LONG-TERM RECOVERY OF ECOSYSTEM SERVICES FOLLOWING FOREST HARVEST IN COASTAL TEMPERATE RAINFORESTS OF VANCOUVER ISLAND, BRITISH COLUMBIA, CANADA

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ABSTRACT

All ecosystems, and the ecosystem services (ES) they provide, are susceptible to potentially lasting impacts of resource extraction. For example, in forests, timber harvesting provides near-term services (such as wood products), but can be responsible for declines in other services such as carbon storage or wild edible foods, which may take decades or even centuries to recover. Some ES may recover quickly with forest regrowth, while others recover either slowly or not at all. However, the long-term recovery of multiple forest ES has rarely been quantified. My fundamental goal in this thesis is to build an improved understanding of how multiple ES recover following forest harvest, using the heavily harvested coastal temperate forests of western Vancouver Island, British Columbia, Canada, as my study system.

First, I used a forest chronosequence to estimate the recovery trajectories for eight ES over a 212-year period. I used changes in key forest structures to estimate the provision of the following services: wood volume, carbon storage, potential nesting platforms used by an emblematic old-growth associate bird species the marbled murrelet (*Brachyramphus marmoratus*), habitat services provided by coarse woody debris, habitat services provided by dead trees, large heritage trees, wild edible berries, and large redcedar (*Thuja* plicata) used in traditional First Nations carving. ES recovered along varying non-linear trajectories and within markedly different timeframes. Wood volume stocks, dead tree biomass, and carbon storage recovered the fastest, reaching their maximum rates of recovery at around 65 years. In contrast, recovery of wild edible berries, heritage large trees, and habitat for marbled murrelet did not even commence until 70-100 years. Large heritage trees and large redcedar did not recover to old-growth baseline (forests >250 years old) during the 212-year period of my chronosequence.

Second, I examined how ES recovery differed in two forest types: riparian and upland forests. With field assistance from a local First Nations crew, I estimated ten ES in old-growth (late seral stands >250 years in age) and second-growth stands (~35 years age) within each forest type. In addition to those services sampled in Chapter 1, I also estimated cedar bark for use in traditional

First Nations weaving, salal (*Gualtheria shallon*) merchantable greenery, and fish habitat provided by instream woody debris. The abundance of ES differed significantly by forest type and forest age. For example, large cedar and potential nesting platforms for marbled murrelets were absent in second-growth stands, and significantly higher in riparian sites relative to their presence in upland forests. Old-growth riparian forests were hotspots of many ES, providing the highest levels of all services except salal merchantable greenery.

The long timeframes and varying trajectories of recovery highlight the need to avoid ES declines proactively, for example by preserving sites with high levels of ES or working with First Nations to identify key areas with high levels of desired ES. Forest age and forest type have significant and major effects on multiple ES, and are thus two key variables for managing multiple ES in forested landscapes. Overall, this thesis provides insights into the effects of forest harvesting on multiple ES of ecological, cultural and economic importance. By applying forest ecological understanding to track changes in a bundle of ES, I identify influences of site conditions, long timeframes of successional recovery, and impacts from management to gain a broader understanding of the factors shaping forest ES. By building an improved empirical and conceptual understanding of multiple ES and their change through time, I have provided novel insights as well as practical solutions towards the challenge of long-term forest planning to sustain multiple ES.

RÉSUMÉ

Les écosystèmes, et les services écosystémiques (SE) qu'ils fournissent, sont vulnérables aux effets à long terme engendrés par l'extraction des ressources naturelles. Dans les écosystèmes forestiers, par exemple, la sylviculture peut fournir des services à court terme par l'entremise des produits sylvicoles, mais ce gain se fait souvent au détriment d'autres services comme la séquestration de carbone ou l'approvisionnement en produits comestibles, qui requièrent souvent des décennies voir même des siècles à se régénérer. Quoique certains SE peuvent se régénérer rapidement avec la succession de la forêt suivant un coupe, d'autres se régénèrent lentement ou s'éteignent complètement. En milieux forestiers, la régénération des SE sur de longues périodes a rarement été quantifié. Le principal objectif de cette thèse est d'approfondir nos connaissances sur la régénération de multiples SE suivant la succession des écosystèmes après une coupe forestière, et ce dans les écosystèmes des forêts tempérés fortement exploitées de la zone côtière de l'ouest de l'île de Vancouver.

