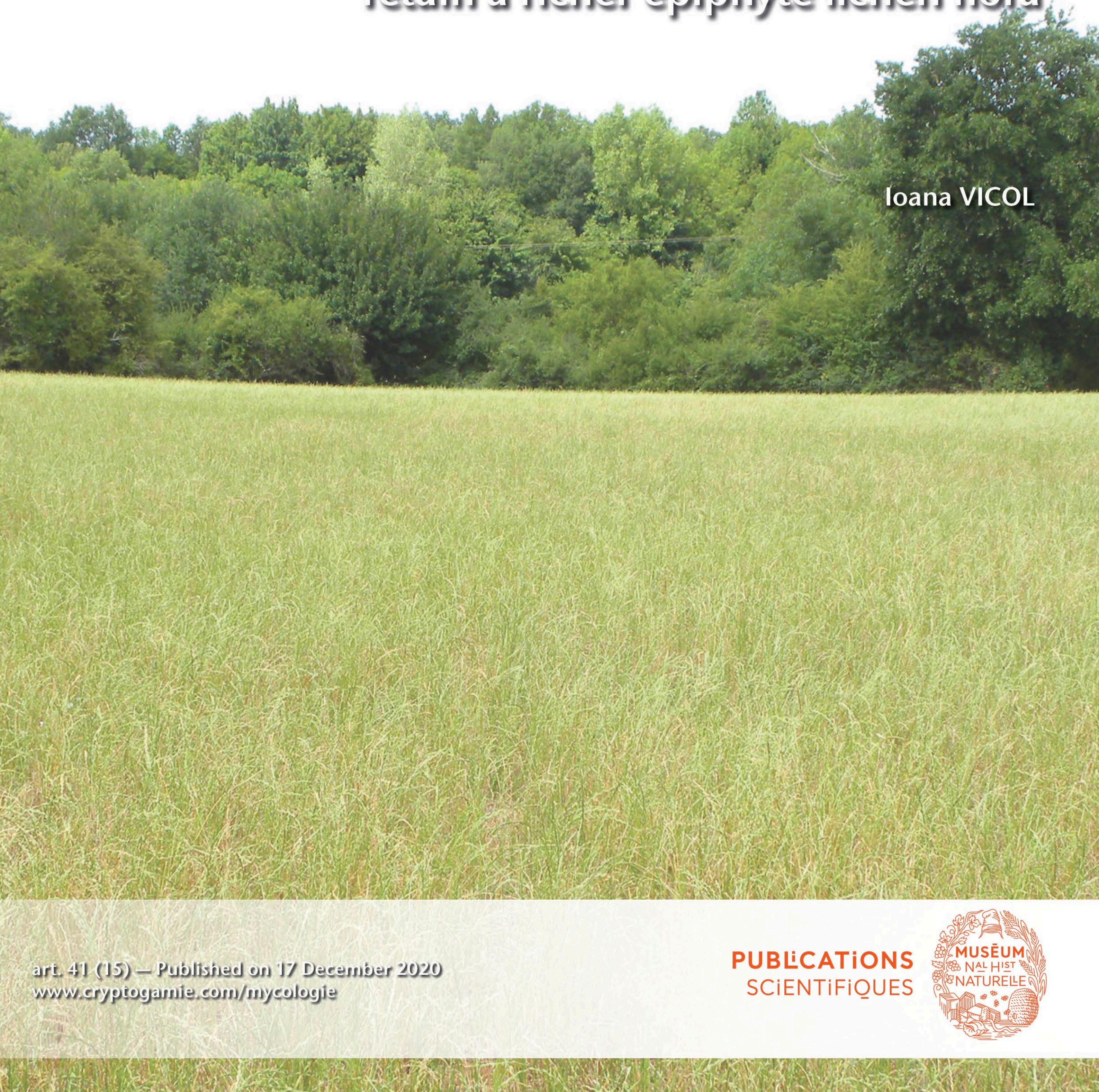

Ioana VICOL

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Multi-aged forest fragment surrounded by meadows in the "Zone Atelier Plaine et Val de Sèvre"./ Fragment de forêt multi-âge entouré de prairies dans la "Zone Atelier Plaine et Val de Sèvre". Photo: Vicol Ioana, 30.07.2017

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Multi-aged forest fragments in Atlantic France that are surrounded by meadows retain a richer epiphyte lichen flora

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ABSTRACT
This project was focused on identifying the effect of environmental factors on epiphytic lichen species by using a multiscale design applied within multi-aged forest fragments. The field investigations were performed within 20 forest fragments, of which 14 were surrounded by crops and six were surrounded by meadows. Sampling units of 10 by 10 m were selected from the exterior to the interior of each forest fragment following the perimeter line; other sampling units were selected following the same perimeter line to the centre of the forests. The spatial gradient represented by the exterior and interior parts of the forest fragments, surrounding matrix and forest structure (i.e., the presence of larger trees) significantly supported patterns of lichen abundance and diversity. Lichen abundance and diversity were significantly influenced by microhabitat and macrohabitat drivers on the relatively large trees in the forest fragments surrounded by both crops and meadows. Lichen species replacement was significantly described by both larger and thinner trees situated in the interior and at the exterior of the forest fragments surrounded by meadows. The lichen richness was significantly higher on larger trees situated in the interior of the forest fragments surrounded by meadows. The mature structure of forests and the surrounding matrix significantly determined the pattern of epiphytic lichen species. Furthermore, larger and thinner trees harbour very rare lichen species within forest fragments surrounded by both crops and meadows. Forest management practices based on selective cutting on a short rotation cycle did not exert a negative impact on epiphytic lichen.

KEY WORDS
Larger trees,
lichen diversity,
lichen abundance,
surrounding matrix,
thinner trees,
tree species.

RÉSUMÉ

Les fragments de forêt multi-âge en France atlantique entourés de prairies conservent une flore de lichens épiphytes plus riche.

Ce projet s'est concentré sur l'identification de l'effet des facteurs environnementaux sur les espèces de lichens épiphytes en utilisant une conception multi-échelle appliquée au sein de fragments de forêt multi-âge. Les recherches sur le terrain ont été effectuées dans 20 fragments de forêt, dont 14 étaient entourés de cultures et six de prairies. Des unités d'échantillonnage de 10 mètres sur 10 ont été sélectionnées de l'extérieur vers l'intérieur de chaque fragment forestier en suivant la ligne de périmètre; d'autres unités d'échantillonnage ont été sélectionnées en suivant la même ligne de périmètre jusqu'au centre des forêts. Le gradient spatial représenté par les parties extérieures et intérieures des fragments de forêt, la matrice environnante et la structure de la forêt (c'est-à-dire la présence d'arbres plus grands) a permis de soutenir de manière significative les modèles d'abondance et de diversité des lichens. L'abondance et la diversité des lichens ont été significativement influencées par les facteurs de microhabitat et de macrohabitat sur les arbres relativement grands des fragments de forêt entourés à la fois de cultures et de prairies. Le remplacement des espèces de lichens a été décrit de manière significative par des arbres à la fois plus grands et plus fins situés à l'intérieur et à l'extérieur des fragments de forêt entourés de prairies. La richesse en lichens était significativement plus élevée sur les grands arbres situés à l'intérieur des fragments de forêt entourés de prairies. La structure mature des forêts et la matrice environnante ont déterminé de manière significative le schéma des espèces de lichens épiphytes. En outre, les arbres plus grands et plus minces abritent des espèces de lichens très rares à l'intérieur des fragments de forêt entourés de cultures et de prairies. Les pratiques de gestion forestière basées sur la coupe sélective sur un cycle de rotation court n'ont pas eu d'impact négatif sur le lichen épiphyte.

