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Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests

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Abstract   Testing the relations between tree parameters and the richness and composition of lichen communities in near-natural stands could be a first step to gather information for forest managers interested in conservation and in biodiversity assessment and monitoring. This work aims at evaluating the influence of tree age and age-related parameters on tree-level richness and community composition of lichens on spruce in an Alpine forest. The lichen survey was carried out in four sites used for long-term monitoring. In each site, tree age, diameter at breast height, tree height, the first branch height, and crown projection area were measured for each tree. Trees were stratified into three age classes: (1) <100 years old, immature trees usually not suitable for felling, (2) 100–200 years old, mature trees suitable for felling, and (3) >200 years old, over-mature trees normally rare or absent in managed stands. In each site, seven trees in each age class were selected randomly. Tree age and related parameters proved to influence both tree-level species richness and composition of lichen communities. Species richness increased with tree age and related parameters indicative of tree size. This relation could be interpreted as the result of different joint effects of age per se and tree size with its area-effect. Species turnover is also suspected to improve species richness on over-mature trees. Similarly to species richness, tree-level species composition can be partially explained by tree-related parameters. Species composition changed from young to old trees, several lichens being associated with over-mature trees. This pool of species, including nationally rare lichens, represents a community which is probably poorly developed in managed forests. In accordance to the general aims of

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near-to-nature forestry, the presence of over-mature trees should be enhanced in the future forest landscape of the Alps especially in protected areas and Natura 2,000 sites, where conservation purposes are explicitly included in the management guidelines.

Introduction

Epiphytic lichen communities are influenced by several factors whose importance depends on the scale of the analysis. For example, regional patterns in lichen community composition depend strongly on climatic or topographic gradients (Peterson and Mc Cune 2001; Jovan and Mc Cune 2004; Berryman and Mc Cune 2006), while at the landscape level tree composition, stand age, stand heterogeneity, and the presence of coarse wood are more important (e.g. Hyvärinen et al. 1992; Humphrey et al. 2002). At the tree-level, tree age influences both the richness and the abundance of macrolichens, with several species preferring old trees (Uliczka and Angelstam 1999). Recently, Johansson et al. (2007) has demonstrated that tree age and size have an important role in explaining tree-level species richness and composition on ash trees in southern Sweden. However, the effect of tree age and size are difficult to disentangle. The former is related to the time available for colonization, whilst the latter is more related to the available surface for lichen establishment. Furthermore, other tree features could influence epiphytic lichens, e.g. canopy structure due to its relation with light availability. The results of former studies proved to be relevant for planning conservation strategies and management of forests, since they suggest that some simple parameters related both to stand identity and tree features could be used to assess the potential of forests for lichen diversity. For example, the tree-level occurrence of rare or red-listed species is known to be enhanced by increasing tree age and diameter, indicating that old and large trees are crucial for lichen conservation (Uliczka and Angelstam 1999).

In the Alps, despite the noticeable reduction of human activities since the beginning of the twentieth century, spruce forests are still intensively managed for timber production (Motta 2002). Management practices are mainly based on the shelterwood system or on clear-cut over small surfaces (<1 ha) in which mature trees (120–180 years) are felled. In managed spruce forests trees with more than 200 years are usually absent or rare and remnant stands with 'old-growth structures' tend to be scattered and small-sized in the Italian Alps (Motta 2002). The increasing interest on near-to-nature forestry has favored a scientific-based and multi-purpose management approach whose models are often developed on the basis of ecological studies in the remnant near-natural sites. This could apply also to epiphytic lichens, whose role in biodiversity conservation in managed forests of the Southern Alps is still largely unknown (but see Nascimbene et al. 2007). Testing the relations between tree parameters and the richness and composition of lichen communities in near-natural stands could be a first step to gather information for forest managers interested in conservation and in biodiversity assessment and monitoring. Thus, this work aims at evaluating the influence of tree age and age-related parameters on tree-level richness and community composition of lichens on spruce.

