

Substrate age influences species richness and community composition of calicioid lichens and fungi on wooden buildings

Author(s): Kate Petersen, Lalita M. Calabria, Jesse E. D. Miller, Jesse Brown-Clay, Lillian Hynson, Trygve Steen, Kelli Johnston, Amanda Ulbrich, Erol Chandler, Maysa Miller, and John Villella

Source: *The Bryologist*, 120(1):19-24.

Published By: The American Bryological and Lichenological Society, Inc.

DOI: <http://dx.doi.org/10.1639/0007-2745-120.1.019>

URL: <http://www.bioone.org/doi/full/10.1639/0007-2745-120.1.019>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Substrate age influences species richness and community composition of calicioid lichens and fungi on wooden buildings

Kate Petersen^{1,6}, Lalita M. Calabria¹, Jesse E. D. Miller², Jesse Brown-Clay¹, Lillian Hynson¹, Trygve Steen³, Kelli Johnston³, Amanda Ulbrich³, Erol Chandler³, Maysa Miller⁴ and John Villella⁵

¹ Evergreen State College, 2700 Evergreen Parkway NW, Olympia, WA 98505, U.S.A.; ² Department of Environmental Science and Policy, University of California, Davis, 1 Shields Way, Davis, CA 95616, U.S.A.; ³ Department of Environmental Science and Management, Portland State University, PO Box 751, Portland, OR 97201, U.S.A.; ⁴ Opal Creek Ancient Forest Center, 721 NW 9th Avenue, Suite 236, Portland, OR 97209, U.S.A.; ⁵ Siskiyou Biosurvey, 324 Avery Street, Ashland, OR 97520, U.S.A.

ABSTRACT. Identifying processes that drive epiphytic lichen diversity and succession is important for directing conservation efforts and developing forest management plans for the maintenance of biodiversity and forest health. Stand age has been implicated as a key factor in driving epiphytic species diversity and community composition. However, understanding the influence of substrate age, independent of the many confounding variables that affect live and dead wood substrates in a forest habitat, can be difficult. To test the hypothesis that substrate age has distinct effects on lichen community assembly independent of surface area, we sampled communities of calicioid lichens and fungi growing on wooden buildings that ranged from 2 to 82 years old. We found a total of 17 species, with a strong positive correlation between species richness and substrate age. We also tested the effects of surface area on species richness and found no relationship between the two variables. Our results indicate that substrate age influenced community composition; non-lichenized calicioid species acted as early colonizers and six calicioid species were recorded only on the oldest substrate. Old-growth associate species were found on substrates of varying ages, implying that additional variables may also be responsible for the colonization of old-growth associate species.

KEYWORDS. *Chaenotheca*, *Calicium*, *Mycocalicium*, *Chaenothecopsis*, *Cyphelium*, *Microcalicium*, old-growth forest, chronosequence, Oregon.



Identifying processes that drive epiphytic cryptogam diversity and succession patterns is important for directing conservation efforts and developing forest management plans that maintain biodiversity and forest health. Predicting how individual species will respond to climate change and forest disturbances also depends on understanding mechanisms underpinning species distributions on the landscape. Late-successional habitats, such as old-growth forests, are known to be hotspots for lichen diversity. However, the relative importance of factors that influence epiphyte diversity in old-growth forests remains incompletely understood.

Many studies have demonstrated positive correlations between tree age and lichen diversity, as well as influences on species composition (Fritz et al. 2009; Hilmo 1994; Nascimbene et al. 2009; Ranius et al. 2008; Ruchty et al. 2001; Uliczka & Angelstam 1999). However, researchers have also shown that age correlated surface area increases (Johansson et al. 2007; Rolstad & Rolstad 1999) and specific microhabitat development (of sap flows and bark furrows; Fritz et al. 2009; Ranius et al. 2008) may be more important drivers of community patterns than substrate age per se. Due to the nearly ubiquitous correlations between tree surface area, tree age and microhabitat formation, disentangling these variables is challenging in natural forest systems. However, forest managers would benefit greatly

⁶ Corresponding author's e-mail: katespetersen@hotmail.com
DOI: 10.1639/0007-2745-120.1.019



Figure 1. Jawbone Flats, OR in the Opal Creek Wilderness Area in 1947, showing many of the buildings used in this study. Photograph provided by Tom Atiyeh.

from this kind of nuanced understanding of the ecological factors driving forest diversity.

