Silvicultural strategies for lichen conservation: Smaller gaps and shorter distances to edges promote recolonization

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Abstract
Conservation of epiphytic lichens in managed forest landscapes relies on understanding limitations to their dispersal and establishment after harvesting. A hot spot for cephalo- and cyanolichens, the Kispiox inland temperate rainforest of British Columbia, Canada, is an example of where forest managers seek silviculture options that allow for forest harvesting to continue, while also conserving threatened species. To characterize colonization of these lichens (including the nationally threatened *Nephroma occultum* and *Lobaria retigera*), we quantified thalli on 25-year-old regenerating spruce trees at varying distances from forest edges in logged openings of different sizes surrounded by mature (160 years) or old-growth (≥350 years) forest. Lichen colonization 25 years after logging was influenced by distance from the forest edge, surrounding forest age, and opening size. Total mean colonization and number of species per three branches were 81 thalli and 8 species at the forest edge, declining to 18 and 4, respectively, approximately 50 m into the openings. Colonization of most species reached minimum levels within 80 m. Nationally threatened species and old-forest associates had higher abundances and longer colonization distances in openings surrounded by old-growth forests; whereas widespread species had greater colonization when surrounded by mature forests. Logged gaps <0.6 ha promoted higher and more diverse lichen colonization than clearcuts (>3.8 ha). This study demonstrates that forest managers should consider the spatial patterning of harvesting, with smaller openings and shorter distances between edges (likely in tandem with higher levels of retention) in forests rich in epiphytic lichens to facilitate their recolonization and conservation.

KEYWORDS
Canopy retention, cyanolichens, dispersal, epiphytic lichens, logging, temperate rainforest

INTRODUCTION

Current forestry practices and climate change are predicted to reduce globally significant temperate rainforests in British Columbia and their lichens (Bezzola & Coxson, 2020; Coxson et al., 2019). The Kispiox inland temperate rainforest (hereafter “Kispiox rainforest”) supports a rich lichen flora, owing to clean air and an oceanic macroclimate of high humidity and frequent low-intensity summer rain (Coxson et al., 2019).
The recognition of the Kispiox rainforest as a global hot spot of epiphytic cephalo- and cyanolichens was emphasized in the 1990s (Goward, 1994, 1995; Goward & Pojar, 1998) and later supported by Goward and Arsenault (2000a). Cyano- and cephalolichens containing cyanobacteria as their primary or secondary photosynthetic partner, respectively, account for unusually high proportions of the epiphyte diversity in these forests (Goward & Arsenault, 2000a; Goward & Pojar, 1998). These lichens are globally important due to their role in nitrogen fixation and nutrient cycling, their association with unpolluted old forests and sensitivity to environmental disturbance (Rikkinen, 2015; Rose, 1988). Two canopy lichens in the Kispiox rainforest are threatened in Canada, >12 are at risk in British Columbia, and >4 are endemic to northwestern North America (British Columbia Conservation Data Centre [B.C. Conservation Data Centre], 2021; Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2018, 2019).

Boreal and temperate rainforests are globally important for epiphytic lichens (DellaSala, 2011). In the Kispiox, few of these old forests are protected from logging; only 7% is protected formally (910 km²) of which <1% (110 km²) is known to be rich in lichens (Bezzola & Coxson, 2020; Coxson et al., 2019). Given the low level of legal protection of old forests, the progressive harvesting and fragmentation, and the projected edge effects of the remaining lichen-rich stands (Bezzola & Coxson, 2020), silvicultural prescriptions meeting lichens’ ecological requirements are needed to maintain species diversity across managed forest landscapes.

In some temperate rainforests, forest managers prescribe that patches of live trees be retained around occurrences of threatened lichens to meet forest stewardship objectives and certification standards. Live-tree retention in logged areas has been proposed to conserve canopy lichens in the managed landscape (Price et al., 2017; Rosenvald & Löhmus, 2008). Retaining live trees in the harvest units may permit old forest-dependent organisms to persist through the harvest cycle (“life-boating,” sensu Franklin et al., 1997) and act as sources of propagules for colonization of regenerating forests (Baker et al., 2013; Beese et al., 2019; Fedrowitz et al., 2014).

The viability of rare cephalo- and cyanolichen species in retained old forest reserves within cut-blocks was recently shown to decline as far as 90–120 m into the forest interior from recently cut edges (Gauslaa et al., 2019). Using this metric, retention patches >240 m in diameter would be necessary to avoid harmful effects to these lichens even in the center of the patches. The ability of retained lichens to survive and grow over longer periods, disperse from retained patches, and successfully recolonize logged areas has not been well studied.

The indirect (shading, buffering) and direct impacts of distance to intact forest on disturbed areas are known as “forest influence” (Baker et al., 2013; Keenan & Kimmins, 1993). The ability of an organism to recolonize a regenerating forest depends on its dispersal capacity and life history characteristics, plus retained habitat quality and biotic interactions, which vary with forest influence (Baker et al., 2013). Dispersal distance and establishment success influence the abundance of epiphytic lichens in forests (Dettki et al., 2000; Hilmo & Sästad, 2001; Peck & McCune, 1997; Sillett et al., 2000), yet knowledge on how lichens disperse and establish is sparse, particularly for threatened species. Here, we aim to address this gap and quantify the depth and magnitude of forest influence on recolonization. Our goal was to determine which cephalo- and cyanolichens colonize previously logged areas and to estimate effective colonization distances for each species, a simple metric for forest managers to use to develop strategies for conserving these lichens. Colonization distances for threatened or target species could be used to design silvicultural prescriptions for appropriate levels and configuration of retention in the harvested areas and on the landscape to ensure their long-term persistence.

Our overall hypothesis was that lichen colonization would decrease with distance from the intact forest edge until a changepoint that would represent an effective colonization distance. Because cephalo- and cyanolichen abundance is higher in older forests (Esseen et al., 1996; Price et al., 2017; Price & Hochachka, 2001), resulting in higher availability of diaspores, we predicted that openings in old-growth forests would support more thalli and greater lichen diversity than those in mature forests, resulting in different colonization patterns between age classes. We also predicted that small canopy gaps would have more lichens than large clearcuts because small openings have less direct sunlight and higher day-time humidity (Coates, 1998), and because distance from sources of lichen propagules is shorter (i.e., greater forest influence). Finally, we predicted that north-facing edges would allow longer colonization distances and higher abundances than south-facing edges exposed to direct sunlight.