Materials and methods

Study area

The study was carried out in the Paneveggio spruce forest (Paneveggio-Pale di San Martino Natural Park, N-Italy, Trentino-Alto Adige; 46°18′N, 11°45′E), extending over a 6,000 ha surface. The average annual temperature is 2.4°C, annual rainfall is c. 1,200–1,300 mm year^{-1}. The bedrock is porphyry, the soils are rankers and podsols.

The lichen survey was carried out in four sites used for long-term monitoring since 1993 (Motta 2002; Motta et al. 2002). Their main features are reported in Table 1. The first two sites are in dense mono-layered spruce stands which were not managed in the last 30–50 years and whose establishment started after an intensive logging activity, probably shelterwood cutting in small groups, approximately in 1,820 in site 1, and in 1,790 in site 2. Sites 3 and 4 are in multi-layered, open-canopied stands which were not managed in the last 50 years. Site 3 was managed for at least the past three centuries with single-tree or small-group selection system. Site 4 was probably a pasture with sparse trees up to the end of the ninetieth century (Motta 2002).

Tree parameters

In each site, tree age (AGE) was measured for each tree by extracting cores with an increment borer and preparing according to standard procedures (Stokes and Smiley 1968; Swetnam et al. 1985). Tree rings were counted, corrected, and each series was dated both visually and using the programs TSAP (Rinn 1996) and COFECHA (Holmes 1983). Tree size was represented by tree diameter at breast height, measured in two direction and averaged (DBH), and tree height (HEIGHT). The first branch height (CR-INS) was measured in two directions and averaged, and crown projection area (AREA) was evaluated by measuring the branch length, perpendicularly to the stem, at four cardinal directions, and computing the area of the resulting irregular ellipsoid.

Lichen survey

For lichen surveying, trees were stratified into three age classes potentially corresponding to different stages of the management process: (1) <100 years old, immature trees usually not suitable for felling, (2) 100–200 years old, mature trees suitable for felling, and (3) >200 years old, over-mature trees normally rare or absent in managed stands. In each site,

Table 1 Main features of the four sites

	Site1	Site2	Site3	Site4
Altitude (m)	1695	1815	1865	1980
Slope (°)	17	25	20	15
Aspect	NW	NW	N	N
Number of living trees (n ha^{-1})	484	557	477	846
Proportion (%)				
Picea abies	100	100	99	75
Larix decidua	0	0	0	18
Pinus cembra	0	0	1	7

Table 2 Descriptive statistics of sampled trees within each age class and each site

	Age 1	Age 2	Age 3	Site1	Site2	Site3	Site4
Number of *Picea abies*	28	28	28	21	21	21	21
Mean tree diameter (cm)	31 ± 14	43 ± 15	57 ± 10	43 ± 12	51 ± 10	38 ± 22	44 ± 19
Mean tree age (y)	85 ± 15	149 ± 27	271 ± 62	163 ± 58	173 ± 85	179 ± 102	159 ± 101
Total number of lichen species recorded on the sampled trees	43	55	57	41	42	42	44
Mean number of lichen species/tree	8 ± 2.8	12 ± 2.9	14 ± 3.4	12 ± 4	13 ± 2	10 ± 4	11 ± 5

Mean values are given with standard error (SE)

seven trees in each age class were selected by random sampling, for a total of 84 trees (Table 2).

Sampling followed the guidelines proposed by Stofer et al. (2003) for the Forest BIOTA project (Giordani et al. 2006), which are based on the European guidelines for lichen monitoring (Asta et al. 2002; Scheidegger et al. 2002a). Lichen diversity was sampled using four standard frames of 10×50 cm as sampling grids, subdivided into five 10×10 cm quadrats, which were attached to the tree trunk at the cardinal points with the shorter lower side at 100 cm from the ground. All lichen species inside the frames were listed and their frequency was computed as the number of 10×10 cm quadrats in which the species occurred. Lichen cover was visually estimated in each frame as percentage of surface occupied by lichens and the values of the four cardinal points were averaged for each tree.