Premièrement, j'ai utilisé un chronoséquence forestière pour estimer la trajectoire de renouvellement de huit SE sur une période de 212 ans de succession forestière. J'ai utilisé les changements dans les caractéristiques importantes de la structure de la forêt pour estimer l'approvisionnement et la disponibilité des services comme le volume de bois, la séquestration de carbone, le potentiel de nidification du guillemot marbré (*Brachyramphus marmoratus*), les services d'habitats potentiels offerts par les débris ligneux grossiers, les services d'habitats potentiels offerts par les grands arbres morts, les grands arbres ayant un patrimoine culturel, les baies sauvages comestibles et les thuyas géants (*Thuja plicata*) traditionnellement utilisés pour la sculpture par les Premières nations. Les SE se sont renouvelés suivant une variété de trajectoires non linéaires sur des échelles temporelles différentes. Le volume de bois, la biomasse d'arbres morts et la séquestration de carbone se sont régénérés le plus rapidement, atteignant un taux de régénération maximale après une période d'environ 65 ans. Par contre, d'autres SE comme les baies sauvages, les grands arbres ayant un patrimoine culturel et l'habitat du guillemot marbré commencent à peine à se rétablir après une période de 70 à 100 ans. Les grands arbres ayant un patrimoine culturel et les thuyas géants n'ont pas eu l'opportunité de se rétablir au point de

référence des forêts anciennes (plus que 250 ans) sur la période de 212 ans disponible dans la chronoséquence utilisé.

Deuxièmement, j'ai étudié la divergence de la trajectoire de régénération des SE dans deux types de forêts, soit des forêts riveraines et des forêts des hautes terres. À l'aide d'assistants de terrain d'une Première nation locale, j'ai estimé 10 SE dans des forêts anciennes (plus de 250 ans) et dans des forêts de peuplements de seconde venue (environ 35 ans). En plus des SE étudiés dans mon premier chapitre, j'ai estimé la disponibilité de l'écorce de thuya pour le tissage de paniers traditionnelles par les Premières nations, la disponibilité du salal (*Gaultheria shallon*) pour l'économie traditionnelle et les habitats aquatiques créés par les débris ligneux. L'abondance des SE diverge significativement selon le type et l'âge de la forêt. Par exemple, les cèdres géants et les sites potentiels de nidification du guillemot marbré étaient complètement absents dans les forêts de peuplements de seconde venue, et plus abondants dans les forêts riveraines que dans les forêts des hautes terres. Les SE étaient le plus abondant dans les forêts anciennes riveraines qui abritaient la plus grand potentiel d'approvisionnement pour tous les SE, sauf la disponibilité de la salal.

Les longues périodes et la variété des trajectoires caractérisant la régénération des SE soulignent l'importance de gérer les compromis de manière proactive, soit en préservant des sites abritant une abondance de SE ou en travaillant avec les Premières nations afin d'identifier des sites abritant le plus de SE désirables pour les activités traditionnelles. Le type et l'âge de la forêt ont le plus d'influence sur la variété et l'abondance des SE disponibles et consistent donc des deux variables les plus importantes pour la gestion des SE en milieux forestiers. Dans son ensemble, cette thèse identifie les dynamiques spatiales et temporelles des SE afin de comprendre les effets de l'exploitation forestière sur l'approvisionnement des SE d'une importance écologique, économique et culturelle. En appliquant des concepts écologiques pour faire un suivi des changements d'abondance des SE au fil du temps, j'identifie l'influence des types de sites, des échelles temporelles de la succession végétale et des impacts de gestion de la forêt afin de mieux comprendre les facteurs influençant les SE en milieux forestiers. En améliorant notre compréhension empirique et conceptuelle des changements d'abondance des SE au fil du temps,

cette thèse contribue aux connaissances nécessaires à l'adoption de méthodes de gestions requises pour assurer la disponibilité d'une variété de SE sur de longues périodes.

Dedicated to the inspiring places in this world that turn ordinary
lives into meaningful adventures. And to my parents, brother, friends and mentors
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PREFACE

This thesis is manuscript-based, consisting of two stand-alone chapters prepared for publication in peer-reviewed journals. Each chapter contains its own Literature Cited section and a connecting statements explaining how the chapter fits within the broader thesis work. The thesis begins with an introduction section to provide more detailed context of the problems and knowledge gaps that motivates my thesis. At the end of the thesis, I synthesize key contributions from my research and record insights for future research directions. Chapter 1 is an investigation into the long-term recovery trajectories of multiple ecosystem services following logging. It has been prepared for submission to the peer-reviewed journal *Proceedings of the National Academy of Sciences*. The second chapter is an investigation of the effects of forest age and ecological site conditions on multiple ecosystem services. It is based on original data I collected in the field, and is prepared for submission to the peer-reviewed journal *Ecological Indicators*. The formatting of headers and sections roughly follows the thesis of McGill grad Matthew Mitchell, Phd. For consistency, all Literature Cited sections are formatted in accordance with the journal *Proceedings of the National Academy of Sciences's* style guide.

