The Lichenologist **50**(2): 231–237 (2018) doi:10.1017/S0024282918000087

The inclusion of overlooked lichen microhabitats in standardized forest biodiversity monitoring

Arsen GASPARYAN, Harrie J. M. SIPMAN, Lorenzo MARINI and Juri NASCIMBENE

Abstract: Epiphytic lichens are increasingly included in forest biodiversity monitoring schemes, but most of the standardized guidelines consider only lichens colonizing a small part of tree trunks (1·0–1·5 m) and overlook other important microhabitats, such as fallen branches and stumps. In this paper, we present results of a small-scale pilot study to evaluate the possible advantage of including four distinct microhabitats in standardized procedures for assessing epiphytic lichen diversity. Trunk bases, trunks between 100 and 150 cm above the ground, stumps, and fallen branches were each sampled with a different standardized sampling method along a forest age gradient in temperate deciduous forests of the Caucasian region. Plot-level species richness was contrasted between the standardized sampling procedures of different substrata and a non-probabilistic floristic sampling. The interactions between sampling procedure and stand age were analysed using linear mixed models, and non-metric multidimensional scaling (NMDS) and multi-response permutation procedures (MRPP) were used for comparing species composition. Overall, 97 species were recorded, their richness increasing with increasing stand age. Results were consistent across the gradient of stand age and demonstrated that the adoption of standardized sampling procedures which include stumps and fallen branches in addition to tree trunks would increase the capability of maximizing species capture. This approach would allow researchers to evaluate lichen patterns by simultaneously considering the response of different communities sensitive to different stand-related factors. Despite the likelihood that a non-probabilistic floristic survey would give a more exhaustive picture of the plot-level lichen diversity, standardized sampling procedures that include tree trunks, fallen branches and stumps are likely to represent a reasonable trade-off between exhaustiveness and cost-effectiveness.

Key words: canopy, coarse woody debris, epiphytic lichens, fallen branches, standardized sampling procedures, stumps

Accepted for publication 30 *October* 2017

Introduction

Forests are complex ecosystems and forest biodiversity assessment and monitoring require multidisciplinary approaches for defining structure and taxon-based indicators (Puumalainen *et al.* 2003; Blasi *et al.* 2010). Different taxonomic groups of organisms are proposed as suitable indicators for monitoring ecological integrity and estimating the biodiversity of forests (Welsh & Droege 2001; Blasi *et al.* 2010). A recent review of biodiversity indicators for forest ecosystems in Europe included lichens among the most valuable indicators for both stand and landscape level analyses (Gao *et al.* 2015).

Lichens make a significant contribution to nutrient and water cycling, as well as to food-webs in forest ecosystems (Galloway 1992; McCune 2000; Ellis 2012; Li *et al.* 2015). Moreover, they are a significant and sensitive component of the forest biota and for this reason are widely used for biomonitoring purposes and are included in continental-scale forest biodiversity assessments and

A. Gasparyan and H. J. M. Sipman: Botanischer Garten und Botanisches Museum, Freie Universität, Berlin, Germany. Email: a.gasparyan@bgbm.org; agasparyan@wwfcaucasus.org
A. Gasparyan: WWF-Armenia, Yerevan, Republic of Armenia.
L. Marini: Department of Agronomy, Food, Natural Resources, Animals and the Environment (DAFNAE), University of Padova, Padova, Italy.
J. Nascimbene: Department of Biological, Geological and Environmental Sciences, University of Bologna, Bologna, Italy.

monitoring programmes (e.g. Forest Health Monitoring program (McCune 2000); ForestBIOTA (Stofer 2006)). In Europe, different sampling guidelines have been developed for lichen diversity monitoring (Asta *et al*. 2002; Scheidegger *et al*. 2002; Stofer *et al*. 2003, 2012; Giordani *et al*. 2009). Recently, the Comité Européen de Normalization (CEN) has adopted a standard procedure for sampling design and assessment of lichen diversity (Ambient air – Biomonitoring with lichens – Assessing epiphytic lichen diversity; European Standard EN 16413:2014). The sampling strategy included in that document was developed mainly for air pollution monitoring activities and focused only on tree trunks (1–1·5 m above ground) (Cristofolini *et al*. 2014), thus overlooking several additional microhabitats relevant for lichens in forest ecosystems. A reduction of sampling effort on tree trunks has been suggested by previous studies (Nascimbene *et al*. 2010) as a potential strategy to redirect the sampling effort to currently overlooked microhabitats, such as the canopy and coarse woody debris (CWD), and to design sampling schemes that would result in a more comprehensive species capture in forest ecosystems.