The rarity of species at the national level was retrieved from Nimis (2003). Eight commonness-rarity classes were used, from extremely rare to extremely common. The 'extremely rare' status is given only to taxa known from less than five localities in Italy, or to those that were not mentioned in the literature in the last 50 years. Recently described or dubious taxa are excluded from this category. In the present work, very and extremely rare species were merged into a single category, and labeled as 'rare'. Nomenclature of lichens follows Nimis and Martellos (2003).

Data analysis

For each site, the Pearson correlation coefficients between tree parameters (AGE, DBH, HEIGHT, CR-INS, AREA) and tree-level lichen richness (mean number of species at tree-level), and lichen cover were calculated. We preferred a strict correlational approach instead of a multiple regression model due to the high collinearity among the explanatory variables.

To examine the effect of tree age on lichen species richness, analysis of covariance (ANCOVA) was applied considering site identity (SITE) as a random factor and AGE as a continuous covariate. To meet assumptions of ANCOVA, the variables were checked for normality, and variance homogeneity. Scatterplots were analyzed to check linearity between the covariate and species richness (Quinn and Keough 2002). AGE was log-transformed to increase linearity and to reach a normal distribution of errors. As only total species richness met the assumptions of ANCOVA, we did not perform this analysis for lichen cover.

Simple linear regression was applied to describe separately the relation between total species richness and tree age and size (DBH and HEIGHT).

Species composition was explored by means of redundancy analysis (RDA) as implemented in the CANOCO package (Version 4.5, Ter Braak and Šmilauer 2002). Since a preliminary detrended correspondence analysis (DCA) showed a total inertia expressed in standard unit of 2.21 SD, linear-based ordination methods were considered suitable for the data set. RDA was tested for significance using a Monte Carlo Permutation Test ($n = 1,000$). Specie frequencies were log-transformed prior the analysis. Tree-related quantitative explanatory variables were: AGE, DBH, HEIGHT, CR-INS, and AREA. Site identity was considered as a dummy variable. First, we tested separately tree-related variables and site identity with a forward selection (Monte Carlo permutation test, $P < 0.01$). Then we performed a variation partitioning analysis to separate the relative effect of tree-related variables and site identity on lichen species composition following the method of Borcard et al. (1992).

An indicator species analysis (ISA; Dufrêne and Legendre 1997) was used to describe differences in species composition and frequency among the three age classes, and to determine how strongly each species was associated to different age classes. For each species, the indicator value (IV) ranges from 0 (no indication) to 100 (maximum indication). Statistical significance of IV was tested by means of a Monte Carlo test, based on 10,000 randomizations. The indicator species analysis and Monte Carlo test were performed by PC-ORD (Mc Cune and Mefford 1999).

Results

Seventy epiphytic lichens and two non lichenised fungi (*Chaenothecopsis pusilla* and *Microcalicium disseminatum*) were found (Table 3). Their number ranges from 43 to 57 in the three age classes and from 41 to 44 in the sites, with an average species number per tree ranging from 8 to 14 in the age classes, and from 10 to 13 in the sites (Table 2). The lowest number of species per tree (3) was found on a 84 years old spruce in site 3, while the highest number was 22 on a 347 years old spruce in site 4. Twelve nationally rare and twelve calicioid species were found (Table 3).

Species richness and lichen cover

Tree size (DBH and HEIGHT) was positively correlated to tree age, while features related to crown structure (CR-INS, and AREA) were correlated with tree age in the two open-canopied sites only (3 and 4, Table 4). In each site, species richness was positively correlated to tree age and size. In the ANCOVA model, no significant interaction was found between site and tree age, indicating that species richness responded similarly to age in each site (Table 5). Species richness increased with age, leveling out at around 250–300 years (Fig. 1a), while it increased constantly with DBH and HEIGHT (Fig. 1b, c). The overall, as well as the mean number of species per tree increased from age class 1 to 3 (Table 2). Tree features related to crown structure seem to be more important for lichen richness in sites 3 and 4 than in the other two sites. Lichen cover was not correlated to tree age in the two dense-canopied sites (1 and 2), while it had a positive relation with age in the two open-canopied sites.