CONTRIBUTIONS OF AUTHORS

My thesis co-advisors, Elena Bennett and Sarah Gergel, are co-authors on manuscript chapters 1 and 2. Sarah and Elena have been highly involved in their role as advisors and contributed to these manuscripts, including conceptualizing the research proposal, providing advice, and helping with final edits. Elena Bennett originally conceived the idea for a study of ecosystem services recovery in a forested system. Previous work by Sarah Gergel on Vancouver Island identified the need to understand impacts of past forest harvesting on First Nations' cedar resources and on forest ecosystem services located in different site conditions. I am the first author of both manuscripts, having led conceptualization of the research, collected and analyzed the data, and assumed the primary role in writing the manuscript chapters.

INTRODUCTION

BACKGROUND TO THESIS TOPIC

Ecosystems, and the benefits they provide to people, are susceptible to potentially lasting impacts from resource extraction (MA 2005, De Groot et al. 2010). For example, while forest harvest provides immediate timber resources, it has long-term impacts on biodiversity (Bunnell et al. 1999) and reduces forest capacity to provide numerous ecosystem services such as carbon storage which regulates global climate (Luyssaert et al. 2008), cultural heritage experiences among large old trees (Blicharska and Mikusiński 2014), and wild foods (Clason et al. 2008). In fact, a fundamental challenge for natural resource management in the 21st century is how to meet increasing demands for economic products (such as food and timber) while sustaining other ecosystem services, now and in the future (Rodriguez et al. 2006, Power 2010, Kline and Mazzotta 2012). Among terrestrial ecosystems, forests are particularly susceptible to lasting impacts of resource extraction due to the slow recovery of trees and other structures (Bunnell and Dunsworth 2010). In this thesis, I identify multiple ecosystem services provided by coastal forests on Vancouver Island, British Columbia, Canada and investigate how they change and recover in the decades following forest harvest.

ECOSYSTEM SERVICES IN RESEARCH AND MANAGEMENT

The ecosystem services (ES) framework helps recognize and account for society's distinct values attributed to ecosystems by acknowledging provisioning, cultural, habitat and regulating services (MA 2005, De Groot and Van der Meer 2010). Provisioning services include the raw materials extracted from ecosystems with economic or subsistence values, such as timber and non-timber forest products from forests. Cultural services include many non-material benefits of nature linked to spiritual, heritage, and aesthetic value (Daniel et al. 2012, Hernández-Morcillo et al. 2013). Habitat (or supporting) services are the ecosystem structures and functions that maintain life cycles of different plants and animals, such as the role of coarse woody debris in providing forest habitat niches (Bunnell et al. 1999, Feller 2003, Pollock and Beechie 2014). Finally, regulating services, such as carbon storage for climate regulation, maintain environmental conditions in a safe and desirable range conducive to human wellbeing and the production of other ES (Villamagna et al. 2013).

Once multiple ES are identified as criteria for management, the ES approach is operationalized by systematically identifying ES indicators based on the key properties of ecosystems that provide ES (Burkhard et al. 2009, van Oudenhoven et al. 2012, Beier et al. in press). While social factors, such as the needs, preferences and customs of people, motivate societal demand for ES, the biophysical properties of ecosystems determine the underlying capacity of ecosystems to provide ES to meet such demands (Villamagna et al. 2013, Wolff et al. 2015). Thus, the first step in understanding how changes in ecosystems will affect human wellbeing is to account for changes in the capacity of an ecosystem to provide ES (Haines-Young and Potschin 2010, Martinez-Harms et al. 2015).

THE TEMPORAL DIMENSION OF ECOSYSTEM SERVICE INTERACTIONS

Facilitating the rapid adoption of the ES approach in management and policy are many recent advances in the science of ecosystem services. Our ability to map, inventory, and evaluate the capacity of landscapes to provide ES has markedly improved in recent years (Fisher et al. 2009, De Groot et al. 2010, Syrbe and Walz 2012, Diaz et al. 2015), yet many practical and theoretical challenges remain (Carpenter et al. 2009, Bennett et al. 2015, Guerry et al. 2015). A key interest now is to uncover the mechanisms by which multiple services interact (Kremen 2005, Qiu and Turner 2013). ES interactions, such as tradeoffs among multiple ES, have been described conceptually (Bennett et al. 2009, Kline and Mazzotta 2012, Cavender-Bares et al. 2015) and observed based on spatial correlation (Willemen et al. 2010, Qiu and Turner 2013), but the mechanisms of interaction that lead to tradeoffs are rarely empirically examined (Wong et al. 2014). In particular, the development and persistence of tradeoffs along temporal gradients are understudied (Cavender-bares et al. 2015). The temporal dimension of tradeoffs is key for assessing sustainability of ES and for predicting how management actions to enhance some specific ES such as food or timber can interact to change entire sets of ES —herein termed ES bundles (Carpenter et al. 2009, Steen-Adams et al. 2015, Cavender-Bares et al. 2015, Guerry et al. 2015).