Forest canopy is a valuable habitat for a variety of organisms, especially cryptogams (Ozanne *et al*. 2003; Ellis 2012; Marmor *et al*. 2013). The vertical stratification of epiphytic lichens has been previously reported by several authors (McCune *et al*. 1997; Fritz 2009; Li *et al*. 2015). However, a survey of canopy lichens is not included in current CEN lichen monitoring guidelines, mainly due to practical constraints. These constraints have been estimated to overlook 38–54% of lichen diversity (Boch *et al*. 2013). It is therefore relevant to explore a possible trade-off that would allow this component to be included in lichen diversity monitoring by, for example, recording epiphytic litter on fallen branches which could provide information on canopy lichens.

Different types of CWD, important for forest biodiversity, provide a key microhabitat for lichens, bryophytes, saproxylic fungi, beetles and birds (Siitonen *et al*. 2000; Travaglini *et al*. 2007; Nascimbene *et al*. 2008*a*, *b*; Spribille *et al*. 2008; Blasi *et al*. 2010; Blasy & Ellis 2014). In managed forests, natural CWD is often removed, and human-induced woody habitats such as tree stumps are the only available microhabitat for deadwood-associated lichens (Travaglini *et al*. 2007; Nascimbene *et al*. 2008*a*). In consequence, stumps could be the most valuable CWD microhabitat to be included in standardized forest lichen monitoring in managed forests.

In this paper, we present results of a small-scale pilot study to evaluate the possible advantage of including four distinct microhabitats in CEN procedures for assessing epiphytic lichen diversity. Trunk bases, trunks between 100 and 150 cm above the ground, stumps, and fallen branches were each sampled with a different standardized sampling method along a forest age gradient in temperate deciduous forests of the Caucasian region. Plot-level species richness, between the standardized sampling procedures and a non-probabilistic floristic sampling, was also contrasted to evaluate the effectiveness of standardized sampling in capturing the plot-level lichen diversity.

Materials and Methods

Study area

The study area is the Noyemberyan Forest (24 942 ha) in the Tavush Province of Armenia. Deciduous stands dominate, occupying the north-western part of the Gugarats mountain range at elevations between 500–1850 m. Dominant trees are *Fagus orientalis*, *Quercus iberica* and *Carpinus betulus* (Ministry of Nature Protection 2008). Annual precipitation is 550–600 mm and mean annual temperature is 10·4 °C.

Lichen sampling design

The fieldwork, July to August 2015, was carried out in 15 circular plots (26 m in diam.) randomly selected in pure stands of *Fagus orientalis* across three age classes (five plots per class): 60-90, 110-130 and 150-180 years old. The forest stands are subjected to the same management type and are at comparable elevations (1000-1250 m). The distance between plots of the same age class was > 1 km. In each plot, the 5 trees (DBH (diameter at breast height) >18 cm) closest to the plot centre were selected for the lichen survey. Lichen diversity was sampled using a standardized probabilistic method with two 10 × 50 cm frames subdivided into five

10 × 10 cm quadrats attached to the tree trunk at the N and S cardinal points, the shorter lower side positioned 1 m above the ground. Two additional 10 × 50 cm frames were placed at the base of the trunk at the same cardinal points. All lichen species inside the frames, including sterile crustose lichens, were listed and their frequency determined as the number of 10 × 10 cm quadrats in which they occurred. The lichen richness of the trunks was also recorded by carefully examining the whole surface of the trunks from the base up to 2 m according to a non-probabilistic sampling approach.