Table 3 Species list

Species	NRS	Cal	Frequency in the three age classes			Age IV	Frequency in the four sites				Site	IV
			1	2	3		1	2	3	4		
Arthonia mediella			4	0	0	3.6	0	0	0	5	4	4.8
Bacidia globulosa			4	0	0	3.6	0	0	5	0	3	4.8
Bacidia subincompta			4	0	0	3.6	0	0	0	5	4	4.8
Biatora chrysantha			7	0	0	7.1	0	0	10	0	3	9.5
Buellia punctata			4	0	0	3.6	5	0	0	0	1	4.8
Cladonia coniocraea			4	0	4	1.8	0	10	0	0	2	9.5
Hypogymnia tubulosa			11	11	0	5.4	0	10	0	19	4	13.3
Lecanora argentata			14	4	4	13.0	0	0	5	24	4	15.5
Lecanora leptyrodes			4	4	0	1.8	5	5	0	0	1	2.4
Lecanora symmicta			11	0	0	10.7	5	0	0	10	4	4.3
Lopadium disciforme	+		4	4	4	1.8	5	10	0	0	2	4.8
Melanelia exasperatula	+		4	0	0	3.6	0	0	0	5	4	4.8
Mykoblastus affinis			39	36	36	14.8	76	71	0	0	1	45.0**
Parmeliopsis hyperopta			43	32	21	27.9*	14	48	19	48	4	19.4
Rinodina capensis			7	4	0	6.1	0	0	0	14	4	14.3*
Vulpicida pinastri			29	11	7	22.4*	5	5	5	48	4	39.1**
Biatora efflorescens			0	4	0	3.6	0	5	0	0	2	4.8
Bryoria capillaris			14	32	21	16.7	0	29	38	24	3	16.9
Buellia griseovirens			11	21	18	12.5	33	5	14	14	1	19.7*
Buellia schaereri			0	14	11	6.5	0	0	19	14	3	11.1
Caloplaca herbidella	+		0	4	0	3.6	0	0	5	0	3	4.8
Cetraria sepincola			0	4	0	3.6	0	0	5	0	3	4.8
Chaenotheca hispidula	+	+	0	7	4	4.8	0	10	5	0	2	7.9
Chaenotheca laevigata	+	+	25	25	18	11.2	52	29	10	0	1	28.3**
Hypogymnia physodes			89	96	93	34.1	95	100	76	100	1	37.3**
Lecanora cadubriae			0	7	4	5.0	0	0	5	10	4	4.8
Lecanora circumborealis			7	18	4	15.1*	0	10	19	10	3	11.0
Lecanora hypoptoides			0	4	0	3.6	5	0	0	0	1	4.8
Lecanora pulicaris			11	11	4	5.2	19	10	0	5	1	10.4
Lecanora varia			0	7	4	3.6	0	0	5	10	4	7.1

