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Long-term recovery of epiphytic communities in the Great Bear Rainforest of coastal British Columbia

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ABSTRACT

The recent Great Bear Rainforest agreement recognises the high biodiversity values of this large intact area of coastal temperate rainforest by calling for old forest targets to be met by 2264. Recruiting young stands has joined conserving existing old stands as a strategy for achieving targets, but the point at which second growth stands recover oldgrowth attributes remains uncertain. We examined the recovery of epiphytes towards oldgrowth conditions by comparing community composition, richness and abundance between young (55–100 year old), mature (101–250 years old) and oldgrowth stands (>250 year old). We felled 77 western redcedar, amabilis fir, western hemlock and Sitka spruce trees, identified all epiphytes, and examined effects of stand age, region, tree species, site nutrient status and presence of residual trees on the epiphyte community. We found 229 taxa, including 49 bryophytes, 98 macrolichens and 82 crustose lichens. Epiphyte community varied by region and among tree species, but not by site productivity or presence of residual trees. In the northern region, trees in oldgrowth supported twice as many epiphyte species, seven times as many unique species, and a significantly different community composition for all functional groups (bryophytes, crustose lichens, hair lichens, cyanolichens and other macrolichens) relative to trees in stands younger than 200 years. Overall similarity between second growth and oldgrowth was about 50%. Young and mature stands overlapped considerably in richness, abundance, and community composition, indicating little recovery between 55 and 200 years. Our study suggests that in the northern region of the Great Bear Rainforest, epiphyte communities need more than 200 years to recover to oldgrowth conditions.

1. Introduction

One of the world's largest areas of relatively intact coastal temperate rainforest lies within British Columbia's (BC) 6.4 million hectare Great Bear Rainforest (DellaSala, 2011). This highly productive, biologically rich, and globally rare ecosystem is characterised by abundant precipitation and a moderate climate (DellaSala, 2011). Due to the extreme rarity of natural stand-replacing disturbances, particularly fire, temperate rainforests are dominated by ancient, structurally-complex forests that can be aged in millennia rather than centuries (Lertzman et al., 2002; Gavin et al., 2003; Daniels and Gray, 2006).

A recent agreement, endorsed by First Nations, the BC Government, environmental organisations and industry, aims to maintain ecological integrity in the Great Bear Rainforest by achieving high levels of oldgrowth ecosystem representation (generally 70% of each ecosystem over 250 years old) by the year 2264, and by limiting future forest harvest to 15% of the area (MFLNRO, 2016). Past logging, however, has already converted many productive ecosystems to even-aged second growth forests (e.g., productive western redcedar [*Thuja plicata*]-leading ecosystems have less than 10% oldgrowth; Holt and MacKinnon, 2006). Within the managed forest, plans call for 15% of each forest stand to be retained. Given the desire for sustainable, ecosystem-based management in the Great Bear Rainforest (Price et al., 2009; MFLNRO, 2016), important ecological questions include "How quickly will harvested stands develop oldgrowth characteristics?" and "How well will 15% in-stand retention maintain oldgrowth associates and facilitate recovery?"

Epiphyte communities are good indicators of ecological integrity, because of their slow recovery following disturbance and because of their various ecological functions as habitat, forage

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and nitrogen-fixers (Ellis, 2012). Wherever epiphytes have been studied in temperate and boreal ecosystems, old forests have supported a higher abundance and different communities of epiphytes than young or mature stands (e.g., Rose, 1976; Lesica et al., 1991; McCune, 1993; Neitlich, 1993; Goward, 1994; Esseen et al., 1996; Enns et al., 1999; Price and Hochachka, 2001; Campbell and Freeden, 2004). These changes have been related to potentially interacting variables including tree characteristics (e.g., substratum), stand characteristics (e.g., heterogeneity) and forest continuity (Ellis, 2012). Epiphyte communities in humid forests often undergo succession from early-colonising green foliose and crustose lichen species to hair lichens and finally cyanolichens and bryophytes (McCune, 1993; Sillett and Neitlich, 1996). Some cyanolichen species are sufficiently reliable oldgrowth associates that they have been used to indicate forest age and continuity (e.g., Goward and Pojar, 1998; Campbell and Fredeen, 2004).

Green tree retention (Rosenvald and Lõhmus, 2008) has been investigated as a strategy to maintain late successional epiphytes through forest harvest cycles by mitigating microclimate changes (Benson and Coxson, 2002) and dispersal limitations (Sillett and McCune, 1998). Results have varied. In coastal forests in Oregon, hair lichens and cyanolichens were more abundant in young stands with oldgrowth remnant trees (Peck and McCune, 1997), and the amount of oldgrowth-associate litter decreased with distance from remnants (Sillett and Goslin, 1999). However, in boreal ecosystems, remnant trees lost sensitive bryophytes and lichens in the first few years post-harvest likely due to seasonal drying (Perhans et al., 2009; Boudreault et al., 2013), and veteran trees supported a depauperate community of cyanolichens relative to their age-mates in adjacent old forest (Benson and Coxson, 2002; Radies and Coxson, 2004).