In each plot, the three fallen branches (1–2 cm in diam.) closest to the plot centre were surveyed. The first 20 cm of each branch length was divided into four equal parts of 5 cm and sampled for all lichens, starting from the more proximal end (larger diameter/attachment end). Afterwards, a non-probabilistic sampling approach was applied to record the lichen species along the whole branch length. We are aware that the inclusion of epiphytic litter and/or fallen branches for estimating lichen diversity poses several formal issues in terms of sampling design, which deal synthetically with the definition of the reference population from which the sample is sorted. However, we tried to develop a pragmatic approach to the inclusion of the lichen canopy component into a formal monitoring framework.

In each plot, the three tree stumps closest to the plot centre were surveyed. One quadrat (10 × 10 cm) was placed at the centre of the cut surface and four quadrats were placed at the centre of the N, S, E and W vertical parts of the stump. As for the other microhabitats, non-probabilistic floristic sampling on the whole stump surface was carried out.

Lichen identification

When possible, lichens were identified in the field but species identification was based mostly on the study of collected specimens (*c.* 1500) and some voucher specimens stored in the Herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem (B). In particular, crustose lichens were identified in the laboratory using both a stereomicroscope and compound microscope. Standard chemical spot tests and UV-light fluorescence were performed on some specimens. The identification of sterile leprose/crustose lichens (*c.* 120 specimens) was based on standardized thin-layer chromatography (TLC) following the protocols of Orange *et al.* (2010). Nomenclature of lichen species mainly follows Smith *et al.* (2009).

Data Analysis

Species richness

To test the effect of including the four different microhabitats in the sampling procedure, we used the linear mixed model *lme* function in the package nlme (Pinheiro *et al.* 2016). The response variable was the number of species. The model included the sampling procedure (i.e. the four microhabitats), stand age and their interactions as fixed effects and plot ID as a random factor. A paired *t*-test was used to compare species richness estimates between standardized and non-probabilistic sampling strategies. Statistical analyses were implemented in R version 3.2.3. (R Core Team 2015).

Species composition

For each stand age class, differences in species composition among the four types of microhabitat (base of trunks, trunks between 100–150 cm above the ground, stumps and fallen branches) were tested by multi-response permutation procedures (MRPP) as implemented in PC-ORD (McCune & Mefford 1999), using the Sørensen distance measure on rank transformed distance matrices. MRPP was used to test differences between microhabitat types as well as for all the microhabitats *in toto*. The test statistic A in MRPP describes the separation between stand types. The pattern of species composition was also visually evaluated using non-metric multidimensional scaling (McCune & Grace 2002) as implemented in PC-ORD (McCune & Mefford 1999), using the "slow and thorough" autopilot mode with the Sørensen distance measure. This procedure performed 40 runs with the real dataset compared with 50 randomized runs, each run with 400 iterations. This iterative ordination method is based on ranked distances between sample units in the data matrix, known as "species space" (McCune & Grace 2002); it does not assume linear relationships or normally distributed data and is therefore suited for most ecological data.

Results

Species richness

In total, 97 lichen taxa were recorded with non-probabilistic floristic sampling and 92 with standardized sampling methods. Mean species richness per plot was significantly different between non-probabilistic floristic sampling (37·7 ± 5·8) and standardized sampling (32 ± 5·8) ($P < 0·001$). The highest mean number of species per plot was found on tree trunks (23·3 ± 5·11) followed by fallen branches and stumps (13·1 ± 3·76 and 6·40 ± 2·38 respectively). The mean number of species recorded with non-probabilistic floristic sampling increased significantly with increasing stand age ($P < 0·05$): 33·4 ± 7·83 in young stands, 37·6 ± 6·54 in intermediate stands, and 41 ± 3·39 in older stands. Irrespective of stand age, the additional sampling of three currently neglected microhabitats in lichen monitoring surveys (i.e. fallen branches (BR), base of the trunk (TL) and stumps (ST)) increased species richness capture (Fig. 1). Adding only fallen branches led to a steep increase in species capture (51%) while the subsequent addition

of the lower part of the trunks and stumps increased the recorded species richness by 21% and 8%, respectively. The results of the linear mixed model analyses showed that estimates of richness differed between sampling approaches regardless of stand age (Table 1). The survey of the plot by one person identifying/collecting the specimens and one person making notes/records lasted *c.* 3–6 hours. The oldest stands were the most time-consuming.