Table 3 continued

| | NRS | Cal | Frequency in the three age classes | | | Age | Frequency in the four sites | | | | Site | |
			1	2	3	IV	1	2	3	4		IV
Lepraria elobata			0	7	4	4.2	0	14	0	0	2	14.3
Micarea prasina			0	4	0	3.6	5	0	0	0	1	4.8
Ochrolechia alboflavescens		+	4	21	18	11.4	0	0	19	38	4	27.2**
Ochrolechia androgyna		+	4	21	11	11.7	29	14	0	5	1	12.9
Schismatomma pericleum	+	+	25	50	7	35.0*	38	48	24	0	2	17.1
Usnea hirta			0	7	4	5.7	0	5	0	10	4	7.0
Bryoria fuscescens			0	18	25	16.2	5	0	14	38	4	32.5**
Calicium glaucellum		+	7	25	43	20.3	43	33	14	10	1	24.2*
Calicium viride		+	46	79	93	38.8**	57	95	76	62	2	30.5*
Chaenotheca chrysocephala		+	46	39	61	23.3	67	52	71	5	3	41.9***
Chaenotheca ferruginea	+	+	0	4	11	6.0	5	0	14	0	3	12.7*
Chaenotheca trichialis		+	11	21	61	39.5**	24	33	57	10	3	40.7**
Chaenothecopsis pusilla		+	0	0	7	7.1	0	0	5	10	4	9.5
Chrysothrix candelaris			0	11	29	24.1**	48	0	5	0	1	45.8***
Cladonia digitata			0	4	11	8.6	0	14	0	5	2	12.9
Cyphelium inquinans	+	+	0	11	43	41.1**	5	5	33	29	3	26.3**
Cyphelium karelicum	+	+	0	0	54	53.6**	10	19	33	10	3	23.7*
Cyphelium tigillare	+	+	0	0	4	3.6	0	0	0	5	4	4.8
Evernia divaricata			18	50	54	27.8	24	19	52	67	3	27.2
Hypogymnia austerodes			0	4	7	3.6	0	0	0	14	4	14.3
Hypogymnia bitteri			4	18	18	9.6	29	5	0	19	1	11.0
Hypogymnia farinacea			4	7	14	7.6	0	0	5	29	4	24.8**
Imshaugia aleurites			0	7	11	9.3	0	0	0	24	4	23.8**
Lecidea leprarioides			11	7	18	9.5	43	5	0	0	1	38.1**
Lepraria rigidula			0	0	4	3.6	0	0	5	0	3	4.8
Letharia vulpina			0	4	11	9.5	0	0	0	19	4	19.0*
Microcalicium disseminatum		+	0	0	11	10.7	0	0	10	0	3	8.4
Mykoblastus sanguinarius			4	4	7	4.7	14	5	0	0	1	11.6
Ochrolechia arborea			0	4	7	4.8	5	10	0	0	2	6.3
Ochrolechia microstictoides			36	29	43	19.9	43	86	0	14	2	58.1**

Table 3 continued

	NRS	Cal	Frequency in the three age classes			Age	IV	Frequency in the four sites				Site	IV
			1	2	3			1	2	3	4		
Parmelia saxatilis			46	71	68	3	26.4	95	86	48	19	1	53.2**
Parmelia sulcata			11	7	25	3	9.0	19	5	19	14	1	11.1
Parmeliopsis ambigua			86	100	100	3	36.5	81	100	100	100	4	31.9**
Pertusaria amara			7	14	25	3	12.5	33	24	5	0	1	17.7
Platismatia glauca			46	57	82	3	34.7*	95	100	33	19	1	46.1**
Pseudevernia furfuracea			39	68	68	3	28.0	19	86	52	76	4	38.2**
Ramalina farinacea			0	0	7	3	7.1	0	5	5	0	2	2.4
Ramalina obtusata	+		0	0	4	3	3.6	0	0	5	0	3	4.8
Ramalina thrausta	+		4	0	4	3	2.1	5	0	5	0	3	2.9
Tuckermannopsis chlorophylla			0	21	46	3	33.5*	10	24	5	52	4	34.2**
Tuckneraria laureri	+		0	0	14	3	14.3*	5	14	0	0	2	11.9
Usnea sp.pl.			11	36	39	3	25.4*	14	33	24	43	4	24.7*

Species are ordered according to the age class (Age) in which the indicator value (IV) is maximum, following the results of the indicator species analysis

NRS Nationally rare species

Cal Calicioid species

Frequency in the three age classes: species frequency in each age class (1, 2, 3) is expressed by the percentage of trees of each class in which the species occurred

Frequency in the four sites: species frequency in each site (1, 2, 3, 4) is expressed by the percentage of trees of each site in which the species occurred

IV: maximum indicator value

* Marks significant indicator species at $P < 0.05$, ** $P < 0.01$

Table 4 Pearson correlation coefficients for the independent variables, species richness, and lichen cover