MOTS CLÉS
Arbres plus grands, diversité des lichens, abondance des lichens, matrice environnante, arbres plus fins, espèces d'arbres.

INTRODUCTION

European mixed forests have a complex pattern of tree species diversity, with various microhabitats that are closely related to cryptogamic diversity (Aragón *et al.* 2010; Kubiak & Osyczka 2017). Human activities have changed forest habitat complexity by reducing the heterogeneous interior structures of forests, with deleterious effects on epiphytic lichen species (Leppik *et al.* 2011; Otálora *et al.* 2011; Ellis 2012; Hauck *et al.* 2012); therefore, in this respect, sustainable forest management is needed (Nascimbene *et al.* 2013; Benesperi *et al.* 2018). In addition, the structural heterogeneity of interior forest areas creates favourable environmental conditions for their dependent species (Lindenmayer & Franklin 2002). Habitat quality and forest continuity are important drivers of the distribution of epiphytic lichen species (Ranius *et al.* 2008; Belinchón *et al.* 2009; Otálora *et al.* 2011). Different management practices, such as selective cutting, the prolongation of the rotation cycle and the retention of small patches of larger trees, ensure lichen species continuity and conservation (Nascimbene *et al.* 2013). In this context, multiscale approaches across forest habitats that integrate a greater heterogeneity of environmental factors affecting patterns of epiphytic lichen species could contribute to better management practices for epiphytic lichens (Ellis 2012; Nascimbene *et al.* 2013; Merinero *et al.* 2014). The surrounding matrix has an impact on the biodiversity of the forest interior (Lindenmayer & Franklin 2002). Furthermore, the degradation of forests and land use intensification in the temperate zone exerts intense pressure on forest habitats (Jüriado *et al.* 2009; Ellis 2012; Nascimbene *et al.* 2013).

In this study, a multiscale approach was used to identify environmental effects on epiphytic lichen species assessed within multi-aged forest fragments surrounded by a matrix of different types of land management. This research addressed the following questions: a) Which are the main environmental factors affecting lichen abundance and diversity? b) Does forest structure (e.g. larger and thinner trees) across the interior and exterior of forest fragments and surrounding matrix (crops and meadows) affect the abundance and diversity of epiphytic lichen species? c) Do lichen abundances on thinner and larger trees differ between the exterior and interior forest fragments? d) Is the surrounding matrix important in the differentiation of lichen abundances? and e) How does the epiphytic lichen diversity in the interior of forest fragments vary compared with that at the exterior of forest fragments, taking into account tree size (i.e., larger and thinner trees) and the surrounding matrix?

The hypotheses addressed in this study are as follows: a) The interiors of forest fragments retain higher quality substrata than the exteriors of forest fragments due to the presence of relatively larger and scattered trees; therefore, it is expected that the abundance and richness of lichen species are greater in the forest interior than in the forest exterior; and b) The traditional matrix surrounding forest fragments (i.e., meadows), rather than agricultural land use, exerts a positive effect on the abundance and richness of lichen species. In this respect, the abundance and richness of epiphytic lichen species are significantly higher in

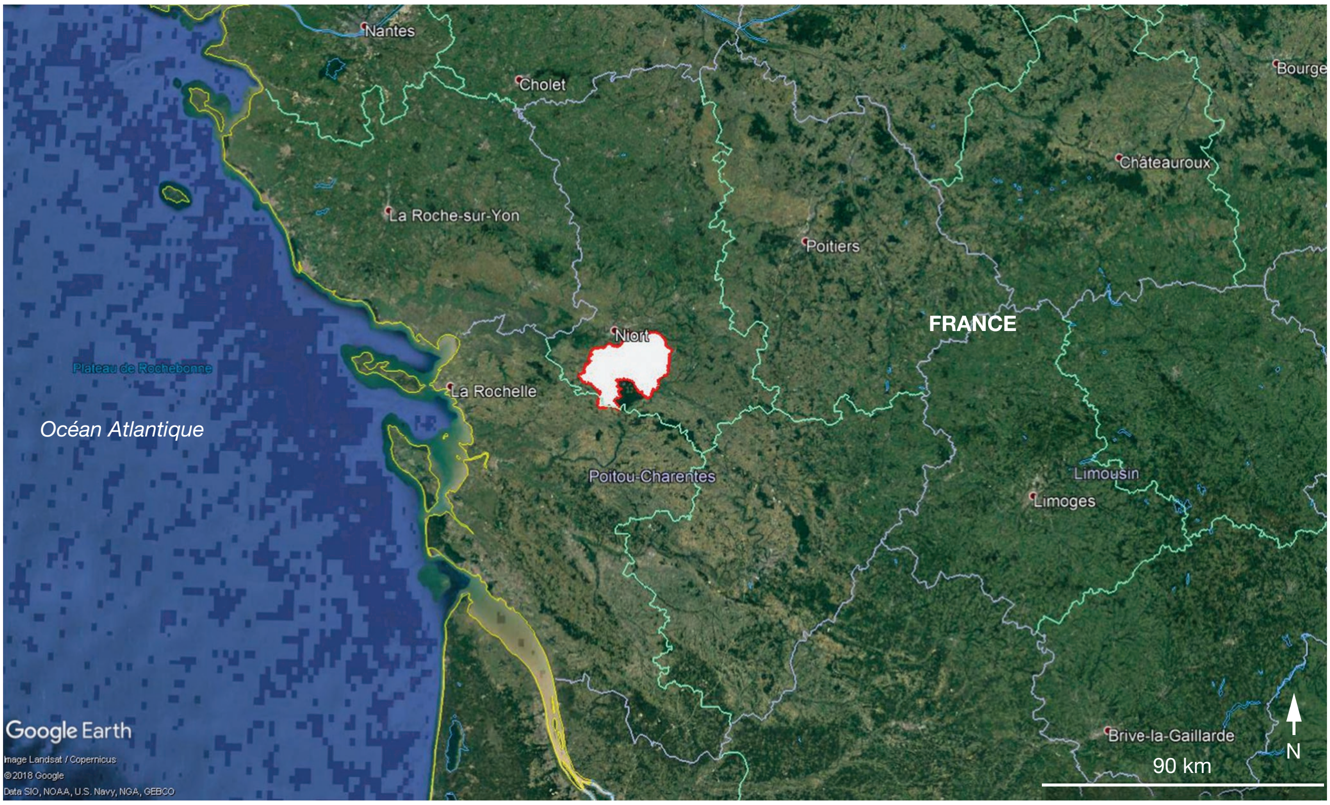

Fig. 1. — The location of the study area within the Poitou-Charentes region (western France). Source: Google Earth Pro V 7.3.2.5776. (14 December 2015). France. 45°21'34.14"N, 0°12'32.38"W, Eye alt 340.93 km. SIO, NOAA, U.S. Navy, NGA, GEBCO. US Dept of State Geographer. Landsat/Copernicus 2018. http://www.earth.google.com (13 February 2019).

forest fragments surrounded by a traditional matrix than agricultural land use.