Species composition

In each stand age class, significant differences in species composition were found among trees, fallen branches and stumps (Table 2). These differences increased with stand age, as indicated by the increasing *A* values from young to old stands. In contrast, communities at the base and at 100–150 cm on the trunks did not differ in species composition. This result was consistent across stand age classes. Overall, MRPP results were corroborated by the visual interpretation of the NMDS ordinations (Fig. 2A–C). For each stand age a final 2-dimensional solution was selected (young = stress 11%, instability 0·00001; intermediate age = stress 14·5%, instability 0·00021; old = stress 10·8%, instability 0·00001). For young stands the two axes accounted for 70% of the total variation in species composition, for intermediate age stands 76·8%, and for old stands 80·8%.

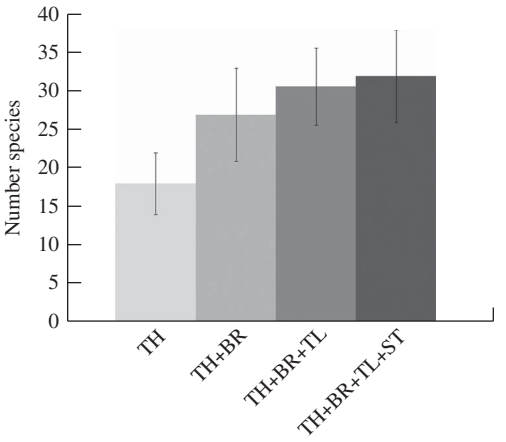

FIG. 1. Plot level species richness recorded in standard sampling of tree trunks (TH) and incremental increases in species richness when neglected habitats are incorporated into surveys. BR = fallen branches; TL = base of trunks; ST = stumps. Mean values ($n = 15$) are plotted ± 1 SE.

In accordance with the NMDS ordinations (Fig. 2A–C), the main pattern expressed along axis 1 is that related to compositional differences among assemblages recorded on fallen branches and stumps. However, assemblages on these two microhabitats clearly separated from those recorded on trees, as indicated by the pattern expressed along axis 2. This compositional difference between trees and the other two microhabitats was most evident in the old stands (Fig. 2C). On the other hand, assemblages recorded at the base of the trunk and at 100–150 cm above the ground strongly overlapped in the species space, indicating similar community composition.

Discussion

Our results demonstrate that the inclusion in CEN standardized sampling procedures (European Standard EN 16413:2014) of stumps and fallen branches in addition to tree

TABLE 1. *The effect of stand age and sampling strategy on lichen species richness using linear mixed models.*

	df	SS	MS	F value	*P* value
Between plots					
Age	1	202·5	202·5	3·14	0·0998
Residuals	13	838·3	64·49		
Within plots					
Sampling strategy	3	2030·2	676·7	158·735	<0·001
Age × sampling	3	23·3	7·8	1·822	0·1592
Residuals	39	166·3	4·3		

TABLE 2. *Summary results from multi-response permutation procedures (MRPP) carried out on the lichen species composition in four microhabitat types and three stand age classes of* Fagus orientalis. *MRPP was used to test differences both between pairs of microhabitat types and among all four microhabitats. All data are included in the analysis considering all the four microhabitats while for pairwise comparisons between microhabitats only the relevant subsets of data are used. The test statistic A in MRPP describes the separation between microhabitat types and* P *values indicate its significance level. TL = base of the tree trunks; TH = between 100–150 cm on the tree trunks; BR = fallen branches; ST = stumps available in the plot.*

		Young stands	Intermediate age stands	Old stands
Among all microhabitats	*A*	0·39	0·44	0·53
	P	<0·0001	<0·0001	<0·0001
TL vs TH	*A*	0·06	0·08	0·07
	P	0·8	0·95	0·88
TL vs BR	*A*	0·33	0·40	0·45
	P	<0·01	<0·01	<0·01
TL vs ST	*A*	0·27	0·29	0·35
	P	<0·01	<0·01	<0·01
TH vs BR	*A*	0·34	0·38	0·45
	P	<0·01	<0·01	<0·01
TH vs ST	*A*	0·27	0·27	0·38
	P	<0·01	<0·01	<0·01
BR vs ST	*A*	0·27	0·37	0·41
	P	<0·05	<0·01	<0·01