METHODS

Study site and opening selection

We examined lichen colonization on 25-year-old planted trees in logged openings of the Date Creek Silvicultural Systems Study near Hazelton, in northwestern British Columbia (55°22’N, 127°50’W; 400—665 m; Coates et al., 1997). The Date Creek study occurs on the
traditional territory of the Gitxsan First Nation and in the Hazelton variant of the moist cold subzone of the Interior Cedar Hemlock biogeoclimatic zone (Banner et al., 1993). It is part of the Kispiox rainforest (Coxson et al., 2019), transitional between the wetter, temperate rainforests of the Pacific coast and the drier, colder, continental interior forests. Even though mean annual precipitation is just 800 mm, as much as 45% of the days in three warmest months receive rain (150 mm, Environment Canada, 2020). Predicted summer moisture deficit is low (64 mm) reflecting wet, cool summers and shelter from coastal winds (Coxson et al., 2019; Wang et al., 2012).

Two age classes of primary forest, mature and old growth, originated after stand-destroying fires in ~1855 and ~1630, respectively. Mature forests (~160 years old) were dominated by Tsuga heterophylla with varying amounts of Thuja plicata, Abies lasiocarpa, hybrid spruce (a complex of Picea glauca, P. sitchensis, and on occasion P. engelmannii var engelmannii), Pinus contorta var. latifolia, Betula papyrifera, Populus tremuloides, and Populus trichocarpa. Old-growth forests (~380 years), dominated by T. heterophylla with varying amounts of T. plicata, Abies lasiocarpa, and A. amabilis, had larger trees and greater structural diversity, but less diverse tree species. The average maximum tree height among plots from preharvest measurements was 30 m for both age groups. Mean stand basal area was also similar between age groups (66 and 63 m² ha⁻¹ for old and mature forest, respectively); however, old-growth stands had fewer, but thicker stems (596 and 929 stems ha⁻¹ for old and mature forests, respectively). Mature closed forests had low understory light levels and were poor in epiphytic lichens, especially infrequent species. In contrast, open mature forests and old forests, especially where groundwater accumulates, had more light and were richer in lichen species. Preharvest lichen surveys detected 54 epiphytic macrolichens, of which 21 were cephalo- or cyanolichens: three restricted to mature forests, six to old-growth, and 12 in both (Goward, 1993).

The Date Creek study was established to investigate the effects of different levels and patterns of retention on timber production and biodiversity (Coates et al., 1997). The treatments created a range of overstory retention and opening sizes in 20-ha forest stands replicated once in old-growth forests and three times in mature forests. Stands comprised mainly mesic site series (average soil moisture and nutrient regimes) on morainal soils (Coates et al., 1997). Clearcutting and retention treatments (40% and 70% retention) were completed in the fall and winter of 1992–1993. In the clearcuts, all overstory trees were removed, except for scattered deciduous stems. In the retention treatments, which mimicked the natural disturbance regime of canopy gap dynamics (Coates & Burton, 1997), logging created a range of gap sizes from single-tree to ~0.6 ha in size. In May 1993, gaps and clearcuts were planted with 1-year-old seedlings of T. heterophylla, T. plicata, hybrid spruce, P. contorta, and A. lasiocarpa.

We characterized cephalo- and cyanolichen colonization across a range of opening sizes surrounded by either mature or old-growth forest in 28 logging-created openings (0.009–0.52 ha) and five clearcuts (3.8–39 ha). In each of the three mature 40% retention treatment units, we randomly selected one small (0.002–0.03 ha) and one medium (0.03–0.1 ha) gap, the smallest of the large (0.1–0.52 ha) gaps and the largest gap (12 gaps in total). In the single old growth 40% retention treatment unit, we sampled all 12 medium to large gaps; and, in the 70% retention treatment unit, we sampled four randomly selected small gaps, for a total of 16 old-growth gaps. Three of the five clearcuts sampled were treatment units in the Date Creek study; two were mature forest and one was old growth. Two nearby mature clearcuts of similar age were also sampled. The area of experimental openings was calculated using the formula for an ellipse for small openings and GIS software for large openings and clearcuts (see Coates et al., 1997).

### Data collection

In June to October 2017, we established a north–south transect through the center of each logged opening, keeping the east and west edges as equidistant from the transect as possible (Figure 1). The transect was the longest possible north–south line from one canopy edge to the other and was adjacent to a row of planted hybrid spruce. We sampled along the transect in a systematic manner, without seeking out high-potential areas in timed searches (e.g., Hilmo, Ely-Aastrup, et al., 2011; Resource Information Standards Committee, 2018). Distance to nearest north or south forest edge was recorded. The transect represented a gradient from high (north end and center) to low (south end) light exposure. Satellite imagery was used to avoid roads and clumps of residual mature stems (Google Earth Pro, 2017). The maximum distance from forest edges was 200 m in openings surrounded by old-growth forests and 400 m in mature forests. Lichens were sampled on planted hybrid spruce because (1) preliminary observations and other studies (Goward & Arsenault, 2000b; Hilmo et al., 2005) showed that it hosted more lichens than other tree species; (2) planted spruces were readily distinguished from naturally regenerated trees, which controlled for tree age; and (3) planted spruces were frequent and could be found across the transects.
We sampled 213 trees at varying distances from forest edges (Figure 2). For clearcuts and large gaps with a transect length ≥100 m, we sampled one tree every 10 m until 50 m, then every 25 m afterward. For gaps with transects 50–70 m, we sampled a tree every 10 m. For smaller gaps, we sampled five trees as equally distributed along the transect as possible. At each distance from the canopy edge, we selected the tree with highest lichen diversity and abundance in a search zone. For large gaps and clear-cuts, we used a 20-m² search zone (5 m × 2 m on either side of transect) at each transect distance; whereas search zones were reduced in smaller gaps. Sampling the best-colonized tree at each distance may overestimate lichen colonization rates but compensates for the fact that not all trees are suitable hosts for cephalo- and cyanolichens due to fine-scale environmental gradients (e.g., unbalanced elemental supplies; Gauslaa et al., 2020). Sampled tree diameters were recorded (0–24 cm; corresponding to estimated heights of 1.2–16.6 m using allometric equations). The mean estimated height of sampled trees per logged opening was 10.5 m in

**FIGURE 1** Diagram of north–south transects through (a) 0.03- and 0.5-ha gaps in a 40% retention treatment unit, and (b) 15.8-ha clearcut treatment unit at the Date Creek Silvicultural Systems Study

**FIGURE 2** Distribution of sampled trees across opening sizes, across different distances from the forest edge, and surrounded by mature forest (orange triangles) or old-growth forest (blue circles) for (a) all sampled trees (*n* = 213) and (b) sampled trees in gaps <0.6 ha (*n* = 124)
clearcuts, 9.1 m in large gaps, 4.6 m in medium gaps, and 3.4 m in small gaps.