Here, we investigate the recovery of epiphyte communities in young and mature forests of the Great Bear Rainforest. Secondarily, we assess the potential effectiveness of remnant trees at facilitating recovery, but a retrospective study design, including sites with and without remnant trees, allows us to explore patterns rather than infer causation. We predicted that trees in oldgrowth would support unique epiphyte communities and that recovery would be slow. We predicted that oldgrowth-associated epiphytes would be positively affected by remnant trees, assuming that seasonal drying would pose a minor challenge in this maritime ecosystem. To understand epiphyte distribution among and within trees of the study area better, where there are known differences in tree composition and structure between second growth and oldgrowth stands (Banner and LePage, 2008; LePage and Banner, 2014), we also considered the effects of tree species and vertical canopy position on epiphyte communities.

This study forms part of an interdisciplinary investigation into the recovery trajectories of a variety of ecosystem attributes in coastal BC. As well as the epiphyte communities described in this paper, studies have examined stand structure and tree species composition (LePage and Banner, 2014), understory vegetation (Banner and LePage, 2008), forest growth and productivity, and soil properties including faunal communities.

2. Methods

2.1. Study area

The Great Bear Rainforest encompasses the coastal temperate rainforest of the central and northern BC coast (51°–55°N). Within this area, ecosystem recovery studies focussed on low elevation forests of the Very Wet Hypermaritime Coastal Western Hemlock biogeoclimatic subzone (CWHvh2; Banner et al., 1993) that grow on coastal islands and a mainland fringe between northern Vancouver Island and southeast Alaska. The mild, very wet (Banner et al., 1993) climate limits fire ignition and spread. Most stand-replacing natural disturbances are small and initiated by landslides, wind and alluvial flooding (Price and Daust, 2003; Banner et al., 2005). Gap-phase dynamics dominate stand regeneration, leading to uneven-aged oldgrowth stands that can be thousands of years old, considerably older than the oldest live tree (Lertzman et al., 1996; Daniels and Gray, 2006). Forests grow on moderate to steep slopes, while bogs cloak gentler terrain (Banner et al., 1993, 2005). Forested stands typically include a mix of western hemlock (*Tsuga heterophylla*), western redcedar, amabilis fir (*Abies amabilis*) and Sitka spruce (*Picea sitchensis*). Following stand-replacing disturbance, young CWHvh2 forests have a dense closed canopy for the first century. The canopy opens up between 100 and 160 years, and oldgrowth characteristics (large old trees, downed wood, snags, vertical and horizontal heterogeneity) develop over the next hundred years (Franklin et al., 2002; LePage and Banner, 2014).

Small-scale commercial harvesting in the Great Bear Rainforest began about a century ago; most cutblocks harvested were small (<20 ha; many much smaller); today, they contain residual trees (small and less desirable species left after logging), and are surrounded by oldgrowth. Although stands vary in their development, 80–100 year-old harvested stands in the study area have a 40–55% structural similarity to oldgrowth stands, with nutrient-rich sites developing large trees faster than mesic sites (LePage and Banner, 2014).

2.2. Sample sites

The sites were located in two accessible areas, one in the north and one in the central region of the Great Bear Rainforest (Fig. 1). Second growth site selection was severely limited due to the paucity of stands meeting age criteria (young: 55–100 years old; mature: 101–250 years old) in the region. Second growth stands (>1 ha of uniform stand characteristics), accessed from the ocean and narrow inlets, were identified using maps, local knowledge, and visual inspection. Oldgrowth stands (>250 years old) in the northern region were accessed from roads near the ocean and were selected to match plant community characteristics of second growth stands. As a group they were slightly farther from the ocean and higher in elevation (2.2–2.4 km and 33–189 m elevation) than the second growth sites (0.1–0.5 km and 1–59 m elevation) due to timing and access logistical limitations. All sites were sheltered by islands rather than exposed to the open Pacific, controlling somewhat for oceanic influence. Slope and aspect varied (0–86% and 12–354°, respectively). The 29 sampled sites included 11 young stands initiated by harvesting, 13 mature stands initiated by harvesting, windthrow or fire (sometimes with a mix of disturbance types) and five uneven-aged oldgrowth stands.

Northern sites were colder than central sites (mean annual temperature: 6.9 ± 0.06 °C and 8.1 ± 0.02 °C respectively), and had slightly higher mean annual precipitation (3200 ± 105 and 3000 ± 40 mm/year respectively), with relatively less spring precipitation and more summer and fall precipitation (interpolated 1960–1990 climate normals for sites were extracted from ClimateBC; Wang et al., 2016).

At each site, we cored four of the largest diameter, non-residual trees and defined stand age as the age of the oldest cored tree. Oldgrowth stands were assigned an age of 250+ years because rotten tree cores prevented accurate tree ring counts and because stands are frequently older than the oldest tree. We determined site productivity, based on the BC biogeoclimatic ecosystem classification system (Banner et al., 1993; Kranabetter et al., 2003). Most sites had sub-mesic to mesic soil moisture (two were hygric), but varied in nutrient regime. We grouped sites (using Banner et al., 1993) into "rich" (CWHvh2/05 and /06 site series), "medium"