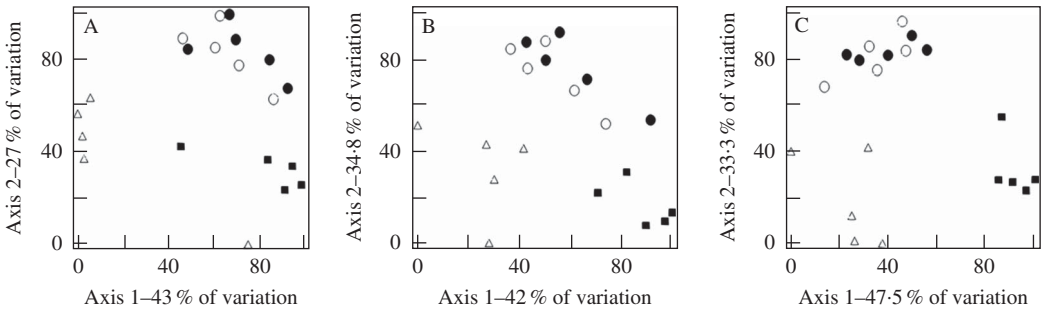

FIG. 2. Non-metric multidimensional scaling (NMDS) ordination plots for lichen species composition in four microhabitats and three stand age classes. A, 60–90 years old; B, 110–130 years old; C, 150–180 years old. Microhabitats: closed circles = between 100–150 cm on the tree trunks; open circles = base of the tree trunks; closed square = fallen branches; open triangle = stumps.

trunks increases the effectiveness of lichen monitoring procedures in estimating lichen diversity. On one hand, our findings indicate that the inclusion of the basal parts of the trunks only slightly increases species capture at the plot level. This result could be habitat-dependent and would require further tests in other forest types. However, similar findings were found by Nascimbene & Marini (2015) exploring lichen diversity in spruce forests of the Alps along elevational gradients. On the other hand, the survey of fallen branches results in the highest increase of species capture, confirming previous findings addressing the flaws of lichen diversity estimates that do not include the canopy microhabitat (Boch *et al.* 2013; Marmor *et al.* 2013). When fallen branches are accounted for, the further inclusion of stumps adds only a moderate contribution indicating that most of the species could be recorded on trunks and fallen branches. The positive effect in terms of species capture of surveying currently neglected microhabitats, such as basal parts of the trunks, fallen branches, and stumps, are consistent across stand age classes. This indicates that the adoption of improved monitoring procedures

that include these microhabitats would produce consistent results across forests of different ages, allowing comparisons across successional stages.

Except for the basal part of the trunks, the increase in plot-level species richness values corresponding to the inclusion of an increasing number of microhabitats is related to differences in species composition that are consistent across the gradient of stand age. This suggests that the inclusion of currently neglected microhabitats in standardized monitoring procedures would improve the chance of evaluating lichen patterns by simultaneously considering the response of different subcommunities indicative of different stand-related factors (Ellis 2012). This pattern is particularly evident for older stands, where the compositional differences among trunks, fallen branches and stumps are more evident than in younger stands. This probably reflects a pattern of increasing substratum specialization of lichen communities with stand aging (Lie *et al.* 2009; Nascimbene *et al.* 2009; Ellis 2012). However, inclusion of the additional microhabitats would also increase the duration of the plot sampling procedures by 1–2 hours.

Despite the fact that standardized sampling procedures allowed us to record *c.* 95% of the overall species recorded by non-probabilistic floristic sampling, plot-level richness values differed between the two strategies, indicating that non-probabilistic floristic survey could allow the recording of a higher number of species. However, standardized sampling procedures that include tree trunks, fallen branches and stumps could represent a reasonable trade-off between exhaustiveness and cost-effectiveness (McCune & Lesica 1992). Moreover, standardized sampling procedures would allow higher reproducibility and comparability of results that are indispensable for long-term monitoring programmes based on data comparisons over time. We are aware that the relatively small sampling size and the inclusion of one forest type in our sampling design could hinder the general applicability of our results. However, we feel that the results of this pilot study could stimulate further tests with larger sample sizes and including different forest types across Europe.