Calicioids, a cosmopolitan, polyphyletic group of ascomycetes with saprotrophic, lichenized and parasitic species, are particularly interesting model taxa because they are widely considered to be important indicators of forest stand age and ecological continuity (Rose 1976; Selva 2003, 2014). They tend to have specific habitat requirements at the stand level (Löhmus & Löhmus 2011), often occurring on old-growth legacy features, such as vertical to overhanging snags, channels in bark of old trees and pockets between roots with limited exposure to precipitation (Holien 1996; Peterson & Rikkinen 1999; Selva 1994; Tibell 1992).

To test the influence of substrate age on lichen species richness and community composition, independent of surface area and microhabitat formations, we surveyed calicioid lichens and calicioid non-lichenized fungi colonizing an 82-year chronosequence of buildings in an old-growth temperate rainforest in Jawbone Flats, Oregon, U.S.A., a former mining town. These buildings provided a unique model for evaluating effects of substrate age on the epiphyte community because their features remain relatively static over time; their surface area does not change and they do not exhibit microhabitat features such as bark furrows or sap flows. Additionally, these buildings are situated within a narrow valley surrounded by the largest continuous tracts of low elevation old-growth forest in Oregon (**Fig. 1**). This exposes the buildings to the ambient environmental

conditions of an old-growth forest and places them in close proximity to old trees and habitat features known to harbor diverse calicioid communities in surrounding forest stands (Rikkinen 2003; Hardman et al. 2017).

The main objectives of our study were to: 1) conduct a survey of building-dwelling calicioid species in a Pacific Northwest old-growth forest setting; and 2) determine the effects of substrate age and surface area on calicioid species richness and community composition.

METHODS

Site description. Jawbone Flats (**Fig. 1**) is a thirteen-acre site that was established as a mining town in 1929 and is now owned and operated as an environmental education facility by the Opal Creek Ancient Forest Center. The site is situated in the Willamette National Forest in Oregon at the confluence of Battle Axe Creek and Opal Creek (44°50'48.14"N, 122°12'32.79"W) and is bordered by the Opal Creek Wilderness (33,226 acres) and neighboring Bull of the Woods Wilderness (27,427 acres). This area is the largest low-elevation, relatively undisturbed forested watershed remaining in Oregon. Forests within the town site are early- to mid-seral, and the surrounding forests are dense old-growth dominated by Douglas-fir (*Pseudotsuga menziesii*), western yew (*Taxus brevifolia*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*), with bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) in the creekside areas. Dominant shrubs include salal (*Gaultheria shallon*), dwarf Oregon grape (*Berberis nervosa*), western sword fern (*Polystichum munitum*) and Pacific rhododendron (*Rhododendron macrophyllum*). The closest weather station to Jawbone Flats is Detroit Dam and data for the period of 1954–2013 shows average annual precipitation of 227 cm, average high temperature in July of 26°C and average low temperatures in January of 1°C (Oregon Climate Data 2013).

Buildings description. The buildings in Jawbone Flats include cabins, a workshop, a mess hall, sheds and outbuildings, of different sizes and aspect orientations. Sixteen buildings were surveyed. Eight were built in 1930, one in 1942, one in 1974, two in 1980, two in 2001, one in 2007, and one in 2010. Wood used in construction was either western hemlock (*Tsuga heterophylla*) or Douglas-fir (*Pseu-*

dotsuga menziesii). All buildings were built from wood logged and milled on site. The siding is board and batten construction. None of the buildings analyzed have treated, impregnated, painted or otherwise altered siding. An exception is a 70-year-old building that was vandalized, and some of the siding destroyed. All of the buildings have been colonized primarily by calicioids, with only very rare and intermittent algae, bryophyte and macrolichen colonies. All surveyed buildings were determined to have wooden surfaces that were analogous to snag decay class 5, defined as “a clean hard snag with no bark remaining” (Maser et al. 1979). The ages of the buildings were determined using Opal Creek Ancient Forest Center historical records.