ES dynamics are particularly important in managed forest landscapes where periodic timber harvesting events drive temporal cycles of disturbance, forest regrowth and ES recovery. The distinct temporal interactions of forest ES, and the prevalence of these interactions in managed forests worldwide, make it an important system in which to study ES interactions and their change over time. Furthermore, a well-established body of theory and methods within the domain of forestry (e.g., forest ecology, stand dynamics, management tradeoffs) means that forests are a model system for understanding ES interactions over long timeframes (Oliver and Larson 1990, Franklin et al. 2002, Bauhus et al. 2009, Grêt-Regamey et al. 2013).

KNOWLEDGE GAPS FOR MANAGING FOREST ECOSYSTEM SERVICES

Interest to sustainably manage forest ES —which underpin the livelihoods of 1.6 billion people worldwide (IUCN 2007)— is rapidly growing. An international convention, the Rio Earth Summit of 1992, first introduced principles to include biodiversity and indigenous cultural resources in forest management (Bunnell and Dunsworth 2010). In 2005, The Millennium Ecosystem Assessment provided impetus to further incorporate diverse ecological, socio-cultural, and economic values into forest management through development of indicators for measuring ES (MA 2005, De Groot and Van der Meer 2010). However, amidst momentum for sustainable management of ES, several knowledge gaps impede implementation.

Among terrestrial ecosystems, society perceives forests as particularly important for the diverse services they provide, yet linking societal appreciation of forests to specific structures or compositions, that can be used as indicators in management is a persistent challenge. Among all emerging paradigms for sustainable ES management, such as those emphasizing greater First Nations participation in land-use planning, indicators are needed for inventory, mapping and predicting changes in ES.

Another important gap is to better understand timeframes of ES recovery in degraded or logged forests —now comprising nearly 65% of forests globally (FAO 2010). Considerable research in tropical regions has identified that recovery of tropical forest structure and composition is rapid, sometimes reaching baseline levels after 60-80 years (Chazdon 2008, Edwards et al. 2011, Goldstein 2015). In contrast, loss of forests with characteristically long-lived tree species, may impart permanent losses (Lindenmayer et al. 2014), though, few studies have captured recovery timeframes beyond 100 years (but see Wells 1996, Gerzon et al. 2011, LePage and Banner 2014, Freund et al. 2015). Furthermore, no study to date has developed a set of ES indicators and linked changes in forest structure to track the long-term recovery of a complete bundle of ES towards baseline condition. Identifying the recovery of ES is needed to inform the persistence of impacts from forest harvesting, thus providing a means to define forest harvesting tradeoffs and to predict potential consequences of alternative decisions that may affect ES.

Considerable uncertainty also surrounds the distributional occurrence of ES across heterogeneous forested landscapes (Andrew et al. 2015). Local site conditions influence plant species composition and productivity, therefore likely affecting forest ES and their recovery patterns. For example, small areas such as riparian corridors may contain larger, faster growing trees than less productive upland sites, and be important for ES such as carbon storage, fish habitat, and culturally symbolic wildlife species. Local differences in vegetation growing conditions are incorporated into nearly all aspects of forest research and forestry planning (Price et al. 2009, Thompson and Gergel 2008). Meanwhile, ES assessments often generalize over such differences by relying on broad-scale forest cover mapping to predict ES (Eigenrod et al. 2010). An improved understanding of differences in ES over heterogeneous landscapes is needed to identify potential ES hotspots such as riparian areas and to improve accuracy of assessments.

Three core knowledge gaps impeding efforts to sustainably manage forests ES are thus: (1) being able to account for and maintain the full set of services people receive from forests, by using indicators to identify ES of ecological, socio-cultural and economic importance (De Groot and Van der Meer 2010, Patterson 2014), (2), empirically tracking ES recovery towards baseline condition for improved prediction of forest harvesting impacts and (3) understanding the distributional occurrence of ES across heterogeneous landscapes to inform planning and to identify key conservation areas. In this thesis, I aim to gain insights and develop practical tools to address these three core challenges, using forests on the west coast of Vancouver Island, BC, Canada as my study system.