AG is grateful to Dr Karen Manvelyan (WWF-Armenia), Mr Vasil Chilingaryan (Director) and other staff members of the Noyemberyan Forest Enterprises of the "Hayantar" SNCO for assistance in the organization of fieldwork, and for financial support from the DAAD (German Academic Exchange Service) and the project "Developing Tools for Conserving the Plant Diversity of the Transcaucasus" financed by the Volkswagen Foundation. AG and JN are grateful to Professor Pier Luigi Nimis (Italy) for his assistance. AG also thanks Professor Mark Seaward (United Kingdom) for improving the English language of the manuscript.

References

Asta, J., Erhardt, W., Ferretti, M., Fornasier, F., Kirschbaum, U., Nimis, P. L., Purvis, O. W., Pirintsos, S., Scheidegger, C., Van Haluwyn, C., *et al.* (2002) Mapping lichen diversity as an indicator of environmental quality. In *Monitoring with Lichens – Monitoring Lichens* (P. L. Nimis, C. Scheidegger & P. A. Wolseley, eds): 273–279. Dordrecht: Kluwer Academic Publishers.

Blasi, C., Marchetti, M., Chiavetta, U., Aleffi, M., Audisio, P., Azzella, M. M., Brunialti, G., Capotorti, G., Del Vico, E., Lattanzi, E., *et al.* (2010) Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. *Plant Biosystems* **144:** 160–170.

Blasy, V. & Ellis, C. J. (2014) Life on deadwood: cut stumps as a model system for the succession and management of lichen diversity. *Lichenologist* **46:** 455–469.

Boch, S., Müller, J., Prati, D., Blaser, S. & Fischer, M. (2013) Up in the tree – the overlooked richness of bryophytes and lichens in tree crowns. *PLoS ONE* **8:** e84913.

Cristofolini, F., Brunialti, G., Giordani, P., Nascimbene, J., Cristofori, A., Gottardini, E., Frati, L., Matos, P., Batič, F., Caporale, S., *et al.* (2014) Towards the adoption of an international standard for biomonitoring with lichens – consistency of assessment performed by experts from six European countries. *Ecological Indicators* **45:** 63–67.

Ellis, C. J. (2012) Lichen epiphyte diversity: a species, community and trait-based review. *Perspectives in Plant Ecology, Evolution and Systematics* **14:** 131–152.

Fritz, Ö. (2009) Vertical distribution of epiphytic bryophytes and lichens emphasizes the importance of old beeches in conservation. *Biodiversity Conservation* **18:** 289–304.

Galloway, D. J. (1992) Biodiversity: a lichenological perspective. *Biodiversity Conservation* **1:** 312–323.

Gao, T., Nielsen, A. B. & Hedblom, M. (2015) Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators* **57:** 420–434.

Giordani, P., Brunialti, G., Benesperi, R., Rizzi, G., Frati, L. & Modenesi, P. (2009) Rapid biodiversity assessment in lichen biomonitoring surveys: implications for quality assurance. *Journal of Environmental Monitoring* **11:** 730–735.

Li, S., Liu, W. Y., Li, D. W., Song, L., Shi, X. M. & Lu, H. Z. (2015) Species richness and vertical

stratification of epiphytic lichens in subtropical primary and secondary forests in southwest China. *Fungal Ecology* **17:** 30–40.

Lie, M. H., Arup, U., Grytnes, J. A. & Ohlson, M. (2009) The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. *Biodiversity Conservation* **18:** 3579–3596.

Marmor, L., Tõrra, T., Saag, L., Leppik, E. & Randlane, T. (2013) Lichens on *Picea abies* and *Pinus sylvestris* – from tree bottom to the top. *Lichenologist* **45:** 51–63.

McCune, B. (2000) Lichen communities as indicators of forest health. *Bryologist* **103:** 353–356.

McCune, B. & Grace, J. B. (2002) *Analysis of Ecological Communities*. Gleneden Beach, Oregon: MjM Software.

McCune, B. & Lesica, P. (1992) The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests in Montana. *Bryologist* **95:** 296–304.