Field protocol. We collected every taxon encountered on each of the 16 buildings. Field recognizable morphological characteristics were used to distinguish taxa when possible. Those species not reliably distinguished in the field were collected. For these, two specimens were collected from each aspect of each building where they were encountered. Building number and aspect were recorded for each specimen. Surface area measurements of the buildings were taken by measuring their dimensions and excluding areas which were inhospitable to lichen colonization or could not be surveyed due to windows or propane tanks.

Lab techniques. We made preliminary identifications at the Opal Creek Ancient Forest Center and at the Evergreen State College. We curated and identified specimens using standard techniques (Brodo et al. 2001). Thallus fragments and ascomata were mounted in tap water and viewed on a light microscope to identify photobionts and anatomical features. References used to identify specimens included Peterson (2012), Tibell (1999) and Goward (1999). Upon closer inspection, some specimens were found to have other, less noticeable, calicioid species growing near or amongst the intentionally collected thalli. When this occurred, the additional calicioid species were also identified. Eight specimens were found to be non-calicioid and were omitted from the data. Experts later verified all collections. Voucher specimens were deposited in the Evergreen State College Herbarium (EVE).

Statistical analysis. To analyze drivers of calicioid richness, we performed a regression with building age as the predictor variable and building-level species richness as the response variable. We

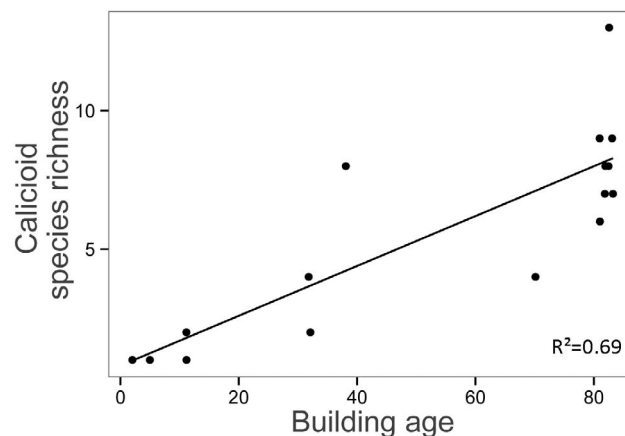


Figure 2. Relationship of calicioid species richness with building age, on an 82-year chronosequence of wooden buildings at the Opal Creek Ancient Forest Center.

natural log-transformed the species richness of individual building walls to improve its distributional properties to better meet assumptions of statistical tests. To test whether surface area influenced species richness, we performed a regression with building surface area as the predictor variable and building-level species richness as the response variable. To test whether substrate age affected community composition, we used permutational multivariate analysis of variance (PERMANOVA). PERMANOVA is a versatile semi-parametric multivariate procedure that is appropriate for analyzing how community composition responds to ecological drivers (Anderson 2001). We performed the PERMANOVA using the Jaccard index with 1,000 permutations, with species presence as the response matrix and building age as the fixed effect. All analyses were performed in R version 3.1.0 (R core team 2014), and the PERMANOVA was performed using the Vegan package 2.2-0 (Oksanen et al. 2013).

RESULTS

Species richness on each building ranged from 1–17, and significantly increased with substrate age ($R^2=0.69$, $p<0.001$) (Fig. 2). There was no significant relationship between building surface area and calicioid species richness ($R^2=0.03$, $p=0.493$). We collected one hundred thirty-two calicioid specimens, and seventeen calicioid species from four families (Table 1) were identified.