	SITE	AGE	DBH	HEIGHT	CR-INS	AREA	Species richness
DBH	1	0.38*					
	2	0.57*					
	3	0.85*					
	4	0.64*					
HEIGHT	1	0.45*	0.89*				
	2	0.45*	0.59*				
	3	0.78*	0.83*				
	4	0.87*	0.84*				
CR-INS	1	–	–	–			
	2	–	–	–			
	3	0.6*	0.63*	0.7*			
	4	0.79*	0.75*	0.8*			
AREA	1	–	0.56*	0.38*	−0.19		
	2	–	0.58*	–	−0.45*		
	3	0.6*	0.82*	0.61*	0.51*		
	4	0.59*	0.81*	0.68*	0.57*		
Species richness	1	0.52*	0.59*	0.58*	–	0.38*	
	2	0.55*	0.66*	0.53*	–	–	
	3	0.6*	0.68*	0.69*	0.61*	0.6*	
	4	0.73*	0.76*	0.7*	0.77*	–	
Lichen cover	1	–	0.4*	0.55*	–	–	0.43*
	2	–	–	–	–	–	–
	3	0.62*	0.63*	0.7*	0.49*	0.52*	0.58*
	4	0.53*	0.7*	0.62*	0.46*	–	0.72*

* Marks significant correlations ($P < 0.05$)

Table 5 Results of ANCOVA for total lichen species richness site identity (SITE) as a random factor and tree AGE as covariate

Source of variation[a]	df	SS	MS	F-value	P	Slope
SITE	3	127.94	42.65	4.9534	<0.01	
Ln(AGE)	1	490.59	490.59	56.98	<0.01	4.77
Residuals	79	680.17	8.61			

Results refer to the ANCOVA testing the main effects assuming slope homogeneity

[a] The non-significant interaction was removed from the model, before testing the main effects

Species composition

Among tree-related variables, the RDA forward selection included AGE, DBH, HEIGHT, and AREA. Site identity was also significant. Total variation in species composition explained by all significant variables (tree-related and site) was 36.5% ($P < 0.01$). The pure effect of tree-related variables was 11.1% ($P < 0.01$), while that of site identity accounted for 11.5% ($P < 0.01$). The joint effect between the two groups accounted for 13.9% of the total variation.

Considering the pure effect of tree-related variables (Fig. 2a), several species were positively influenced by increasing tree age and size (DBH and HEIGHT) irrespective of tree age, e.g. *Calicium viride*, *Cyphelium inquinans*, *C. karelicum*, *Chaenotheca trichialis*, and *Tuckermannopsis chlorophylla*, others, e.g. *Parmeliopsis hyperopta* and *Vulpicida pinastri* were negatively influenced by these parameters. Also crown structure (AREA) positively
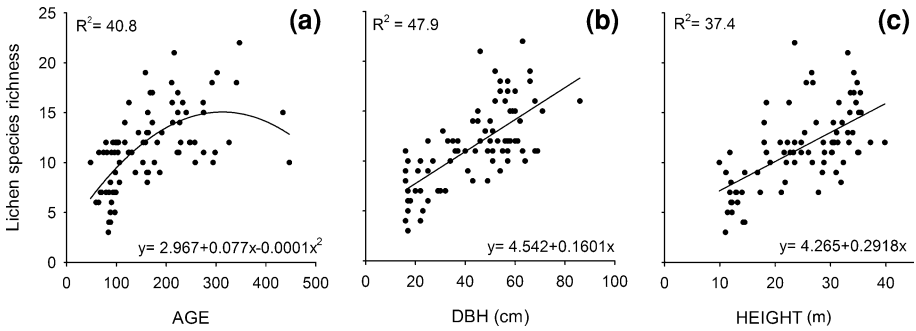
Fig. 1 Scatterplots of the number of lichen species vs. (**a**) tree age (AGE), (**b**) tree diameter (DBH), and (**c**) tree height (HEIGHT). Trends are shown by fitting linear and quadratic functions when significant (*F*-test, *P* < 0.01)
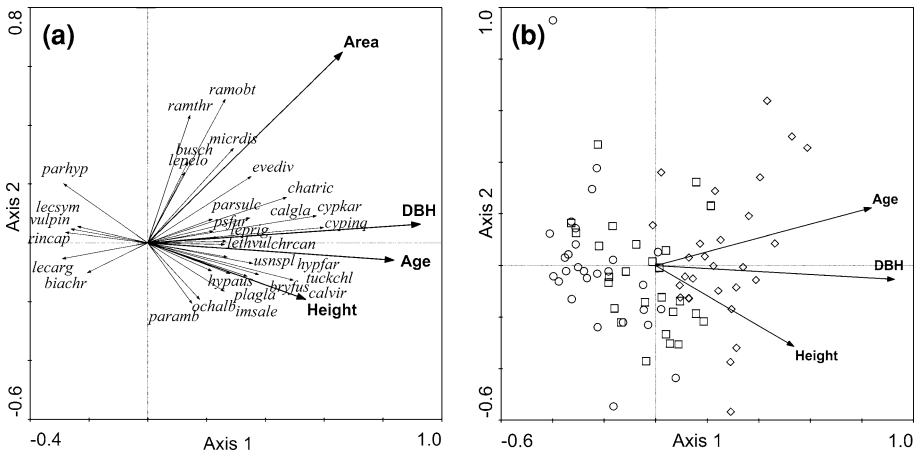
Fig. 2 (**a**) Plot species x pure effect of tree parameters; (**b**) Plot trees x pure effect of tree parameters. Trees are classified according to the three age classes (○ = <100 years; □ = 100–200 years; ◇ = >200 years)