At each tree, the three best-colonized branches attached below 1.5 m were selected based on diversity and cover of cephalo- and cyanolichens. All thalli >0.1 cm² were counted and measured. To ensure capture of old-growth associated species (Goward & Pojar, 1998), we broadened the sampling to all branches below 1.5 m for species known to be locally infrequent (with the exception of *N. isidiosum*).

We used a 1 cm × 1 cm wire grid to estimate the surface area of each lichen thallus. The grid was placed on top of each lichen and the grid cells or fractions of grid cells occupied by the lichen were estimated. This approach gave a repeatable method of measuring thallus area compared to more subjective visual estimates. The same person selected trees, branches and measured all lichens to decrease measurement bias and error. Taxonomically difficult specimens, as well as voucher specimens from each site, were examined in the laboratory. Nomenclature follows Esslinger (2019).

**Data analysis**

Using likelihood methods and Akaike’s information criterion (AIC) in a multiple alternate hypothesis framework (Burnham & Anderson, 2004; Canham & Uriarte, 2014), we examined the relationship between various measures of abundance per sample tree (total number of thalli, number of species [richness], number of thalli of each taxon) and distance from the closest forest edge along a north–south bearing (Model 1). We also examined three additional effects on lichen colonization: age of the surrounding forest (Model 2), size of the logged opening (Model 3), and position within the opening (distance from north vs. south edge; Model 4). We compared the models to a null model, which estimated lichen abundance as a simple mean multiplied by the tree size modifier (Table 1).

Models are presented in Table 1 and further described in Appendix S1. Briefly, a piece-wise linear function with a y-intercept (Y.INT), a negative slope (k), a change-point (z), and a calculated minimum value (MIN = Y.INT + k × z) represented the decrease in lichen abundance from a maximum at the forest edge to a minimum at a distance (z) from the edge in Model 1. Parameters Y.INT, k, and z (but not MIN) could vary for trees in openings surrounded by old-growth forest for Model 2, and for trees closer to the south edge of an opening for Model 4. An additive parameter (s) in Model 3 allowed gaps and clearcuts to differ in abundance. Models 3 and 4 were tested for only total abundance, species richness, and for the five species with observations on >100 trees. A tree size modifier was included in all models (except with *Lobaria oregana*) to account for the smaller branch surface area on smaller trees. The number of lichen thalli increased steeply with tree diameter from DBH = 0 to 5 cm and then leveled off and reached an asymptote at DBH = 12 cm, corresponding to the increase in branch length with tree diameter for a small sample of trees (Appendix S1: Figure S1).

The model with the lowest AIC value was considered to have the most support from the data. When models differed by AIC values (ΔAIC) less than two, the more parsimonious (fewer parameters) model was considered superior. A simulated annealing algorithm (likelihood package; Murphy, 2015) using R statistical software (version 3.5.1) calculated maximum-likelihood estimates and approximate 95% support intervals for the parameters in each model after 40,000–100,000 iterations (Goffe et al., 1994; R Development Core Team, 2018).

**Lichen size distributions**

To better understand the timing and dynamics of lichen colonization during the 25 years since logging, we examined thallus size distributions for the five most abundant species (>100 trees). A range of thallus size classes with a reverse-J distribution would indicate that lichens are colonizing trees continuously and that a portion of juvenile thalli are surviving and growing. We visually compared the size class distributions found in the gaps to those in clearcuts close to the edge (<50 m) and in clearcuts far from the edge (>50 m) to assess population growth in gaps versus clearcuts. We selected 50 m as the threshold because longer distances from edges were rare in gaps.

**RESULTS**

**Lichen species**

At 25 years after logging, 213 planted spruce trees in gaps and clearcuts supported >9539 thalli of 22 species (treated as 18 taxa) of epiphytic cephalo- and cyanolichens (Table 2). The epiphytic lichen community supported all but three cephalo- and cyanolichens identified by Goward (1993) prior to logging: *Lichinodium canadense*, *Lobaria silvae-veteris*, and *Leptogium burnetiae* (which were recorded only once each in 1993). *Nephroma helveticum*, *Lobaria pulmonaria*, and *Leptogidium dendriscum* accounted for 75% of observed thalli (Table 2) and most occurred near the forest edge (Y.INT = 28, 35, and 13 thalli, respectively; Table 3,
Figures 3 and 4). Sticta fuliginosa (when surrounded by old growth) and Nephroma parile (by mature forests) had an average of eight thalli at the forest edge. The other species were rarer with ≤3 thalli per three branches at the forest edge (Table 3). We detected 87 thalli of Nephroma occultum and 36 Lobaria retigera, which are threatened in Canada (COSEWIC, 2018, 2019). One single thallus of the provincially red-listed Dendriscosticta