Calicioid community composition was significantly related to substrate age (PERMANOVA: $F_{1,14}=5.19$, $R^2=0.27$, $p=0.001$). Only the non-liche-

Table 1. Calicioid species recorded on an 82-year chronosequence of wooden buildings at Opal Creek Ancient Forest Center, Oregon, U.S.A. Species organized by family. Species indicated with bold were present only on the oldest substrate in the study. Species considered old growth associates by one or more authors (Holien 1998; Löhmus & Löhmus 2011; Selva 2003; Tibell 1992) are denoted with the superscript numeral 1.

| Family | Calicioid species | Building age (years) | | | | | | |
|-----------------------------------|---|---|---|----|----|----|----|----|
| | | 2 | 5 | 11 | 32 | 38 | 70 | 82 |
| Mycocaliciaceae | <i>Chaenothecopsis nana</i> | | | | | | | x |
| | <i>Chaenothecopsis pusiola</i> | | x | x | | x | | x |
| | <i>Mycocalicium subtile</i> | x | | x | x | | | x |
| Coniocybaceae | <i>Chaenotheca brunneola</i> group ¹ | | | x | x | x | x | x |
| | <i>Chaenotheca chlorella</i> ¹ | | | | x | | | x |
| | <i>Chaenotheca chrysocephala</i> | | | | | x | | x |
| | <i>Chaenotheca ferruginea</i> ¹ | | | | | x | x | x |
| | <i>Chaenotheca furfuracea</i> | | | | | | | x |
| | <i>Chaenotheca hispidula</i> | | | | x | | | x |
| | <i>Chaenotheca laevigata</i> ¹ | | | | | x | | x |
| | <i>Chaenotheca phaeocephala</i> | | | | | | | x |
| | <i>Chaenotheca subroscida</i> ¹ | | | | | | | x |
| | <i>Chaenotheca trichialis</i> ¹ | | | | | | x | x |
| | Caliciaceae | <i>Calicium glaucellum</i> ¹ | | | | x | x | x |
| <i>Calicium viride</i> | | | | | | x | x | x |
| <i>Cyphelium inquinans</i> | | | | | | | | x |
| Microcaliciaceae | <i>Microcalicium disseminatum</i> ¹ | | | | | | | x |

nized calicioid species *Mycocalicium subtile* and *Chaenothecopsis pusiola* were found on two- and five-year-old substrates. Lichenized species were first observed on an 11-year-old-substrate (*Chaenotheca brunneola* group; **Table 1**). Six calicioid species appeared only on the oldest (82-year-old) substrate: *Chaenotheca furfuracea*, *Chaenotheca phaeocephala*, *Chaenotheca subroscida*, *Chaenothecopsis nana*, *Cyphelium inquinans*, and *Microcalicium disseminatum* (**Table 1**). Two of these, *Chaenothecopsis nana* and *Microcalicium disseminatum* are non-lichenized. Of the seventeen species found, eight are considered to be old-growth associates or late successional species by one or more authors (Holien 1998; Löhmus & Löhmus 2011; Selva 2003; Tibell 1992; **Table 1**).

DISCUSSION

Species richness. Our study takes advantage of an unusual opportunity to examine the role of substrate age effects on calicioid community dynamics on an 82-year chronosequence of wooden buildings. We found that calicioid species richness increased significantly with substrate age, independent of surface area. This differential response is in conflict with findings from previous studies of substrate age and surface area on live trees (Lie et al. 2009; Nascimbene et al. 2009; Uliczka &

Angelstam 1999) suggesting that factors influencing calicioid species richness patterns cannot be generalized with regard to substrate type (live trees vs. anthropogenic structures).

Community composition. We also found that community composition was influenced by substrate age; we observed that non-lichenized species colonized substrates earlier in the chronosequence than lichenized species and that some calicioid species were restricted to the oldest buildings. While these patterns were observed on a relatively short time scale (2–82 years), they demonstrate that the ecological role of substrate changes through time and mirror studies which demonstrate the role of old snags and trees in supporting biodiversity (Berg et al. 1994; Holien 1996; Odor et al. 2006; Selva 2003). This suggests that retaining legacy features such as snags could promote lichen diversity in managed forests.