STUDY SITE RATIONALE AND SOCIAL-ECOLOGICAL CONTEXT OF VANCOUVER ISLAND, BC, CANADA

In the humid climate on the west coast of Vancouver Island, BC, Canada, stand-replacing disturbances such as fire are rare (fires occur at 700-6000 year return intervals), and very old forests develop. Forests are mainly composed of coniferous tree species: western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*), Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), and western red-cedar (*Thuja plicata*). These species can live more than 1000 years and reach more than 80m in height in old-growth forests, which are locally defined as >250 years old (Parish and Antos 2004, Mackinnon 2003). Old-growth forests develop a complex structure including presence of large trees, large dead trees, high accumulations of woody debris, and a heterogeneous canopy that transmits light down to understory plants (Kimmins 2003).

Vancouver Island, BC, Canada has rugged mountainous topography and vegetation varies according to climatic gradients classified as per the BC Biogeoclimatic Ecosystem Classification (BEC, Meidinger and Pojar 1991). In this thesis I focus on coastal forests along western and northern Vancouver Island in the maritime (CWH vm1) and hypermaritime zones (CWH vh1).

Prior to European settlement, old growth forests covered most of western Vancouver Island, BC, Canada, and provided multiple ES to a substantial population of First Nations inhabitants (Mackinnon 2003). First Nations harvested vast amounts of wild edible berries from understory plants, stripped the bark of cedar trees to weave rope and clothing, and selected large cedar trees as logs to build ocean-going canoes. In addition to providing many ES, the old-growth forests sustained a high diversity of plants and animals (Bunnell et al. 1999, Pollock and Beechie 2014, Burger et al. 2010). The old-growth forests also contain high stocks of the provisioning service of timber, which quickly became a mainstay in the BC coastal economy following European settlement in the late 1800's. Forest harvesting became increasingly widespread with the advent of industrial clear-cut methods (Green 2007) and throughout much of the 1900's the main policy aim in coastal BC forest management was to sustain the rate of timber provisioning. The majority of old-growth forests on Vancouver Island, especially at lower elevation productive sites, are now young and recovering stands (Mackinnon 2003). Recovering second-growth forests have a reduced, relatively homogenous structure that lacks many habitat niches found in old-growth forests (Bunnell et al. 1999, Burger et al. 2010). Also, previous studies have documented that forest harvesting can result in reduced ecological functions linked to ES, such as slope stabilization (Jakob 2000, Guthrie 2002), regulation of environmental quality in salmon spawning streams (Hartman et al. 1996), forest carbon storage (Wells and Trofymow 1997), cultural cedar stands (Green 2007, LePage and Banner 2014), and provision of non-timber forest products (van Kooten and Bulte 1999). Despite knowledge of the impacts of forest harvesting on ecological functions related to ES, few studies have tracked ES recovery.

Beginning in the 1980's, initiatives from concerned local as well as international communities motivated a shift in BC forest policy towards managing a broader set of ES (Bunnell et al. 2003). Conservation of biological diversity became an important objective (Bunnell et al. 1999). Recognition of First Nations rights and title is increasing today (*Tsilhqot'in Nation v British Columbia*, 2014 SCC 44) and they mandate sustainable management of cultural cedar resources (Hoberg and Morawski 1997, Haida Gwaii Strategic Land Use Agreement 2007). A highlight among these rapid shifts in policy is the recent implementation of ecosystem-based management over 5 million ha of coastal forest in northern BC, Canada, which prioritizes maintenance of ecological integrity and seeks to ensure a diversity of options for future human livelihood (Price et al. 2009). New market opportunities have opened up, such as carbon credit agreements and international trade in non-timber forest products (Hobby et al. 2010). However, local forest management is now challenged by the key knowledge gaps I have outlined above facing sustainable management of forest ES.

RESEARCH OBJECTIVES

My fundamental goal in this thesis is to build an improved understanding of how multiple ES recover following forest harvest in the coastal temperate forests on western Vancouver Island, BC, Canada. Within this broader goal, my three specific objectives are to:

1) Build a set of indicators for measurement and tracking of ES based on structural attributes of forest stands. (Chapters 1 and 2).
2) Track the recovery timeframes and trajectories for multiple ES spanning from immediately post-harvest towards old-growth condition. (Chapter 1).
3) Contrast old-growth baseline ES and recovering forest ES in riparian and upland forest types. (Chapter 2)

In Chapter 1, I use a chronosequence approach (with available governmental databases) to track the post-harvest recovery of eight ES. I assess how recovery timeframes and trajectories differ for eight distinct services and for the entire bundle of ES. By combining the ecosystem services framework with the chronosequence approach, I am able to track recovery over a 212-year period, thus gaining insight into recovery of ES provided by old-growth forests. In this chapter (as well as the subsequent chapter), I develop and refine a novel set of indicators to measure and track changes in multiple services, including relatively understudied services such as edible berries and First Nations traditional use of cedar.