MATERIAL AND METHODS

Studied area

The field work was performed in the "Zone Atelier Plaine et Val de Sèvre", a long-term ecological research site situated in the western part of France in the Poitou Charentes region, Deux Sèvre department (Fig. 1). The study area covers 45 000 ha and has predominantly calcareous rocks. The climate is temperate oceanic, with an average annual precipitation of 840 mm. The vegetation is represented by mixed forests, with oak as the dominant element, accompanied by maple, ash, elm, beech, cherry, etc. (Odoux *et al.* 2014). The crops are represented especially by cereals, followed by maize, sunflower, and rape. Other crops include fodder, such as clover, lucerne, sainfoin, rye-grass, fescue, orchard grass, and foxtail millet (Munier-Jolain *et al.* 2012; Odoux *et al.* 2014). The hedgerows are widely spread in the study area and border livestock farming areas and crop parcels (Odoux *et al.* 2014).

Sampling procedure

The research activities were performed within 20 forest fragments (FFs). In the study area, 14 FFs were surrounded by crops, and six were surrounded by meadows. Within each FF, sampling units of 10 by 10 m (Prigodina-Lukošienė & Naujalis 2006) were selected from the exterior to the interior of the forests as follows: 1) at the exterior of the forest fragments, sampling units were selected following the perimeter line; and 2) the remaining sampling units were selected from the perimeter line to the centre of each forest fragment. The distance between the sampling units was approximately 60 m within patches with a greater area and approximately 3 m within patches with a smaller area. A total of 209 sampling units of 10 × 10 m (of which 112 were selected at the FF exteriors and 97 were selected in the FF interiors) were selected within the FFs surrounded by crops, while within the FFs surrounded by meadows, a total of 82 sampling units of 10 × 10 m (of which 43 were selected at the exterior and 39 were selected in the interior) were selected. The structure of the FFs was multi-aged; therefore, within a given sampling unit, both thinner and larger trees were sampled. Thus, within the 10 by 10 m sampling units in the FFs surrounded by crops, 164 trees with large circumferences (of which 81 were at the FF exteriors and 83 were in the FF interiors) and 78 trees with small circumferences (of which 52 were at the FF exteriors and 26 were in the FF interiors) were selected. Within the 10 by 10 m sampling units in the FFs surrounded by meadows, 66 trees with large circumferences (of which 40 were at the FF exteriors and 26 were in the FF interiors) and 27 trees with small circumferences (of which 11 were at the FF exteriors and 16 were in the FF interiors) were selected. In total, 335 trees were sampled, with oaks being the most well represented, followed by maple and ash trees (Table 1). For each tree (including those with both large and small circumferences) in the FFs surrounded by both crops and meadows, 20 × 20 cm and 5 × 10 cm frames (for the trees with large and small circumferences, respectively) were placed on the tree trunks 1 m above the ground at each cardinal point. A total of 884 20 by 20 cm sampling units were obtained, of which 628 were from trees in FFs surrounded by crops and 256 were from trees in FFs surrounded by meadows. A total of 412 5 × 10 cm sampling units were obtained from trees with small circumferences; 296 units were obtained from trees in the FFs surrounded by crops and 116 were obtained from trees in the FFs surrounded by meadows. The circumferences of the thinner trees varied between 0.21 and 0.56 cm, and those of the large trees varied between 0.56 and 2.97 m (Table 2).

To determine the lichen abundance, all the patches of each species were counted within each 20 by 20 cm and 5 by 10 cm sampling units. Abundance was calculated as the sum of all the patches of each species in the four sampling units (20 by 20 cm or 5 by 10 cm, one in each cardinal direction) on each selected tree. Within each sampling unit, at the tree level, the depth of the bark crevices was measured in cm within each of the quarters of the sampled frames, i.e., 4 quadrats each of 10 cm and 2 quadrats each of 5 cm. Thus, four and two measures, respectively, were recorded on each cardinal face of the tree trunk, i.e., 16 and 8 measures per tree trunk.

The microvariables (tree-level variables) measured during the field activities within the 20 by 20 cm and 5 by 10 cm sampling units were as follows: host tree species, tree circumference, bark crevice depth, and cover of mosses and algae. The macrovariables (forest-level variables measured within 10 by 10 m sampling units) taken into account were as follows: forest area, spatial gradient represented by the interior and exterior parts of the FFs, distance from the forest edge to each 10 by 10 m sampling unit, elevation, canopy density, and shrub cover. The number of lichen and their abundances were treated as response variables.

The macrovariables (canopy density and shrub cover) and microvariables, such as the cover of mosses and algae, were adapted from Mistry & Berardi (2005) based on an ordinal scale that varied between 1 and 3:

1 refers to open canopies and lower shrub, moss and algae cover (0%-33%);

2 refers to moderately open canopies and moderate shrub, moss and algae cover (33%-66%); and

3 refers to closed canopies with high shrub, moss and algae cover (66%-99%).

Laboratory survey

The collected lichen species were identified using a stereomicroscope and an optical microscope. Chemical reagents, such as potassium hydroxide, calcium chloride, chlorine, iodine-potassium iodide, and paraphenylenediamine, were used in lichen identification. Dichotomous keys were used in the identification of lichen species according to Purvis *et al.* (1994), Ciurchea (2004), and Sipman (2006). Information about the taxonomy, ecology and conservation status of the identified lichen species was found in the scientific literature (Almborn 1989; Van Haluwyn *et al.* 2010; Roux 2012; Roux *et al.* 2017).

Cormophytes were identified using the following sources: Bonnier & Douin (1990a), Bonnier & Douin (1990b), Ciocârlan (2009), Schwarz (1964), Tison & Foucault (2014), www.tela-botanica.org, and http://siflore.fcbn.fr/?cd_ref=&r=metro. Spatial identification of forest fragments and land use types was performed by accessing the following website: http://www.geoportail.gouv.fr.

Statistical analysis

The host tree species and aspect were taken into account as dummy variables. Thus, a score of 1.0 was attributed to the same dummy variable of a sample and a score 0.0 was attributed to the other dummy variables of the same sample (Lepš & Šmilauer 2003).

The normality of the response variables and quantitative environmental variables (macrovariables and microvariables) was checked using a Shapiro-Wilk *W* test (Mărușteri 2006). The normality test indicated a non-normal distribution ($p < 0.05$) of the data set. Thus, the quantitative data were log-transformed to better approximate the normality assumptions (McCune & Grace 2002). The normality test did not indicate a normal distribution ($p > 0.05$) of the log-transformed data.