Several abiotic and biotic factors may help explain the differences in calicioid community assemblages observed in our study. As dead wood decays, there are changes in pH, nutrients and physical properties (Christensen & Vesterdal 2004), which could create ideal conditions for different species at different time intervals, but would not be captured by the standard snag decay class criteria used in our study. Life history traits such as spore

size may play an important role in lichen establishment time frames (Johansson et al. 2007), as smaller spores and those with ornamentation are more easily transported by animal and wind vectors than larger spores (Tibell 1994). Disparate time scales for colonization by lichenized and non-lichenized species may also be explained by the availability of appropriate photobionts, whose populations are influenced by microhabitat and climate regimes (Marini et al. 2011); it may take time for a new substrate to develop appropriate conditions for photobiont colonization.

Old-growth associates. Old-growth associated calicioid species were not confined to the oldest age classes in our study and were found on buildings of varying ages. This suggests that, while substrate age clearly drives calicioid diversity on these buildings, it is likely not the only factor influencing colonization by old-growth associated species. The fact that an old-growth associated species could be found on an 11-year-old building in our study suggests that, in addition to substrate age, other attributes of old forest ecosystems such as overall moisture and light regimes (Chen et al. 1993), air quality (Nash & Gries 1991), and proximity to propagule sources (Sillett et al. 2000) may be concurrent variables in driving calicioid diversity.

Management implications. We found that species richness and community composition were positively correlated with substrate age and that proximity to old trees and habitat structures characteristic of the surrounding old-growth forest were probably important factors in determining calicioid diversity in our study. Forest managers should consider retaining legacy features such as old snags to promote lichen diversity in managed forests. While old legacy features may harbor diversity themselves, they may also provide source populations to colonize new substrates. Thus efforts to enhance the abundance of calicioid lichens and fungi in managed forests should also include retention of nearby old-growth stands and features.

ACKNOWLEDGMENTS

Thanks to the Opal Creek Ancient Forest Center for allowing us to conduct this study on their property. Thanks to Eric Peterson, Steve Selva and Daphne Stone for confirming or identifying all of the specimens. We thank the Evergreen State College Herbarium for use of facilities and resources for identification of specimens. We would like to give special thanks to Opal Creek historians and past

caretakers Tom Atiyeh, George Atiyeh and Peter Scrivens for providing us critical data on building construction dates.

LITERATURE CITED

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.
- Berg, Å., B. Ehnström, L. Gustafsson, T. Hallingbäck, M. Jonsell & J. Weslien. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology* 8: 718–731.
- Brodo, I. M., S. D. Sharnoff & S. Sharnoff. 2001. *Lichens of North America*. Yale University Press, New Haven & London.
- Chen, J., J. F. Franklin & T. A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and forest meteorology* 63: 219–237.
- Christensen, M. & L. Vesterdal. 2004. Physical and chemical properties of decaying beech wood in two Danish forest reserves. *Nat-Man Working report* 25.
- Fritz, Ö, M. Niklasson & M. Churski. 2009. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Applied Vegetation Science* 12: 93–106.
- Goward, T. 1999. *The Lichens of British Columbia, Illustrated Keys. Part 2. Fruticose Species*. British Columbia Ministry of Forests, Victoria.
- Hardman, A., D. Stone & S. Selva. 2017. Calicioid lichens and fungi of the Gifford Pinchot and Okanogan-Wenatchee National Forests. *Opuscula Philolichenum* 16: 1–14.
- Hilmo, O. 1994. Distribution and succession of epiphytic lichens on *Picea abies* branches in a boreal forest, central Norway. *Lichenologist* 26: 149–169.
- Holien, H. 1996. Influence of site and stand factors on the distribution of crustose lichens of the Caliciales in a suboceanic spruce forest area in Central Norway. *Lichenologist* 28: 315–330.
- Holien, H. 1998. Lichens in spruce forest stands of different successional stages in central Norway with emphasis on diversity and old growth species. *Nova Hedwigia* 66: 283–324.
- Johansson, P., H. Rydin & G. Thor. 2007. Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. *Ecoscience* 14: 81–91.
- Lie, M., U. Arup, J. Grytnes & M. Ohlson. 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.
- Löhmus, A. & P. Löhmus. 2011. Old-forest species: the importance of specific substrata vs. stand continuity in the case of calicioid fungi. *Silva Fennica* 45: 1015–1039.
- Marini, L., J. Nascimbene & P. L. Nimis. 2011. Large-scale patterns of epiphytic lichen species richness: photobiont-dependent response to climate and forest structure. *Science of the Total Environment* 409: 4381–4386.
- Maser, C., R. G. Anderson, K. Cromack Jr., J. T. Williams & R. E. Martin. 1979. Dead and down woody material. Pages 78–95. In: J. L. Parker, R. A. Mowrey, G. M. Hansen & B. J. Bell (eds.), *Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington*. U.S. Government Printing Office, Washington, D.C.
- Nascimbene, J., L. Marini, R. Motta & P. L. Nimis. 2009. Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. *Biodiversity and Conservation* 18: 1509–1522.