| Table 1 | Tested model functional forms, parameters, and corresponding hypotheses using the variables host tree diameter (DBH), host tree distance from the forest edge (and north and south edge; DIST, DISTN, DISTS), surrounding forest age class (AGE), and opening size (SIZE) to predict lichen abundance per tree |
|---------|-----------------------------------------------------------------------------------|
|         | Model Function form | Parameters | Hypothesis tested |
|         |                     |            |                  |
| Null    | \( \mu \times (1 - e^{-0.28 \times (DBH + 0.15)}) \) | \( \mu \): mean abundance | Abundance is only dependent on host tree size |
| 1       | \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \leq z \)  
          \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \geq z \)  
          \( \times (1 - e^{-0.28 \times (DBH + 0.15)}) \) | \( Y.\text{INT} \): abundance at the forest edge  
          \( k \): rate of decrease in abundance with increasing distance from edge  
          \( z \): effective colonization distance | Abundance depends on distance from edge |
| 2       | \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \leq z \) and AGE \( \leq 250 \)  
          \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \geq z \) and AGE \( \leq 250 \)  
          \( \text{OLD.\text{INT}} \times k_{\text{old}} \times \text{DIST} \) if DIST \( \leq z_{\text{old}} \) and AGE > 250  
          \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \geq z_{\text{old}} \) and AGE > 250  
          \( \times (1 - e^{-0.28 \times (DBH + 0.15)}) \) | \( Y.\text{INT} \): abundance at mature forest edge  
          \( \text{OLD.\text{INT}} \): abundance at the old-growth edge  
          \( k \): rate of decrease in abundance with increasing distance from edge  
          \( z_{\text{old}} \): rate of decrease in abundance with increasing distance from old-growth edge  
          \( z_{\text{old}} \): effective colonization distance for mature edge  
          \( z_{\text{old}} \): effective colonization distance for old-growth | Abundance depends on distance from edge and surrounding age class |
| 3       | \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \leq z \)  
          \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \geq z \)  
          \( \times (1 - e^{-0.28 \times (DBH + 0.15)}) \) if SIZE \( \leq 0.6 \text{ ha} \)  
          \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \leq z \)  
          \( Y.\text{INT} + k \times \text{DIST} \) if DIST \( \geq z \)  
          \( \times (1 - e^{-0.28 \times (DBH + 0.15)}) + s \) if SIZE \( \geq 0.6 \text{ ha} \) | \( s \): difference in abundance between gaps and clearcuts | Abundance depends on distance from edge and opening size |
| 4       | \( Y.\text{INT} + k \times \text{DIST}_N \) if DIST \( \leq z \) and DIST \( \leq \text{DIST}_S \)  
          \( Y.\text{INT} + k \times \text{DIST}_S \) if DIST \( \geq z \) and DIST \( \leq \text{DIST}_S \)  
          \( Y.\text{INT} + k_3 \times \text{DIST}_S \) if DIST \( \leq z_3 \) and DIST \( \leq \text{DIST}_N \)  
          \( Y.\text{INT} + k_3 \times \text{DIST}_S \) if DIST \( \geq z_3 \) and DIST \( \leq \text{DIST}_N \)  
          \( \times (1 - e^{-0.28 \times (DBH + 0.15)}) \) | \( Y.\text{INT} \): abundance at the north edge  
          \( \text{S.\text{INT}} \): abundance at the south edge  
          \( k \): rate of decrease in abundance with increasing distance from edge  
          \( k_3 \): rate of decrease in abundance with increasing distance from south edge  
          \( z_3 \): effective colonization distance from north edge  
          \( z_3 \): effective colonization distance from south edge | Abundance depends on distance from edge and opening position |
oroborealis, and almost 300 thalli of blue-listed lichens were detected (Table 2; B.C. Conservation Data Centre, 2021).

**Colonization as a function of distance from intact forest and the impact of forest age**

Total cephalo- and cyanolichen colonization, species richness, and colonization of many species, was highest near the forest edge (5–10 m) and declined steeply with distance into the logged openings (Figures 3 and 4, Appendix S1: Tables S1 and S2), consistent with our prediction that abundance decreases at increasing distances from the edge. A linear piece-wise regression model with a minimum $y$-value provided a reasonable fit ($R^2 = 0.34$; Model 2) for the abundant *L. pulmonaria* (Table 2). For all species, openings and forest age classes, the number of thalli near the edge was variable: ranging from 0 to 250 thalli with an average of 92 thalli per three branches.

| Branches                        | Best model                  | Species                        | No. thalli or species | Model 1, distance from edge | Model 2, surrounding forest age |
|---------------------------------|-----------------------------|--------------------------------|------------------------|------------------------------|----------------------------------|
|                                 |                             | Total lichen                   | 9539                   | 1974                         | 1974                             |
|                                 |                             | Number of species              | 23                     | 919                          | 923                              |
|                                 |                             | *Nephroma bellum*              | 158 39                 | 367                          | 367                              |
|                                 |                             | *Nephroma helveticum*          | 2723 145               | 1342                         | 1343                             |
|                                 |                             | *Leptogidium dendriticum*      | 2162 185               | 1406                         | 1389                             |
|                                 |                             | *Lobaria pulmonaria*           | 2297 117               | 1154                         | 1102                             |
|                                 |                             | *Nephroma isidiosum*           | 59 38                  | 271                          | 268                              |
|                                 |                             | *Nephroma parile*              | 583 137                | 905                          | 888                              |
|                                 |                             | *Nephroma resupinatum*         | 22 9                   | 112                          | 104                              |
|                                 |                             | *Peltigera collina*            | 78 20                  | 217                          | 205                              |
|                                 |                             | *Sticta fuliginosa*            | 890 178                | 1062                         | 1041                             |
| All branches$^a$                 | No surrounding age effect   | Pannariaceae group$^{c,d}$     | 46 26                   | 220                          | 220                              |
|                                 |                             | *Dendriscocaulon spp.*$^e$     | 196 71                  | 493                          | 447                              |
|                                 |                             | *Lobaria oregana*              | 30 9                   | 95                           | 87                               |
|                                 |                             | *Lobaria retigera*             | 36 25                  | 198                          | 192                              |
|                                 |                             | *Lobaria scrobiculata*         | 107 60                 | 398                          | 387                              |
|                                 |                             | *Nephroma occultum*            | 87 40                  | 303                          | 269                              |
|                                 |                             | *Lobaria anomal*               | 47 48                  |                               |                                  |
|                                 |                             | *Lobaria hallii*               | 17 12                  |                               |                                  |
|                                 |                             | *Dendriscosticta oroborealis*  | 1 1                    |                               |                                  |

**Note:** Bolded models have the most support from the data and are the most parsimonious (decrease in AIC by $>2$ points).

*a*Lichens were sampled on three branches or all branches <1.5 m.

*b*Cephalo-lichens. The rest of the species are cyanolichens.

$c$Ranked as special concern (blue list) by the B.C. Conservation Data Centre (2021).

$d$The Pannariaceae group includes five species grouped due to the difficulty in identifying these lichens consistently in the field: *Fuscopannaria ahlneri*, *F. confusa*, *F. ramulina*, *F. alaskana*, and *Parmeliella parvula*.

$e$*Dendriscocaulon spp.* refers to the “dendriscocauloid” forms of *Dendriscosticta* species, recognizing that there are potentially two species in our region (Simon, 2020). *Dendriscocaulon* is not currently ranked in BC because of this uncertainty. We distinguished between the *Dendriscocaulon* (the cyanomorph) and *Dendriscosticta* (the green algal morph) although they share the same mycobiont (Simon, 2020). Their morphs were distinct, behaved differently ecologically, and the foliose morph occurred less frequently.

$f$Ranked as threatened in Canada by COSEWIC (2018, 2019).