In Chapter 2, with field assistance from a First Nations carver, I contrast ES in later seral forests (as an ES baseline) against ES in second-growth (recovering) forests, in two distinct forest types: riparian zones and upland forests. Local site conditions vary substantially in forested landscapes, and are a critical variable for assessing ES because they affect productivity of tree growth, disturbance regimes, and soil edaphic conditions that shape the unique vegetation patterns on forest landscapes. By comparing ES recovery in distinct forest types I build a broader understanding of ES recovery than is gained solely in Chapter 1. Furthermore, through field work with local First Nations I incorporate local knowledge and more direct field sampling of ES, to refine my set of indicators for measuring multiple forest ES.

Given the diverse ecological, socio-cultural and economic values expressed for coastal forests on Vancouver Island, BC, Canada, as well as the legacy of past forest management, this is a compelling region to study ES recovery. By studying ES recovery in these long-lived forests, I can assess the temporal dimension of interactions between timber harvesting and other ES at a timeframe never previously examined —at the scale of 250 years— thus providing insights into the persistence of tradeoffs over long timeframes for multiple ES.

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CHAPTER 1 CONNECTING STATEMENT

To understand how ecosystem services recover after logging, I start by empirically modeling ES recovery using a chronosequence spanning forests from 0 to 250 years old. By examining the influence of forest age on multiple ES, I establish a general empirical framework for predicting the longterm outcomes of forest harvesting. Part of my objective is to assess the impacts and the persistence of ES tradeoffs at the stand-level caused by forest harvest. Identifying the time frames of ES recovery will inform appropriate strategies such as adjusting harvest rotation timing (i.e., the time forest regrows before re-harvesting) to maintain provision of other, non-timber ES. The chronosequence method, a widely utilized space-for-time substitution technique in ecology, allows me to study changes in forest structure over much longer time frames than typically addressed in ES research.

CHAPTER 1: RECOVERY TRENDS FOR MULTIPLE ECOSYSTEM SERVICES REVEAL LONG-TERM TRADEOFFS FOLLOWING FOREST HARVEST IN TEMPERATE RAINFORESTS

ABSTRACT

Most ecosystem services (ES) research focuses on patterns of provision at the current time, and the field generally lacks long-term perspectives on how trade-offs occur and persist over time. In western North America, harvesting old-growth forests (forests >250 years old) yields timber but results in declines in other ES such as carbon storage, wild edible foods, and large trees with ecological and cultural value. Tradeoffs from forest harvest, and their importance through time, remain difficult to quantify and manage as some ES may recover quickly, while others recover slowly or not at all in second-growth forests. I used a 250-year forest chronosequence to estimate recovery of a coastal temperate forest's capacity to provide ES on Vancouver Island, BC, Canada. I empirically estimated changes in eight ES [wood volume, carbon storage for climate regulation, potential nesting platforms used by an emblematic old-growth associate bird species the marbled murrelet (*Brachyramphus marmoratus*), forest floor habitat services provided by coarse woody debris, canopy habitat services provided by large dead trees, large heritage trees, wild edible berries, and large redcedar (*Thuja plicata)* trees used traditionally by First Nations for carving canoes and totem poles] based on forest structural features across the recovery period. ES recovery followed u-shaped or s-shaped trajectories with varying times to reach baseline (i.e. old-growth) condition. Some services remained high post-harvest (e.g., habitat services of coarse woody debris) or recovered quickly in the first 100 years (e.g., carbon storage). However, cultural ES such as large cedar, followed s-shape curves with 200+ year delays in recovery. My empirical models of ES recovery help characterize long-term dynamics of harvest tradeoffs and lead towards multi-ES management solutions. Options include conserving old-growth forests with high levels of specific ES, working with First Nations to inventory cultural ES such as large cedar, or lengthening harvest rotations. Overall, my results demonstrate the importance of tracking temporal tradeoffs over long timeframes.

INTRODUCTION

Tradeoffs arising from the management of ecosystem services (ES) have recently become a focal point in conservation discussions. While advances in ES mapping have helped identify the spatial location and probable causes of tradeoffs, linking research to inform management of the development and persistence of tradeoffs over time could be improved (Tallis et al. 2008, Carpenter et al. 2009, Cavender-Bares et al. 2015, Renard et al. in review). In western North America, harvesting of old-growth forests (i.e. forests > 250 years old) and converting them to managed timber production areas has caused widespread declines in the economic, cultural, and spiritual sustenance people derive from these forests (Oliver 2014, Franklin and Johnson 2011). However, characterizing the tradeoffs for multiple ES requires taking into account the temporal dynamics of forest recovery, during which some ES may recover. Subsequent timber harvests (or rotations) timed to maximize timber production range from 50-100 years in western North America, whereas the recovery of some ES may take much longer (LePage and Banner 2014). As a result, understanding ES recovery is needed to unravel the complex temporal dimensions of tradeoffs and create management strategies that sustain multiple ES.