The variance inflation factor (VIF) was used to identify multicollinearity in the regression analysis. The VIF analysis was performed using the VIF package (vers. 1.0, Lin *et al.* 2011). Environmental variables with VIF values > 5 were excluded from the regression analysis (Legendre & Legendre 2012).

The hierarchical structure of the sampling design was represented by tree and forest levels. Due to this hierarchical structure, with trees represented by sampling units of 20 × 20 cm and 5 × 10 cm nested within sampling units of 10 × 10 m at the forest level, a mixed regression analysis was used, taking into account trees and forests as random effect factors (Pinheiro & Bates 2000). The random effect factors are considered grouping variables; therefore, variance estimation of the response variables is performed within and among these grouping variables. A hierarchical approach reduces the probability of type I and type II errors (Harrison *et al.* 2018). Mixed regression models were performed using the abundance and number of lichen species as the response variables, with four semiquantitative variables (canopy intermingling degree and shrub, moss and algae coverage), three categorical variables (spatial gradient, host tree species and aspect), and five quantitative variables (forest area, elevation, distance from the forest edge to the 10 by 10 m sampling units, bark crevice depth, and tree circumference). The semi-quantitative, categorical, and quantitative variables were treated as fixed effect factors in the regression models.

The relationships between the response and environmental variables, grouped in accordance with the hierarchical structure of the sampling design, were determined using a generalized linear mixed model (GLMM) (Pinheiro & Bates

Table 1. — The data related to the host tree genera, including their numbers calculated as the sums of the small and large circumferences for the FFs surrounded by both crops and meadows.

Host tree genera	FFs surrounded by crops		FFs surrounded by meadows		Total
	Number of trees with small circumferences	Number of trees with large circumferences	Number of trees with small circumferences	Number of trees with large circumferences	
Acer	16	20	4	8	48
Aesculus	0	2	0	0	2
Carpinus	1	0	0	0	1
Cerasus	2	1	0	4	7
Fagus	0	0	0	1	1
Fraxinus	14	12	3	1	30
Populus	0	0	0	8	8
Quercus	37	125	19	44	225
Salix	0	1	0	0	1
Sorbus	3	3	1	0	7
Ulmus	5	0	0	0	5
Total	78	164	27	66	335
M±SD	7.09 ± 11.43	14.90 ± 37.06	2.45 ± 5.66	6 ± 12.98	30.45 ± 66.19
Min ± Max	0.24 ± 0.54	0.56 ± 2.97	0.33 ± 0.47	0.61 ± 2.56	1 ± 335

Table 2. — Floristic composition of the host trees structured according to the range of their circumferences, presented as the mean and standard deviation (M±SD); the minimum and maximum raw values of the range of circumferences are given. Legend: [1]data represented by a single value; NA, data not available.

Host tree genera	FFs surrounded by crops		FFs surrounded by meadows	
	Small circumferences (M ± SD)	Large circumferences (M ± SD)	Small circumferences (M ± SD)	Large circumferences (M ± SD)
Acer	0.38 ± 0.07	0.96 ± 0.40	0.42 ± 0.06	0.59[1]
Aesculus	NA	1.71 ± 0.27	NA	NA
Carpinus	0.51[1]	NA	NA	NA
Cerasus	0.42 ± 0.07	0.97[1]	NA	0.90 ± 0.18
Fagus	NA	NA	NA	1 29[1]
Fraxinus	0.37 ± 0.06	0.92 ± 0.40	0.42 ± 0.06	0.59[1]
Populus	NA	NA	NA	1.94 ± 0.43
Quercus	0.41 ± 0.07	1.12 ± 0.50	0.45 ± 0.05	1.30 ± 0.58
Salix	NA	0.87[1]	NA	NA
Sorbus	0.30 ± 0.07	0.82 ± 0.12	0.33[1]	NA
Ulmus	0.37 ± 0.07	NA	NA	NA
Min ± Max	0.24 ± 0.54	0.56 ± 2.97	0.33 ± 0.47	0.61 ± 2.56

2000). The GLMM analysis was performed separately for each land use type (crops and meadows), spatial gradient (interior and exterior parts of the FFs), and tree trunk size (small and large circumferences). The first GLMM model included response variables related to all the environmental variables analysed by tree trunk size (5 by 10 cm/20 by 20 cm sampling units) for the trees situated in the interiors of the FFs surrounded by crops/meadows at the tree and forest levels. The second GLMM included response variables related to all the environmental variables analysed by tree trunk size (5 by 10 cm/20 by 20 cm sampling units) for the trees situated in the exteriors of the FFs surrounded by crops/meadows at the tree and forest levels.

GLMMs handle non-normal data using a link function and an exponential distribution. Regarding the abundance of lichen species, the mean Poisson response was greater than 5, indicating that penalized quasi-likelihood was an appropriate GLMM technique (Bolker *et al.* 2009). Data sets with counts are typically analysed using a Poisson distribution with a log link function (Bolker *et al.* 2009). The use of the Poisson distribution requires that the variance be equal to the mean (Bolker *et al.* 2009); however, an analysis showed that the group means and variance were not equal. Therefore, a quasi-Poisson GLMM was adopted (Bolker *et al.* 2009). Overdispersion was corrected using a quasi-Poisson GLMM (Zuur *et al.* 2009). Random effects incorporate the correlation between multiple measurements within an individual unit and the variation within and between individual units (Wu 2010) to reduce the probability of type I and type II errors (Harrison *et al.* 2018). Random effects allow within-group errors to be related (Pinheiro & Bates 2000). The GLMM analysis was performed using the glmmPQL function within the MASS package (vers. 7.3-50, Venables & Ripley 2002). To estimate the fixed-effect parameters, the maximum likelihood (ML) method was used (Harrison *et al.* 2018). The estimated values of the GLMM were presented as the estimator ± the standard error for the fixed effect factors. A deviance analysis based on a Wald chi-squared test was used to examine the significance of the fixed effect factors (Bolker *et al.* 2009). The Wald chi-squared test was performed using the package aod (vers. 1.3, Lesnoff & Lancelot 2012).

With respect to the number of lichen species, the mean Poisson response was less than 5; therefore, the Laplace approximation was selected as the appropriate technique for the GLMM (Bolker *et al.* 2009). Further, the GLMM analysis was performed using the Poisson distribution and log link function (Bolker *et al.* 2009). The glmer function within the lme4 package was adopted to analyse the relationships between the number of lichen species and environmental variables (Bates *et al.* 2015). To estimate the fixed-effect parameters, the maximum likelihood (ML) method was used (Harrison *et al.* 2018). The estimated values of the GLMM were presented as the estimator ± standard error for the fixed effect factors. The dispersion of the glmer model was measured using the dispersion_glmer function within the blmeco package (vers. 1.1, Korner-Nievergelt *et al.* 2015). Overdispersion of the modelled data was not detected. Deviance analysis based on the Wald chi-squared statistic test was used to examine the significance of fixed effect factors (Bolker *et al.* 2009). The Wald chi-squared test was performed using the package aod (vers. 1.3, Lesnoff & Lancelot 2012).