$g$Ranked as threatened (red list) by the B.C. Conservation Data Centre (2021). This species had too few observations to include in models.
TABLE 3  Parameter estimates (and 95% support intervals) for Models 1 and 2

| Species                        | Mature forest parameters | Old forest parameters |
|--------------------------------|--------------------------|-----------------------|
|                                | Y.INT | k     | z     | MIN   | OLD.INT | k_OLD | z_OLD |
| Best three branches <1.5 m     |        |       |       |       |         |       |       |
| Total lichens                  | 81 (78–84) | −1.13 (−1.2 to 1.04) | 55 (51–58) | 18.3  |         |       |       |
| Species richness               | 8.2 (7.9–8.5) | −0.09 (−0.1 to −0.08) | 49 (43–55) | 3.9   |         |       |       |
| Leptogidium dendriticum        | 13 (12–14) | −0.21 (−0.24 to 0.17) | 39 (31–44) | 4.8   | 19 (16–25) | −0.05 (−0.08 to 0) | 200+ |
| Lobaria pulmonaria             | 35 (34–35) | −0.4 (0.4 to 0.4) | 76 (75–77) | 2.0 | 0 (0–6.1) | −2.5 (−5 to 0) | – |
| Nephroma bellum               | 2.9 (2.8–3.1) | −0.19 (−0.21 to 0.17) | 13 (12–14) | 0.3   |         |       |       |
| Nephroma helvetica            | 28 (27–29) | −0.52 (−0.55 to −0.48) | 47 (44–49) | 3.1   |         |       |       |
| Nephroma isidiosum            | 0.8 (0.7–0.9) | −0.02 (−0.02 to 0.01) | 39 (33–43) | 0.2  | 1.1 (0.3–3.6) | −9.6 (−20 to 0.41) | – |
| Nephroma parile               | 8.3 (7.9–8.8) | −0.23 (−0.25 to 0.21) | 27 (24–29) | 0   | 3.8 (0–6.7) | −1.75 (−5 to 0.02) | – |
| Nephroma resupinatum          | 0.3 (0.3–0.4) | 0.003 (0.003 to 0.003) | 115 (108–115) | 0 | 0 (0–0.5) | −0.12 (−5 to 0) | – |
| Peltigera collina             | 1.4 (1.4–1.4) | −0.02 (−0.02 to 0.02) | 58 (55–59) | 2.3 | 0 (0–1) | −0.42 (−5 to 0) | – |
| Sticta fuliginosa             | 4.7 (4.4–5.3) | −0.06 (−0.07 to 0.04) | 39 (29–48) | 2.3 | 8.2 (7–9.6) | −0.03 (−0.08 to 0.01) | 200+ |
| All branches <1.5 m            |        |       |       |       |         |       |       |
| Dendriscocaulon spp.          | 0.4 (0.4–0.5) | 0 (0–0) | 108 (74–121) | 0 | 3.4 (2.9–4.2) | −0.05 (−0.06 to 0.03) | 72 |
| Lobaria oregana               | 0 (0–0) | 0 (0–0) | – | 0.1 | 1.2 (1.1–1.6) | −0.13 (−0.15 to 0.09) | 9 |
| Lobaria scrobiculata          | 0.8 (0.7–0.9) | 0 (0–0) | 400+ | 0 | 0 (0–0.6) | −0.02 (−5 to 0) | 11 |
| Nephroma occultum             | 0.2 (0.2–0.2) | −0.01 (−0.01 to 0.01) | 15 (10–18) | 0.1 | 1.9 (1.5–2.2) | −0.05 (−0.07 to 0.03) | 39 |
| Pannariaceae spp.             | 0.7 (0.6–0.7) | −0.02 (−0.03 to 0.02) | 24 (20–25) |       |         |       |       |

Note: Model 1 parameters are presented for bolded species where the age of the surrounding forest had little or no influence on colonization response, and Model 2 parameters are presented for the remaining species where age of the surrounding forest did influence colonization. Mature forest parameters: Y.INT represents abundance at the edge, k is the slope of the decline, z is the colonization distance, and MIN is the minimum abundance. Old forest parameters: OLD.INT represents abundance at the edge, k_OLD is the slope of the decline, z_OLD is the colonization distance, and MIN is the minimum abundance.

The responses of the colonizing lichens to edge distance and surrounding forest age varied among species, for example, in abundance and in colonization patterns as indicated by the parameter estimates in the colonization model (Figures 3 and 4). Even in a single genus, Lobaria, species differed in their colonization. For the rarer L. hallii and L. anomala, there was no evidence that distance from the nearest edge was a good predictor of colonization (ΔAIC was −1 to 4 between null and other models; see Appendix S1: Table S1). For L. scrobiculata, colonization decreased with distance from the old-growth forest edge, but not with distance from the mature forest edge (Figure 4), whereas L. pulmonaria had one of the strongest decreases in colonization with mature forest edge distance (Figure 3).

As predicted, the colonization of 12 of the 17 taxa was influenced by the age of the surrounding forest (Table 2, Figures 3 and 4). However, openings in old growth did not consistently support more thalli or species than in mature forests. Seven of 12 species affected by age class had higher colonization surrounded by old growth (OLD. INT > Y.INT) and 5 had higher colonization surrounded by mature forest (Table 2, Figures 3 and 4). Importantly, L. retigera and N. occultum primarily depended on old growth (Figure 4), whereas the provincially blue-listed Nephroma isidiosum was more abundant in logged openings in mature forests. Blue-listed Pannariaceae species were lumped with slightly more common species; as a group the family was unaffected by forest age class.