Empirical analysis of multiple ES trajectories over long timeframes has rarely been accomplished (but see Beier et al. in press and Renard et al. in review). Meta-analyses over short time frames (i.e. duration of a restoration monitoring program), show that ES recover along varying asymptotic, linear, unimodal, and stochastic trajectories (Barral et al. 2015, Bullock et al. 2011). Ecosystem recovery is generally a non-linear process controlled by the timing and rates of various ecological processes with specific conditions sometimes required for recovery to commence (Chazdon 2008, Robson et al. 2010).

As a forest is harvested and trees are removed from the site, there is a dramatic increase in the provision of timber, along with immediate to delayed declines in ecosystem capacity to provide other ES. For instance, non-timber ES such as carbon storage for climate regulation, wild edible foods, and cultural heritage experiences among large old trees may decline due to removal of trees and other biophysical forest structures, which underlie these ES. Because many forest ES are mechanistically linked to ecosystem structure, their recovery follows the structural regeneration of the forest through its successional stages. For instance, while tree growth increases timber volume in young forests (Husch et al. 2002), maturation of large trees creates cultural heritage values in old forests (Blicharska and Mikusinski 2014). Understory plants in early and late successional forests provide seasonal stocks of wild edible foods (Clason et al. 2008). Recovery of these forest structural features is driven by a sequence of processes such as tree growth, tree mortality, and understory tree regeneration (Bauhus et al. 2009, Freund et al. 2015). Because forest structural features recover from logging along non-linear and variable trajectories (Trofymow et al. 2003, Pollock and Beechie 2014, LePage and Banner 2014), I hypothesize that the ES derived from them recover along varying trajectories too.

Tracking the long-term recovery trajectories of forest ES could clarify the extent that second-growth forest —now comprising 64% of global forests (FAO 2010)— could provide ES relative to undisturbed old-growth forests (Chazdon et al. 2008, Lindenmayer et al. 2009). Given that the amount of disturbed forests continues to grow annually and that human demand for diverse forest ES is rapidly growing, efforts to resolve this uncertainty are increasing (Bauhus et al. 2010). As such, recent studies have quantified temporal tradeoffs between timber production and climate regulation (Lutz et al. in press) and between timber production and biodiversity (McCarney et al. 2008). However, empirical information is still lacking as to how bundles of ES with diverse economic, ecological and cultural values recover towards old-growth condition. In particular, the recovery of ES beyond typical forestry rotation ages (most often <100 years) is under-examined despite the clear ecological and social value of less disturbed, more pristine areas (Gerzon et al. 2011, Freund et al. 2015).

I investigated the long-term recovery of multiple ES in a region representative of North America's coastal temperate rainforests, which have been extensively harvested for timber (Franklin and Johnson 2011). I tracked a bundle of eight ES, believed to have long timeframes for recovery, including: wood volume, carbon storage for climate regulation, potential nesting platforms used by an emblematic old-growth associate bird species the marbled murrelet (*Brachyramphus marmoratus*), forest floor habitat services provided by coarse woody debris, canopy habitat services provided by dead trees, large heritage trees, and wild edible berries. I also examined culturally sacred large redcedar (*Thuja plicata)* trees used traditionally by First

Nations for carving canoes and totem poles. I used a chronosequence approach (i.e. space-for-time substitution) to estimate post-harvest recovery of ES across 212 years by examining changes in forest stand structure on Vancouver Island, BC, Canada, using government databases (Gerzon et al. 2011, Trofymow et al. 1997). Recovery was assessed relative to an old growth forest baseline, defined as the mean of 12 old-growth forest plots. Forest structural variables, including tree size, understory plants, and coarse woody debris were used as biophysical indicators to assess the capacity of forests to provide ES. My objective was to identify the timeframe and shape of long-term recovery trajectories for multiple ES following forest harvest.

METHODS

I analyzed ES recovery trajectories in three steps. First, I compiled a dataset of change in forest structure spanning a 212-year chronosequence for Vancouver Island, BC, Canada (Figure 1-S1). Second, I used forest structure attributes to estimate the capacity of eight ES throughout the chronosequence (Table 1-1). Third, I fit curves to represent the long-term recovery trajectory of each ES towards baseline condition, calculated as the mean of all old-growth plots.