McCune, B. & Mefford, M. J. (1999) *PC-ORD. Multivariate Analysis of Ecological Data. Version 4.0*. Gleneden Beach: MjM Software.

McCune, B., Amsberry, K. A., Camacho, F. J., Clery, S., Cole, C., Emerson, C., Felder, G., French, P., Greene, D., Harris, R., *et al.* (1997) Vertical profile of epiphytes in a Pacific Northwest old-growth forest. *Northwest Science* **71:** 145–152.

Ministry of Nature Protection (2008) *Management plan of the Noyemberyan forestry*. Yerevan, Armenia.

Nascimbene, J. & Marini, L. (2015) Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy. *Journal of Biogeography* **42:** 1222–1232.

Nascimbene, J., Marini, L., Caniglia, G., Cester, D. & Nimis, P. L. (2008*a*) Lichen diversity on stumps in relation to wood decay in subalpine forests of Northern Italy. *Biodiversity Conservation* **17:** 2661–2670.

Nascimbene, J., Marini, L., Motta, R. & Nimis, P. L. (2008*b*) Lichen diversity of coarse woody habitats in a *Pinus-Larix* stand in the Italian Alps. *Lichenologist* **40:** 153–163.

Nascimbene, J., Marini, L., Motta, R. & Nimis, P. L. (2009) Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. *Biodiversity Conservation* **18:** 1509–1522.

Nascimbene, J., Marini, L., Bacaro, G. & Nimis, P. L. (2010) Effect of reduction in sampling effort for monitoring epiphytic lichen diversity in forests. *Community Ecology* **11:** 250–256.

Orange, A., James, P. W. & White, F. J. (2010) *Microchemical Methods for the Identification of Lichens*, 2nd edn. London: British Lichen Society.

Ozanne, C. M. P., Anhuf, D., Boulter, S. L., Keller, M., Kitching, R. L., Körner, C., Meinzer, F. C., Mitchell, A. W., Nakashizuka, T., Silva Dias, P. L., *et al.* (2003) Biodiversity meets the atmosphere: a global view of forest canopies. *Science* **30:** 183–186.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2016) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-127. Available at: http://CRAN.R-project.org/package=nlme.

Puumalainen, J., Kennedy, P. & Folving, S. (2003) Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. *Journal of Environmental Management* **67:** 5–14.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/.

Scheidegger, C., Groner, U., Keller, C. & Stofer, S. (2002) Biodiversity assessment tools — lichens. In *Monitoring with Lichens – Monitoring Lichens* (P. L. Nimis, C. Scheidegger & P. A. Wolseley, eds): 273–279. Dordrecht: Kluwer Academic Publishers.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology Management* **128:** 211–225.

Smith, C. W., Aptroot, A., Coppins, B. J., Fletcher, A., Gilbert, O. L., James, P. W. & Wolseley, P. A. (eds) (2009) *The Lichens of Great Britain and Ireland*. London: British Lichen Society.

Spribille, T., Thor, G., Bunnell, F. L., Goward, T. & Björk, C. R. (2008) Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. *Ecography* **31:** 741–750.

Stofer, S. (2006) *Working Report Forest BIOTA – Epiphytic Lichen Monitoring*. Available at: http://www.forestbiota.org/docs/report_lichens_20060503.pdf.

Stofer, S., Calatayud, V., Ferretti, M., Fischer, R., Giordani, P., Keller, C., Stapper, N. & Scheidegger, C. (2003) *Epiphytic lichen monitoring within the EU/ICP Forests Biodiversity Test-Phase on Level II plots*. Available at: www.forestbiota.org.

Stofer, S., Calatayud, V., Giordani, P. & Neville, P. (2012) Assessment of epiphytic lichen diversity. Manual part VII. In *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. Hamburg: UNECE ICP Forests Programme Co-ordinating Centre. Available at: http://www.icp-forests.org/Manual.htm

Travaglini, D., Barbati, A., Chirici, G., Lombardi, F., Marchetti, M. & Corona, P. (2007) ForestBIOTA data on deadwood monitoring in Europe. *Plant Biosystems* **2:** 222–230.

Welsh, H. H. & Droege, S. (2001) A case for using Plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. *Conservation Biology* **15:** 558–569.