For many species affected by surrounding forest age, the relationship between thallus number and distance from edge was apparent only for one age class (Figures 3 and 4). Colonization of L. pulmonaria, Nephroma resupinatum, and Peltigera collina decreased with increasing distance only from mature forest edges; few thalli occurred in old-growth openings. Similarly, Lobaria oregana abundance declined with distance from old-growth edges, whereas no thalli occurred in the openings of mature forests (Figure 4). The best parameter estimates for N. isidiosum and N. parile indicated that colonization immediately dropped at old-growth edges but gradually decreased from mature forest edges. Also the distance effects in L. dendriticum, S. fuliginosa, N. occultum, and Dendriscocaulon spp. depended on the age of the surrounding forest (Figures 3 and 4).
FIGURE 3  Number of lichen thalli per best-colonized three branches (<1.5 m in height) with increasing distance from the forest edge in openings surrounded by mature (orange triangles) or old-growth (blue circles) forest. Black lines represent the best model fit: Model 2 for (a) and Model 1 for (b)
FIGURE 4  Number of lichen thalli per tree (on all branches <1.5 m in height) with increasing distance from the forest canopy edge in openings surrounded by mature (orange triangles) or old-growth (blue circles) forest. Black lines represent the best model fit: Model 2 for (a) and Model 1 for (b).
Effect of opening size and position on lichen colonization

Comparison between Models 1 and 3 provided evidence that total abundance, species richness, and the abundance of four of the five most common species were strongly affected by opening size in combination with distance to the forest edge (Table 4). Gaps (≤0.6 ha) had consistently more cephalo- and cyanolichens than clearcuts (3.8–39 ha) at similar distances from adjoining edges (Table 4, Figure 5). Per three branches, there were 1.7 fewer species; 36 fewer thalli and 11, 10, 2, and 3 fewer L. pulmonaria, N. helveticum, N. parile, and S. fuliginosa thalli, respectively, in clearcuts versus gaps (s estimates, Figure 5, Appendix S1: Table S3). Only L. dendriscum showed similar colonization responses along the edge gradient in gaps and clearcuts.

We found no evidence for our prediction that aspect affected colonization. South-facing edges had the same colonization as shady north-facing edges at 25 years after logging when we compared Models 1 and 4 for total colonization, species richness and the most common species (AIC only improved by two points between models; Appendix S1: Table S1).

Effective colonization distances

The effective colonization distances ranged from 9 to 400 m among species (Table 3, Figure 6). Total lichens and species richness reached their minimums 55 and 49 m into openings, respectively. The effective colonization distances into logged openings were <80 m for 10 species in mature forests and 5 species in old forests (Figure 6). In contrast, L. dendriscum and S. fuliginosa were effective colonizers even across the largest old-growth opening (Figure 6). L. scrobiculata was another effective colonizer reaching >400 m into mature forest openings, but with less than one thallus per tree. Dendriscocaulon spp. and N. resupinatum had estimated colonization distances >100 m in mature openings, but thalli were few at those distances.

Three out of four at risk species had colonization distances <40 m when surrounded by old-growth or mature forest. L. retigera had a longer colonization distance (71 m) when surrounded by old growth, and had several instances of long distance dispersal (>200 m) when surrounded by mature (Figures 4 and 6). The different colonization distances in logged openings for each forest age class could be estimated for L. dendriscum, N. occultum, and S. fuliginosa, which colonized further when surrounded by old-growth forest, and for Dendriscocaulon spp. and L. scrobiculata, which colonized further in openings surrounded by mature forest (Figure 6).

Long-distance colonization rates (represented by MIN) varied from 0 to 4.8 thalli depending on the species. Most lichens, even some rare species, could be found far from canopy edges (>200 m, Figures 3 and 4). All common species had minimum thallus numbers between 2.0 and 4.8 (Table 3), indicating that long distance colonization occurred regularly. Even trees in clearcuts hosted ≥2 thalli per species after 25 years. Because colonization rate was based on the best three branches only, it underestimated common species abundances per tree. Infrequent species, apart from L. scrobiculata, had MIN estimates between 0 and 0.1, indicating that long-distance colonization occasionally occurs (10 thalli >200 m from edges; Figure 4).

### Table 4: Comparison of Model 1 (distance from edge) and Model 3 (opening size) for cephalo- and cyanolichens species observed on >100 trees

| Species                  | Model 1 |       |       | Model 3 | Opening size (≤0.6 ha vs. >0.6 ha) |       |       |
|--------------------------|---------|-------|-------|---------|-----------------------------------|-------|-------|
|                          | AIC     | R²    | ΔAIC  | AIC     | ΔAIC    | R²    |
| Total lichen             | 1974    | 0.23  |       | 1953    | −21     | 0.29  |
| No. species              | 919     | 0.19  |       | 914     | −5      | 0.21  |
| Leptogidium dendriscum   | 1406    | 0.11  |       | 1407    | 1       | 0.12  |
| Lobaria pulmonaria       | 1154    | 0.10  |       | 1150    | −4      | 0.14  |
| Nephroma helveticum      | 1342    | 0.15  |       | 1334    | −7      | 0.18  |
| Nephroma parile          | 905     | 0.02  |       | 901     | −4      | 0.04  |
| Sticta fuliginosa        | 1062    | 0.11  |       | 1057    | −5      | 0.14  |

Note: Bolded models have the most support from the data or are the most parsimonious.
Thallus size

Thallus size ranged from 0.1 to 70 cm². On the three best branches, almost half (44.6%) of thalli were <0.3 cm² and 74.9% were <1 cm². Few thalli were >5 cm² (3.1%) or >10 cm² (1.1%) and only 0.4% >20 cm². The size distributions were strongly skewed to small thalli and showed a reverse-J distribution for the common species (Figure 7).

FIGURE 5 Number of lichen thalli or species richness per best-colonized three branches (<1.5 m in height) within 50 m of the forest canopy edge in openings <0.6 ha (gaps) and ≥3.8 ha (clearcuts). Lines represent how Model 3 fit for gaps (black lines) and for clearcuts (gray lines). The Model 1 fit is shown for L. dendricum. Dashed gray lines show the lower and upper support intervals for the parameter estimates from Model 3.
Despite larger numbers of thalli in gaps versus clearcuts, there was no clear difference between the size distributions in gaps versus clearcuts (Figure 7).

**DISCUSSION**

To understand how retention forestry, and specifically silvicultural strategies that create a range of opening sizes, benefit the conservation of cephalo- and cyanolichens, we assessed how distance from the forest edge (the magnitude and depth of forest influence), age of the surrounding forest, opening size, and opening position shape lichen colonization in regenerating openings. Although we could not separate dispersal and establishment limitations, the results showed a consistent decrease in abundance and richness of cephalo- and cyanolichens with increasing distance from the forest edge. In general, the depth of the forest influence was ~80 m, which was 2.7 times the canopy height, similar to the edge influence of three times the canopy height reported on lichen colonization into intact forests (Esseen, 2006; Gauslaa et al., 2019), but higher than one canopy height reported by Keenan and Kimmins (1993). However, species differed in their responses to forest influence, forest age and opening size, thereby emphasizing the importance of species-specific studies in assessing the impact of silvicultural strategies on lichen recolonization and in developing appropriate conservation strategies.