influenced some species such as *Evernia divaricata*. When the sampled trees, classified in the three age classes, are plotted against tree-related variables (Fig. 2b), over-mature trees are clearly separated, while immature and mature trees are largely overlapping, indicating that their lichen communities have a rather similar species composition.

ISA indicated the presence of some over-represented species in each age class, which are therefore indicators of different stages of tree development (Table 3). They represent 18% of the total and their number is higher in age class 3 (9 species), in accordance with the low differentiation in species composition between trees of classes 1 and 2. Among indicators for over-mature trees, there are 3 nationally rare and 4 calicioid species, which completely lack on trees younger than 100 years. A single nationally rare species was found among indicators for mature trees (100–200 years old). Over one-third of the species are over-represented in one of the four sites, confirming the influence of site identity in shaping species composition. Eight old trees associated species are included among over-represented species in the four sites (2, 1, 3, 2 species in site 1, 2, 3, 4, respectively). Nationally rare and calicioid lichens are mostly associated to site 3 (Table 3).

Discussion

Tree age and related parameters proved to influence both tree-level species richness and composition of epiphytic lichen communities on spruce in mature subalpine forests of the Italian Alps. These parameters are well known to be related with epiphytic lichens occurrence, even if their effects are often contrasting and not clearly separated from each other. For example Johansson et al. (2007) demonstrated the joint positive effect of age and size on tree-level lichen diversity in relatively young, planted ash forests, Öckinger et al. (2005) found a positive correlation between age and circumference, Uliczka and Angelstam (1999) concluded that on different tree species lichen richness increases with age, while Rolstad and Rolstad (1999) demonstrated that stand age and tree size were more important than tree age in explaining the occurrence of *Usnea longissima*, an old-growth associated lichen.

In our forest, tree-level species richness proved to increase with tree age and related parameters indicative of tree size, such as DBH and tree height. Tree age had a positive correlation with tree size, hindering the possibility to clearly distinguish their respective effect. In the two open-canopied sites, age is also correlated with crown size, since the crowns are allowed to progressively increase with age and trunk size.

The increase of species richness with tree age could be interpreted as the result of different joint effects of age per se (e.g. time for colonization) and tree size with its area-effect (e.g. surface for lichen establishment). When considered separately, the effects of age and tree size have a rather different pattern, the former leveling with age and therefore being more important in younger trees, the latter progressively increasing. Species turnover, whose importance in enhancing species richness was addressed by Johansson et al. (2007), due to the increasing overall number of species with age, is also suspected to improve species richness on over-mature trees. Over-aged large trees are expected to be more lichen rich and to host more heterogeneous species assemblages than mature and immature trees.