Lichen diversity was analysed taking into account the number of lichen species recorded on larger and thinner trees from the interiors of the FFs surrounded by crops and meadows compared to the number of lichen species recorded on larger and thinner trees from the exteriors of the FFs surrounded by crops and meadows. The analysis of lichen species diversity was performed considering the spatial gradient (interior and exterior parts of the FFs) within the FFs. A multiplicative partition procedure was used due to independence of the alpha by beta components (Baselga 2010). Multiplicative beta partitioning was adopted to reveal whether lichen richness shifts from the exterior to the interior of the FFs, taking into account the surrounding matrix (crops and meadows) and tree size category (larger and thinner trees). Alpha and gamma diversity were obtained by introducing the following two data matrices into the analyses: 1) the first matrix represents the number of lichen species identified on the two categories of tree size within FFs surrounded by crops or meadows; and 2) the second matrix included environmental variables (spatial gradient and tree circumferences). The spatial gradients used for the alpha and gamma diversity analysis had two levels for the exterior and interior areas of the FFs. The Shannon-Wiener index was used to estimate the alpha diversity. Alpha diversity was represented by the average number of lichen species from all the 20 by 20 cm and 5 by 10 cm sampling units per tree, and gamma diversity was represented by the total number of lichen species within the 20 by 20 cm and 5 by 10 cm sampling units over all the trees across the entire studied area. The multiplicative beta diversity indicates the differentiation of the lichen species richness from the exterior to the interior of the FFs and measures how distinct this is for each category of tree size and land use (Chao *et al.* 2012). Beta diversity was calculated by dividing the gamma diversity by the mean alpha diversity minus one. Multiplicative partitioning of diversity was performed using the vegan package (vers. 2.5-2, Oksanen *et al.* 2018). To test the significance of the differences in the lichen richness from the exterior to the interior of the FFs, the chi-square test function within the stats package was used (R Core Team 2018). The differences in lichen abundance between the interior and exterior parts of the FFs were obtained using the multi-response permutation procedure (MRPP) McCune & Grace (2002). The MRPP was performed separately for each category of tree size and each category of land use. The MRPP provides an *A* value, which is chance-corrected for within group homogeneity compared to random expectation, and a *P* value, which indicates the significance of the within group dissimilarities compared to observed dissimilarities. *A* value less than 0.10 indicates within-group heterogeneity (McCune & Grace 2002). The MRPP analysis was performed using the chord distance measure and 999 permutations. This analysis was performed using the mrpp function within the vegan package (vers. 2.5-2, Oksanen *et al.* 2018).

All the statistical analyses were performed in R software (vers. 3.5.1, R Core Team 2018).

RESULTS

In the study area, 30 lichen taxa were identified in total (Table 3). Six of the identified lichen species were very rare (*Arthonia mediella* Nyl., *Arthopyrenia fraxini* Mass., *Lecidea turgidula* Fr., *Lecanora subintricata* (Nyl.) Th.Fr., *Phaeophyscia nigricans* (Flk.) Moberg., and *Wadeana dendrographa* (Nyl.) Coppins et P.James. Of these species, *A. mediella* was endangered and of particular national interest, *A. fraxini* was critically endangered and of particular international interest, *L. turgidula*, *L. subintricata*, and *P. nigricans* were near threatened, and *W. dendrographa* was vulnerable and of particular national interest. All the rare lichen species were found only on larger trees within FFs surrounded by crops (*P. nigricans* and *W. dendrographa*) and meadows (*A. fraxini*, *A. mediella*, *L. subintricata*, and *L. turgidula*).

The pattern of lichen abundance and diversity under the influence of environmental factors along the spatial gradient of the FFs, taking into account the surrounding matrix and tree size categories, was significantly limited to larger trees from FFs delimited by crops and meadows.

Assessment of lichen abundance based on the surrounding matrix and tree size category

At the exteriors of FFs surrounded by crops, on larger trees, lichen abundances were significantly influenced by moss coverage, tree circumferences, and tree species composition (Fig. 2). The lichen abundance was significantly related to moss cover on the northern aspect of tree trunks (Fig. 2A). Additionally, mosses had a moderate to high cover in the majority of the studied FFs, especially on oak trees (Fig. 2B). Lichen abundance was greater on larger trees, especially on oak trees (*Quercus*), followed by maple (*Acer*), ash (*Fraxinus*), horse chestnut (*Aesculus*), and whitebeam (*Sorbus*) trees (Fig. 2C). The pattern of lichen abundance was well represented on trees with circumferences that ranged between 1.0 and 2.5 m (Fig. 2D). The lichen abundance was significantly higher on ash trees than on