In many lichens, long-distance dispersal occurs by sexual fungal spores in apothecia that must disperse to habitats hosting suitable photobionts to re-establish the symbiosis. Apothecia are common for three of the 18 study taxa (\(N. \text{ bellum}\), \(N. \text{ helveticum}\), and \(N. \text{ resupinatum}\)), infrequent for \(L. \text{ pulmonaria}\), \(L. \text{ oregana}\) and Pannariaceae, and absent or rare in the remaining species (Brodo et al., 2001; Fedrowitz et al., 2011; Hilmo, Rocha, & Holien, 2011; Jordan, 1973), which would limit their dispersal distance. Although comprehensive information on propagules is scarce, the main mode of reproduction and dispersal (except for \(N. \text{ bellum}\)) is by the heavier symbiotic propagules: soredia, isidia, and thallus fragments (Fedrowitz et al., 2011; Jüriado et al., 2012; Nelson et al., 2015; Rapai et al., 2012; Stofer et al., 2006; Walser, 2004). Large symbiotic propagules, especially...
**FIGURE 7** Thallus area distribution (percent of total in each size class) by species for common lichens colonizing (a) gaps (124 trees sampled), (b) clearcuts <50 m (32 trees sampled), and (c) clearcuts >50 m (57 trees sampled) from the forest canopy edge. Total number of thalli is presented in each panel.
the lobules of *L. oregana*, but also the coarse soredia of *L. pulmonaria*, have shorter dispersal (*Esseen et al., 1996; Sillett et al., 2000*) than finer soredia and asymbiotic ascospores but higher probability of establishment (*Hilmo, Rocha, & Holien, 2011*).

Of our species, only the dispersal and establishment of *L. pulmonaria* has been well studied. Its propagules have been shown to disperse 140–230 m (molecular techniques, *Walser, 2004*) and frequently >200 m (diaspore traps, *Werth et al., 2006*); whereas effective colonization distances were shorter: 15–30 m (*Juriado et al., 2011*) and 35–75 m (*Öckinger et al., 2005*). Here, effective colonization of *L. pulmonaria* was 77 m from the edge, but it had colonized as far as 400 m 25 years after logging. *Hilmo, Rocha, and Holien (2011)* showed that *L. pulmonaria* established more successfully than *L. scrobiculata* when artificially sown on branches in old forests and clearcuts. *Lobaria pulmonaria* has larger diaspores (more resources for establishment; *Hilmo, Rocha, & Holien, 2011*), but a longer generation time (22–25 vs. 15–22 years, *Larsson & Gauslaa, 2011*) than *L. scrobiculata*, which would prevent early local recruitment within logged openings. A short generation time may explain the unexpectedly large colonization capacity of *L. scrobiculata (>100 m)* which was poorly explained by forest influence.

The dispersal distances of other species were also consistent with diaspore size. *Lobaria oregana* has large, poorly dispersing propagules, a short colonization distance (9 m) and was restricted to old-growth forests. Sillett and Goslin (1999) have likewise documented the short dispersal distance of *L. oregana*, for which propagule size is a main limitation (*Sillett et al., 2000*). In contrast, four species were highly effective colonizers: *S. fuliginosa* and *L. dendriscum* had effective colonization distances >200 m for old-growth forests; *Dendriscocaulon* and *N. resupinatum* colonized distances 108–115 m in mature forests. *Leptogium dendriscum* and *Dendriscocaulon* may reproduce by minute fragments that adhere and develop quickly into new thalli, while *S. fuliginosa* reproduces by isidia that are shed frequently and take only 8–12 months to develop into primary lobes (*Zoller et al., 2000*).

### Forest age effect

Based on research from Europe (*Esseen et al., 1996; Rose, 1976*), and western North America (*McCune, 1993; Price et al., 2017; Price & Hochachka, 2001*) we expected openings in old-growth forests to support more lichens than those in mature forests. Instead, species richness and total abundance were equal between forest ages, consistent with Arsenault and Goward (2016) for humid toe-slope forests. Only *L. oregana* and the red-listed *D. oroborealis* were restricted to openings in old-growth forests. Such discrepancies may have various reasons. First, the Kispiox rainforest has an optimal macroclimate for cephalo- and cyanolichens (*Coxson et al., 2019; Goward & Arsenault, 2000a; Goward & Pojar, 1998*). Second, historic low-intensity, infrequent fires (*Coates et al., 1997*) left a patchwork of interwoven old and mature stands with frequent patches of fire veterans that likely enriched the epiphytic lichen communities (*Neitlich & McCune, 1997; Sillett & Goslin, 1999*). Third, our mature forests have never been logged. Fourth, the experiment was done on favorable topographic positions for lichens such as toe and lower slopes, overriding the effect of forest age (*Arsenault & Goward, 2016; Radies et al., 2009*). More importantly, however, mature forests had high proportions of *Populus* species, facilitating cephalo- and cyanolichens beneath their canopies through a drip-zone enrichment (*Campbell et al., 2010, 2013; Gauslaa & Goward, 2012; Goward & Arsenault, 2000b) of elemental nutrients (*Gauslaa et al., 2020*).

Although forest age classes hardly differed in species richness and total abundance, most species were more common in one age class than the other. For *N. occultum*, *S. fuliginosa*, and *L. dendriscum*, the effective colonization distances were substantially greater in old forests. Such long-distance colonization in old-growth forests is likely due to high diaspore rain from the surrounding forests (*e.g., Hylander, 2019*), favorable microclimate (COSEWIC, 2019; *Radies et al., 2009*) or hospitable sites allowing for quick juvenile development (*Zoller et al., 2000*).

### Opening size and forest edge

In these rainforests, clearcuts >3.8 ha supported many cephalo- and cyanolichens, and occasionally, even at-risk species, contradicting studies showing that such lichens were absent in large gaps (1–3 ha, *Benson & Coxson, 2002*) and regenerating forests (*Berryman & McCune, 2006; Price et al., 2017; Price & Hochachka, 2001; Sillett & Neitlich, 1996*). Nevertheless, the abundance and diversity was lower in clearcuts than in gaps (<0.6 ha). Gaps have greater canopy shading, higher day-time humidity and cooler temperatures than clearcuts (*Gauslaa et al., 2007; Geiger, 1950*), but less dew and rain required to activate cyanolichen photosynthesis (*Lange & Kilian, 1985*). Although the microclimate differences may play a role, gaps most likely have higher colonization rates because distances to forest edges (and thus adjacent propagule sources) were lower than clearcuts. Smaller is not necessarily better; *Neitlich and McCune (1997)* proposed...
that while very small canopy gaps (0.0025 m²) had a negligible effect on lichen diversity, creating openings of 0.1 ha would dramatically enhance lichen diversity within 20–50 years. Our results at 25 years after logging support their prediction.