All tree-level dependent variables, however, are also influenced by site identity (e.g. stand-level factors), indicating that a stand-level approach would be required to clarify the interactions between tree-level and stand-level factors. For example, the relation between tree age and lichen cover suggests that this dependent variable is greatly influenced by stand-level conditions. In the two dense-canopied stands lichen cover is independent from tree age and DBH, probably due to a limiting effect of light availability depending on stand structure. In the two open-canopied stands, light is not a limiting factor, and lichen cover increases with tree age and DBH, similarly to species richness.

Relations among tree features and species richness could provide useful tools for management. The estimate of species richness represents an important issue (Lindenmayer et al. 2000), which is often achieved using biodiversity indicators that can be more easily sampled (Noss 1990; Lawton et al. 1998; Will-Wolf et al. 2002). The selection of indicators, however, may be problematic (e.g. Kerr et al. 2000; Landers et al. 1988; Noss 1990), and their correlation with the overall diversity must be tested (Hedenås and Ericson 2000; Bergamini et al. 2005; Nascimbene et al. 2006; Nordén et al. 2007). For a rapid assessment of tree-level species richness both structural and biological indicators could be used. Tree size, relatively easy to measure, is a suitable structural indicator, while lichen cover (mainly in open-canopied stands), could be another suitable biological indicator.

Similarly to species richness, tree-level species composition can be partially explained by tree-related parameters. As in boreal forests (see Hilmo 1994), species composition on spruce changed from young to old trees. However, the main difference in species composition was between over-mature trees and the other two age classes. Age and tree size tend to select the same species. The biological and ecological mechanism of such a selection is not

completely clear, but relevant changes in chemical-physical features of the bark (see e.g. Hyvärinen et al. 1992) are supposed to be among the main factors driving species turnover. A significant influence on composition is also that of crown structure, whose effects are probably related to light availability and protection from direct rain. Crown structure could be responsible for differences in microclimatic conditions between over-aged trees and those of the other age classes. Among species favored by increasing crown size, *Evernia divaricata* is representative of a pool of species which mainly establish on the lower branches of large trees, while the occurrence of *Microcalicium disseminatum* and other calicioid species might be favored by dry and rain-protected conditions under the crown.

Differences in species composition at tree-level were also confirmed by ISA, indicating that several lichens are strongly associated with over-mature trees. This pool of species, including several nationally rare lichens, represents a community which is probably poorly developed where over-mature trees are normally absent, such as in managed forests. Calicioid lichens, well known as indicators of ecological continuity (Tibell 1992; Selva 2002), have a similar pattern among indicator species in the different age classes, being more represented on over-mature trees. For example *Cyphelium karelicum* was considered by Thor (1998) as indicating continuity in spruce forests of Sweden. The influence of stand-level factors cannot be statistically evaluated with our four sites, but the higher number of rare and calicioid species related to site 3 is in accordance with its longer ecological continuity (Motta 2002).

The rarity and the potential threat of several epiphytic lichens could be interpreted as the output of low availability of over-mature trees in managed spruce forests of the Italian Alps. This is in accordance to Scheidegger et al. (2002b), who emphasized the importance of old trees for the conservation of red-listed epiphytic lichens in Switzerland and to Thor (1998) who stated that trees hosting red-listed species are often older than usually allowed in commercial forestry. Fritz et al. (2008) concluded that old trees might enhance the conservation of red-listed species in beech dominated forests of Sweden, and analogously Pykälä (2003) demonstrated that in an intensively managed forest landscape most of the rare epiphytic lichens are found only in key habitats with a long-term continuity of old trees.

The general aims of near-to-nature forestry include biodiversity conservation. Hence, the presence of over-mature trees should be enhanced in the future forest landscape of the Alps (see also Fritz et al. 2008). Retaining mature trees in management plans could be an effective measure for long-term lichen diversity conservation, especially in protected areas and Natura 2,000 sites, where conservation purposes are explicitly included in the management guidelines.

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