- Nash III, T. H. & C. Gries. 1991. Lichens as indicators of air pollution. Pages 1–29. In: O. Huntzinger (ed.), *Air Pollution*. Springer, Berlin.
- Ódor, P., J. Heilmann-Clausen, M. Christensen, E. Aude, K. W. Van Dort, A. Piltaver, I. Siller, M. T. Walley, T. Standovár & A. F. M. Van Hees. 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biological Conservation* 131: 58–71.
- Oksanen, J., F. Guillaume Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens & H. Wagner. 2013. *Vegan: Community Ecology Package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Oregon Climate Data. 2013: <http://www.ocs.orst.edu/oregon-climate-data>. [accessed on November 21, 2013.]
- Peterson, E. B. & J. Rikkinen. 1999. Range extensions of selected pin-lichens and allied fungi in the Pacific Northwest. *The Bryologist* 102: 370–376.
- Peterson, E. B. 2012. Key of calicioid lichens and fungi for genera with members in temperate western North America. (Draft) published by the author, <http://www.crustose.net/2012/03/14/calicioid-checklist-and-key/> [last accessed on March 10 2015.]
- R Core Team. 2014: R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>.
- Ranius, T., P. Johansson, N. Berg & M. Niklasson. 2008. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *Journal of Vegetation Science* 19: 653–662.
- Rikkinen, J. 2003. Calicioid lichens and fungi in the forests and woodlands of western Oregon. *Acta Botanica Fennica* 175: 1–41.
- Rolstad, J. & E. Rolstad. 1999. Does tree age predict the occurrence and abundance of *Usnea longissima* in multi-aged submontane *Picea Abies* stands? *Lichenologist* 31:613–625.
- Rose, F. 1976. Lichenological indicators of age and environmental continuity in woodlands. Pages 279–307. In: D. H. Brown, D. L. Hawksworth & R. H. Bailey (eds.), *Lichenology: Progress and Problems*. Proceedings of an International Symposium. Academic Press, New York.
- Ruchty, A., L. A. Rosso & B. McCune. 2001. Changes in epiphyte communities as the shrub, *Acer circinatum*, develops and ages. *The Bryologist* 104: 274–281.
- Selva, S. B. 1994. Lichen diversity and stand continuity in the northern hardwoods and spruce-fir forests of northern New England and western New Brunswick. *The Bryologist* 97: 424–429.
- Selva, S. B. 2003. Using calicioid lichens and fungi to assess ecological continuity in the Acadian Forest Ecoregion of the Canadian Maritimes. *Forestry Chronicle* 79: 550–558.
- Selva, S. B. 2014. The calicioid lichens and fungi of the Acadian Forest ecoregion of northeastern North America, II. The rest of the story. *The Bryologist* 117: 336–367.
- Sillett, S. C., B. McCune, J. E. Peck, T. R. Rambo & A. Ruchty. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* 10: 789–799.
- Tibell, L. 1992. Crustose lichens as indicators of forest continuity in boreal coniferous forests. *Nordic Journal of Botany* 12: 427–450.
- Tibell, L. 1994. Distribution patterns and dispersal strategies of Caliciales. *Botanical Journal of the Linnean Society* 116: 159–202.
- Tibell, L. 1999. Calicioid lichens and fungi. *Nordic lichen flora* 1: 20–94.
- Uliczka, H. & P. Angelstam. 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography* 22: 396–405.

manuscript received April 8, 2016; accepted November 11, 2016.