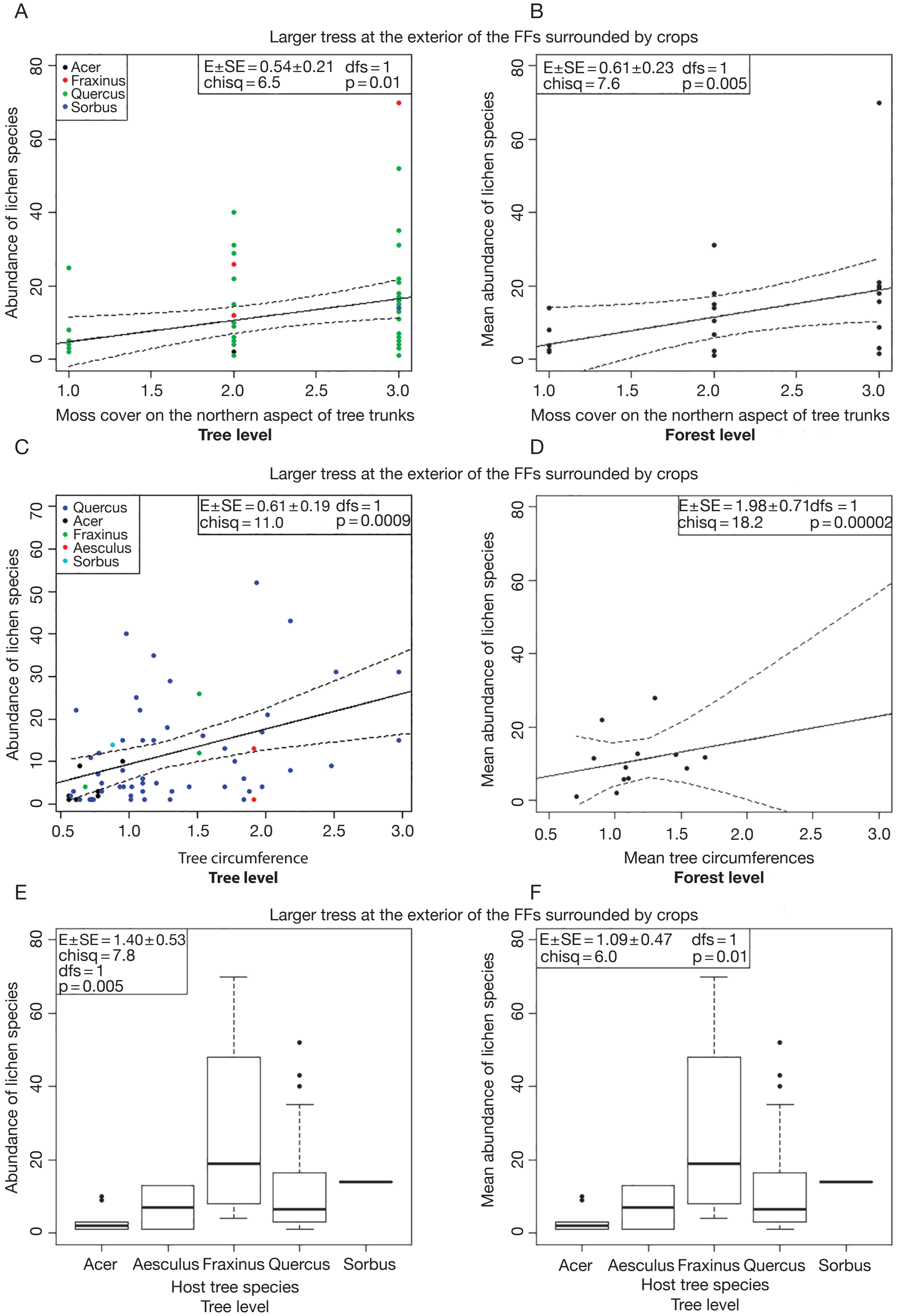

FIG. 2. — The significant effects of: **A**, **B**, moss coverage; **C**, **D**, tree circumference; and **E**, **F**, host tree species on lichen abundance according to a summary of the GLMMs. The values of the estimator (E), standard error (SE), and Wald chi-squared test (chisq), the degrees of freedom (dfs) and significance (p) are presented. The GLMM results are presented for the larger tree category (trees that range in circumference between 0.56 and 2.97) at the tree and forest levels at the exteriors of the FFs surrounded by crops.

TABLE 3. — Details of the identified lichen species, including the conservation status, type of surrounding matrix, and tree size category. Legend: **NA**, data not available; **CR**, critically endangered; **NT**, near threatened; **VU**, vulnerable; **P**, present; **A**, absent.

		Surrounding matrix			
		Crops		Meadows	
Species	Conservation status	Larger trees	Thinner trees	Larger trees	Thinner trees
Arthonia cinnabarina (DC.) Wallr.	NA	A	P	A	A
Arthonia mediella Nyl.	EN	A	A	P	A
Arthopyrenia fraxini Mass.	CR	A	A	P	A
Bacidia näegelii (Hepp.) Zahlbr.	NA	P	A	P	A
Buellia schaereri De Notr.	NA	A	A	P	A
Diploicia badia (Fr.) Szatala	NA	A	A	P	A
Diploicia canescens (Dicks.) A. Massal.	NA	P	A	P	A
Enterographa crassa (DC.) Fée	NA	P	A	A	A
Flavoparmelia caperata (L.) Hale	NA	P	A	P	A
Graphis scripta (L.) Ach.	NA	P	P	A	P
Hyperphyscia adglutinata (Flk.) H.Mayrhofer & Poelt.	NA	A	P	A	A
Lecidea turgidula Fr.	NT	A	A	P	A
Lecanora sambuci (Pers.) Nyl.	NA	P	A	P	A
Lecanora subintricata (Nyl.) Th.Fr.	NT	A	A	P	A
Lepraria sp.	NA	P	P	P	P
Opegrapha rufescens Pers.	NA	P	P	P	P
Opegrapha vulgata Ach.	NA	A	P	P	P
Parmelia sulcata Taylor	NA	A	A	P	A
Parmotrema chinense (Osbeck) Hale & Ahti	NA	A	A	P	A
Pertusaria albescens (Huds.) M.Choisy & Werner	NA	A	P	P	A
Pertusaria hymenea (Ach.) Schaer.	NA	P	A	A	A
Pertusaria pustulata (Ach.) Duby.	NA	P	P	A	A
Phaeophyscia nigricans (Flk.) Moberg.	NT	P	A	A	A
Phaeophyscia orbicularis (Nëck.) Moberg.	NA	P	P	A	A
Physcia adscendens (Fr.) Oliv.	NA	A	P	A	A
Physcia semipinnata (J. F. Gmel.) Moberg.	NA	A	P	A	A
Physconia distorta (With.) J.R.Laundon	NA	A	P	A	A
Punctelia borreri (Sm.) Turner	NA	A	P	A	A
Wadeana dendrographa (Nyl.) Coppins & P.James	VU	A	P	A	A
Xanthoria parietina (L.) Th.Fr.	NA	P	P	P	P
Total		13	15	17	5

the other studied trees (Fig. 2E, F). In the interiors of FF plots surrounded by meadows, on larger trees, lichen abundances were significantly influenced by tree species composition and shrub cover (Fig. 3A, B). The native structure of the studied FFs was represented by oak and ash trees, on which lichen species had a significantly higher abundance (Fig. 3A). Generally, the interior parts of the FFs had a dense shrub layer, and therefore, lichen species were less abundant (Fig. 3B).

At the exterior parts of the FFs surrounded by meadows, on larger trees, lichen abundances significantly decreased, especially on poplar and oak trunks, with increasing canopy density (Fig. 4).

ASSESSMENT OF LICHEN SPECIES NUMBER BASED ON THE SURROUNDING MATRIX AND TREE SIZE CATEGORY

At the exteriors of the FFs surrounded by crops, on larger trees, the number of lichen species increased with increasing maple, ash, and oak circumferences (Fig. 5).

No other significant results between the response variables and environmental factors were obtained using GLMMs.

ASSESSMENT OF LICHEN SPECIES DIVERSITY BY MULTIPLICATIVE PARTITIONING

The total number of lichen species (gamma diversity) was significantly higher on larger trees in the interior of FFs surrounded by meadows (Fig. 6). Traditional landscapes, remarkable because of the specific attributes (they lend to the native structure of habitats), were very important to lichen species diversity. Lichen species replacement (beta diversity) was higher on larger trees from the interiors of the FFs surrounded by meadows (Fig. 7A), while on thinner trees, it was higher at the exteriors of the FFs surrounded by meadows (Fig. 7B). The obtained results show that the forest structures represented by larger and thinner trees harbour significant lichen species replacement along the spatial gradients of the FFs (Fig. 7A, B). No significant results were obtained for alpha diversity.

The MRPP indicated significant differences in lichen abundance on larger trees between the interior and exterior plots of FFs surrounded by meadows (A = 0.02, P value = 0.01).