In European boreal rainforests, most cephalo- and cyanolichens colonized logged openings (0.3–11.3 ha) less frequently and at greater ages (43 and 70 years, respectively; Hilmo, Ely-Aastrup, et al., 2011) than in our temperate rainforests. In these European forests, cyanolichens began to colonize regenerating trees within 20 m of the forest edge at 70–85 years (Hilmo et al., 2009), agreeing with Peterson and McCune (2001) who reported old-forest lichens recolonizing logged stands after 70–110 years in western Oregon. Old-forest lichens are likely more tolerant of logging in humid climates with adequate summer precipitation (Arsenault & Goward, 2016; Gauslaa et al., 2007; Hilmo et al., 2009; Rolstad et al., 2001).

Our results did not support the prediction that north-facing edges would have higher colonization rates than south-facing edges, likely because of cloudy weather and high humidity, and because regenerating trees in the gaps and clearcuts were large enough to buffer the drying light and wind exposure. When the common cephalo- and cyanolichens can effectively colonize distances between 27 and 76 m in mature forests and farther for two species in old forests (200+ m), these lichens can likely colonize the entire area in our gaps. Furthermore, wind events come from the south in these forests (Coates, 1997) and wind as a vector for diasporas may be more important for colonization than edge orientation.

**Thallus size**

Epiphytic lichen populations experience continuous loss (Berryman & McCune, 2006; Caldziz & Brunet, 2006; Lehmkuhl, 2004; McCune, 1994; Stevenson & Coxson, 2003). To compensate for the loss, a high number of new thalli must be produced regularly. Dispersed diasporas may be lost during the critical attachment phase (Hilmo & Såstad, 2001; Scheidegger et al., 1995; Zoller et al., 2000) and the juveniles can be shed (Larsson & Gauslaa, 2011) or grazed (Scheidegger et al., 1995). Zoller et al. (2000) found that 10%–30% of transplanted symbiotic diasporas of three lichens survived and developed into thalli after 16 months in Switzerland (30% for S. fuliginosa). Small populations may not produce enough diasporas to survive. In our study, there was high recruitment in the smallest size class of lichens in gaps and a smaller juvenile proportion in clearcuts. Nevertheless, clearcuts still had a distribution skewed to the smallest sizes. The skewed size distribution toward small juveniles suggests that the five most common cephalo- and cyanolichens efficiently dispersed by diasporas, and that the epiphytic community was still in an early assemblage stage after 25 years.

**Implications for forest management**

The high occurrence of cephalo- and cyanolichens observed in 25-year-old regenerating rainforest openings seems promising for their future survival in managed forests, although this reflects a snapshot in time of the dynamic processes of dispersal, propagule attachment and establishment, growth, mortality, and reproduction (Armstrong, 1988; Hilmo, Rocha, & Holien, 2011; Larsson & Gauslaa, 2011; Scheidegger, 1995). However, the epiphytic community is still developing in these gaps and may not persist through denser and darker successional stages. Monitoring the gaps over longer periods (>25 years) will allow a clearer understanding of how lichen populations develop over time and whether the gaps remain favorable for lichens (e.g., see Radies & Coxson, 2004).

Our results are consistent with others concluding that the conservation of old-forest lichens relies on minimizing distances between the source of lichen propagules and the regenerating trees (Hilmo, Rocha, & Holien, 2011; Peck & McCune, 1997; Sillett & Goslin, 1999). Trees retained in large aggregates better protect the lichens from adverse edge effects such as wind desiccation and direct sunlight, although this is not always the case (Gustafsson et al., 2013). Gauslaa et al. (2019) recommended retention patches >5.7 ha, or buffers ≥120 m to promote survival of lichens in the Kispiox rainforest. Because cephalo- and cyanolichen colonization is restricted to within 80 m of the forest canopy in openings for most species, then live tree patches must be strategically located to minimize dispersal distances.

We have shown that creation of discrete gaps in an intact, or lightly harvested forest matrix greatly improves colonization and likely promotes long-term supply of lichen propagules in the matrix (Neitlich & McCune, 1997; Sillett et al., 2000). This is especially true for rare species with shorter colonization distances (e.g., <40 m for Pannariaceae, N. occultum, L. oregana) that require gaps ≤80 m diameter. Although we have not examined the postlogging growth rates and long-term survival of cyanolichens in the forest matrix in the Date Creek study, the high colonization in the openings suggests that canopy lichens are surviving, growing and reproducing within the 40% and 70% retention units. When adequate
numbers of thalli have reached the reproductive stage in the logged openings, further colonization depends less on diaspores from the surrounding forest matrix. Further studies are needed to identify the time needed for the gaps to change from diaspore sinks to sources.

Conservation strategies for these lichens must consider the interaction between stand and landscape scales. The relatively intact landscape around the Date Creek study, uniquely rich in cephalo- and cyanolichens, provided abundant propagules for colonization of logged openings. In more disturbed landscapes, where old-growth stands are islands in an expanding matrix of young forests, propagules sources for lichen colonization would be diminished. Clearcutting such old-growth islands without adequate retention reduces lichen propagules even more and compromises growth and survival of the “life-boated" lichens in retention patches, leading to local extinctions. At both scales, we must ensure that colonization rates of lichens are higher than local extirpation rates (e.g., Fedrowitz et al., 2012). Sexual reproduction, which enhances genotypic diversity in local populations and increases the probability of survival in a changing climate (Walser, 2004), may depend on coexisting genotypes in outcrossing lichen populations (Walser et al., 2004). Preserving a network of large, well-situated reserves of old and antique forests is essential for maintaining these remarkable lichens in the managed rainforest (Bezzola & Coxson, 2020; Scheidegger & Werth, 2009). Because on-going habitat loss, climate change and air pollution are impacting cephalo- and cyanolichens worldwide, managing for lichen conservation at the stand and landscape levels in the Kispiox rainforest will be important for maintaining these species at the global scale.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data and R scripts (Lilles et al., 2021) are available from Dryad: https://doi.org/10.5061/dryad.k0p2ngf7f.

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Additional supporting information may be found in the online version of the article at the publisher’s website.

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