DISCUSSION

Worldwide, different types of forest management determine different patterns of epiphytic lichen diversity. In the studied area, FFs surrounded by meadows are represented by an old-growth structure due to selective cutting on short rotations (approximately 50 years); therefore, these forests harbour

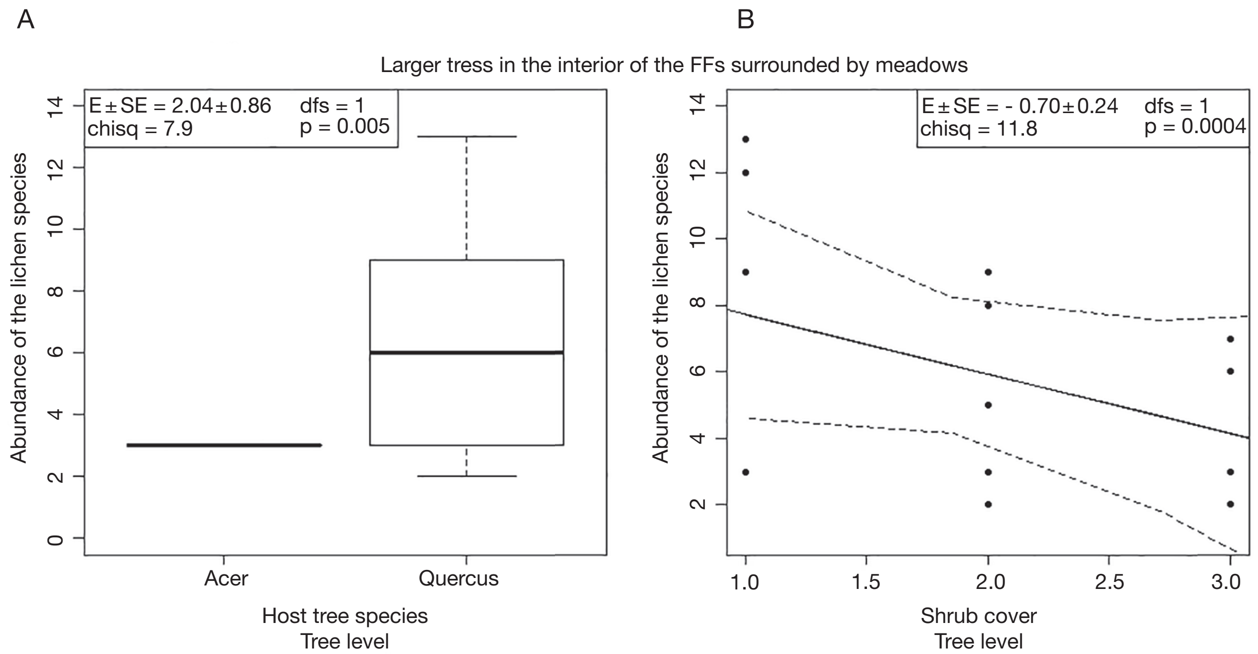

Fig. 3. — The significant effect of host tree species (**A**) and shrub cover (**B**) on lichen species abundance according to a summary of the GLMMs. The GLMM results are presented for the interior forest at the tree level within FFs surrounded by meadows, taking into account the larger tree category (trees that range in circumference between 0.56 and 2.97).

significant epiphytic lichen diversity. Furthermore, human impact on FFs surrounded by traditional land use induced a significant replacement of lichen species richness at both the exteriors and interiors of forests (Hauck *et al.* 2012). The importance of thinner trees for lichen diversity within this study is supported by their contribution to suitable microhabitats characterized by the rough bark of ash, oak, and elm trees (Mežaka *et al.* 2008) and the adequate microclimate induced by the complexity of the forest structure (Campbell & Coxson 2001).

Moss coverage, especially on larger trees, has been related to an increase in lichen abundance. In addition, in the studied forests, not all the fallen trees (of which the majority were larger trees) have been exploited for timber products; therefore, these managed forests appear to be natural reserves, with fallen trees found in an advanced stage of decay with high moss coverage. Important findings have indicated that trees with high moss cover should be maintained due to their capacity for water storage (Benesperi *et al.* 2018). Increases in bryophyte cover are closely related to high humidity, providing suitable substrata for epiphytic lichen species (Belinchón *et al.* 2009). High humidity in the study area is enhanced by climatic conditions characterized by high precipitation (Odoux *et al.* 2014).

The tree's attributes influence epiphytic lichen due to complex interactions of the environment (Ellis 2012). Epiphytic lichen species are more abundant in forests with a very large availability of larger trees (Ellis 2012), which offer habitat quality and microhabitats suitable for epiphytic lichen species (Merinero *et al.* 2014). Dense canopy structure controls light availability at lower levels of tree trunks (Moe & Botnen 1997; Benesperi *et al.* 2018), with a negative effect on epiphytic lichens (Paltto *et al.* 2011; Ellis 2012).

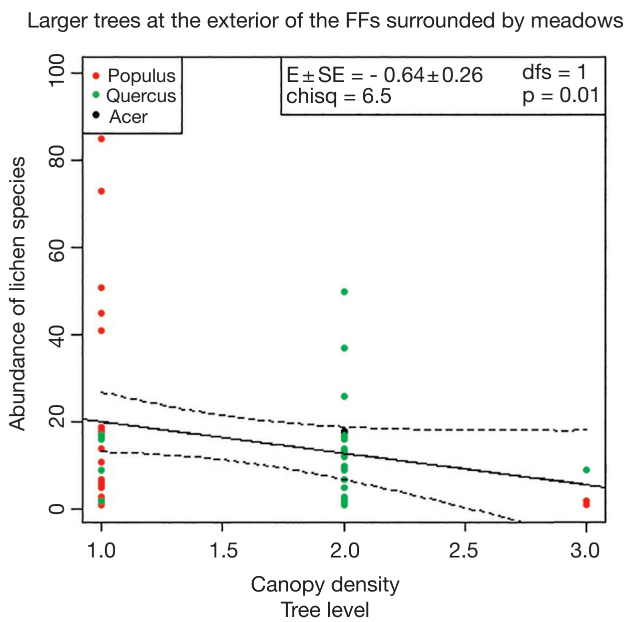

Fig. 4. — The significant effect of canopy density on lichen abundance according to the summary of the GLMMs. The GLMM results are presented for the exterior forest at the tree level within the FFs surrounded by meadows, taking into account the larger tree category (details as in Fig. 2).

At the forest level, structural complexity has a positive influence on epiphytic lichen abundance and richness, which is explained by tree-level heterogeneity and tree species composition (Ellis 2012; Li *et al.* 2019). Different

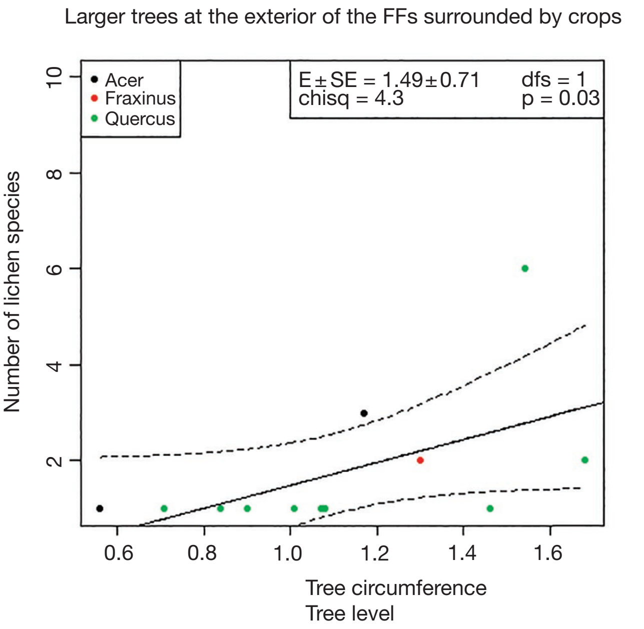

FIG. 5. — The significant effect of tree circumference on the number of lichen species according to the summary of the GLMMs. The GLMM results are presented at the tree level within FFs surrounded by crops, taking into account the larger tree category (details as in Fig. 2).

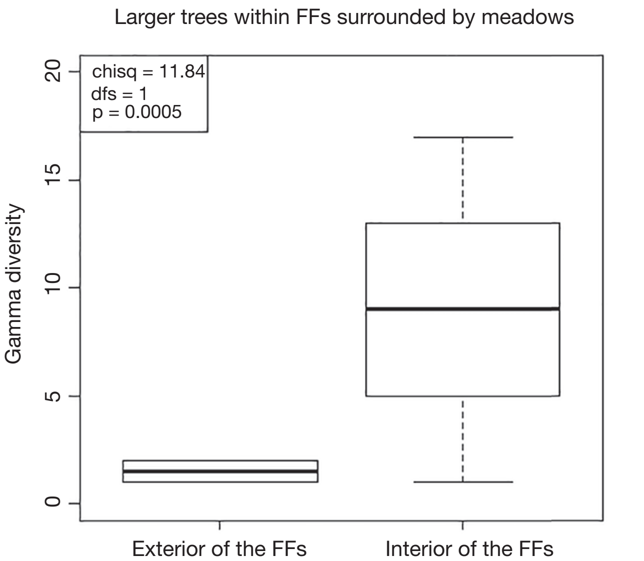

FIG. 6. — The gamma diversity indicated that the highest number of lichen species was recorded on larger trees in the interiors of the FFs surrounded by meadows (legend is as in Fig. 2).

tree species provide a range of features of bark morphology and chemical properties that support opportunities for lichen species colonization (Moe & Botnen 1997; Mistry & Berardi 2005; Belinchón *et al.* 2009; Leppik *et al.* 2011). Mixed forests dominated by oak harbour a high richness of lichen species (Johansson *et al.* 2009; Svoboda *et al.* 2011; Kubiak & Osyczka 2017). Lichen species characteristic of oak forests may be slow growing and require environmental continuity, so larger trees with a high diversity of microhabitats are suitable substrata for epiphytic lichens (Belinchón *et al.* 2009; Leppik *et al.* 2011; Kubiak & Osyczka 2017). Microhabitat quality varies with forest fragment characteristics (tree age and forest structure). Additionally, it is well known that the surrounding matrix affects the distribution of cryptogamic species (Belinchón *et al.* 2009; Chongbang *et al.* 2018). The increase in abundance and richness of lichen species at the exteriors of the studied forest fragments is due to the persistence of remnant larger trees during forest management. Larger trees with rough bark reduce the edge effect through their capacity to retain propagules (Belinchón *et al.* 2009). The continuity of forest structure is the most important driver for epiphytic lichen species richness (Campbell & Coxson 2001), but changes in the native structure of forests lead to a loss of lichen species, especially those closely related to older trees (Paltto *et al.* 2011; Brunialti *et al.* 2012).

According to the findings of this study, the following practical measures are suggested: 1) retain the remnant structural attributes of forest fragments to facilitate the long-term conservation of epiphytic lichen species, which are dependent on these attributes; and 2) maintain tree species diversity and structural heterogeneity within managed forest fragments.

CONCLUSION

Forest management applied within FFs from the "Zone Atelier Plaine et Val de Sèvre" is sustainable due to the maintenance of scattered larger trees during rotation cycles. Larger trees provide suitable microhabitats for epiphytic lichen species within FFs surrounded by both traditional and agricultural matrices. Tree species composition contributes to the diversity of epiphytic lichen species. Furthermore, thinner trees significantly contributed to lichen species turnover along the spatial gradient of the FFs. Therefore, it is important to retain larger tree and tree species diversity to conserve lichen species and their associated habitats.

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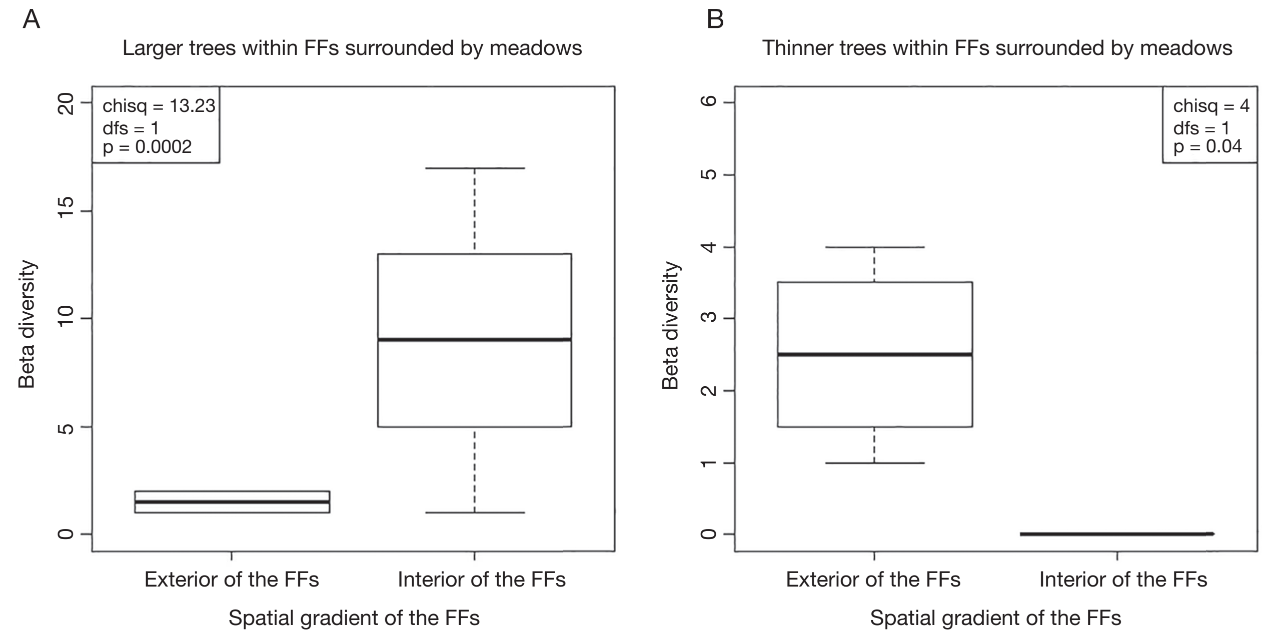

FIG. 7. — The beta diversity indicated significant lichen species replacement on larger trees in the interiors of the FFs surrounded by meadows (**A**). In contrast, lichen species replacement was significant on thinner trees from the exteriors of the FFs surrounded by meadows (**B**).

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