Chronosequence Study Region

My chronosequence includes data from 49 forest field plots collected systematically in two prior studies. Plots were distributed throughout the coastal temperate forest range of Vancouver Island below 600m elevation (Figure 1-1). To reduce environmental variation caused by factors such as topography and soil depth I selected plots situated on mid-slope sites with vegetation characteristics reflecting regional climate, defined as the CWHvm1 01 site series as per BC BEC classification system (Meidinger and Pojar 1991; *SI Text*). Vegetation composition and structure within this ecosystem type reflect the region's cool, humid maritime climate (mean annual precipitation = 2787mm, Meidinger and Pojar 1991). Undisturbed old-growth forests are composed of a mixture of shade tolerant conifers, mainly western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and amabilis fir (*Abies amabilis*).

Table 1-1. Eight ecosystem services provided by coastal temperate forests and the biophysical indicators and method used for their estimation. SI-4 provides descriptions of each service and formulas for estimating services.

Ecosystem services	**Ecosystem services indicators (and unit of measure)**	**Forest attributes measured (from data sets)**	**Method to estimate ecosystem services**
Provisioning of food from wild plants	**Wild edible berries** (proportion abundance)	Percent cover of berry-producing plant species estimated in understory vegetation plots	**Relative abundance** estimated as the cumulative percent cover of five edible berry producing understory shrubs: *Gaultheria shallon, Rubus spectabilis, Vaccinium parvifolium, Vaccinium ovalifolium and Vaccinium alaskense*
Habitat services of forest floor	**Coarse woody debris biomass** (Mg/ha)	Woody debris >7.5cm diameter sampled along line transects	**Allometric equations** for line-transect sampling (Marshall et al. 2003) were used to estimate coarse woody debris biomass using the variables: log diameter at point of transect crossing, species and level of decay.
Habitat services of canopy	**Dead tree biomass** (Mg/ha)	Dead trees >9cm DBH* measured in tree plots	**Allometric equations** using variables tree height, DBH, and species were used to estimate and then sum the dead tree biomass components of stem wood and bark. These equations were developed for the forests of Canada (Ung et al. 2008) (See *SI-4* for Biomass calculation of dead trees with missing tops)
Regulation of global climate	**Above-ground carbon storage** (Mg/ha)	Live and dead trees >9cm DBH* measured in tree plots and Logs >7.5cm diameter sampled along line transects.	**Allometric equations** were used to estimate the biomass pools of live trees, dead trees and cwd, which are then summed together. Their summed biomass was then multiplied by a biomass-to-carbon conversion factor of 0.48 (Preston et al. 1998). Live trees (>9cm DBH) biomass calculated using allometric equations based on the variables tree height, diameter, and species to determine then sum biomass of stem wood, bark, branches and foliage (Ung et al. 2008).
Provisioning of fibre or wood	**Wood volume** (m^3/ha)	Live trees >9cm DBH* measured in tree plots	**Allometric equations** were used to estimate wood volume using the variables: tree height, DBH and species (BC Ministry of Forests 1976)
Cultural existence and bequest values	**Marbled murrelet habitat** (probability of presence)	Large canopy branches (>15cm diameter) at least >10m above the forest floor, observed in tree plots	**Presence/absence** of potential marbled murrelet nesting platforms, defined as tree branches large enough for nesting marbled murrelets (>15cm diameter located more than 10m in the air; Burger et al. 2010). One or more potential nesting platform indicates that this ES is present.
Cultural heritage resources	**Large heritage trees** (probability of presence)	Live trees of any species greater >1m DBH* measured in tree plots	**Presence/absence** of large heritage trees, where large heritage tree is defined as any tree species >1m DBH. One or more large heritage tree indicates that this ES is present.
Culturally sacred resources	**Large redcedar** (probability of presence)	Redcedar trees >1 m DBH* measured in tree plots	**Presence/absence** of large cedar, where large cedar are defined as any redcedar (*Thuja plicata*) tree >1m DBH. I based this size-threshold on the criteria specified for managing large cedar by the Haida First Nation (2007). One or more large cedar indicates that this ES is present.

*DBH = Diameter at breast height (1.34 m above ground), the standard height in BC for measuring tree diameters.

The long time span of my study introduced challenges in meeting the chronosequence assumption that all stands originated following a common disturbance (Walker et al. 2010). Most stands <125 years in age originated following clear-cut forest harvesting; however, those >125 years originated from natural disturbances (wind, fire or insects) before industrial forest harvesting had commenced in the region. To reduce potential effects arising from different types and severities of disturbance, I removed residual trees (present at 6 plots and comprising between 6-36% of total plot live tree volume) from the analysis using the same method as Gerzon et al. (2011) so that my trajectories primarily reflected recent recruitment. I retained residual coarse woody debris (cwd) in the analysis because it would not be possible to accurately identify the point that residual cwd transitions to newly recruited cwd. Also, acknowledging high abundance of cwd post-harvest is important to understand cwd trajectories in second-growth forests (Feller 2003).

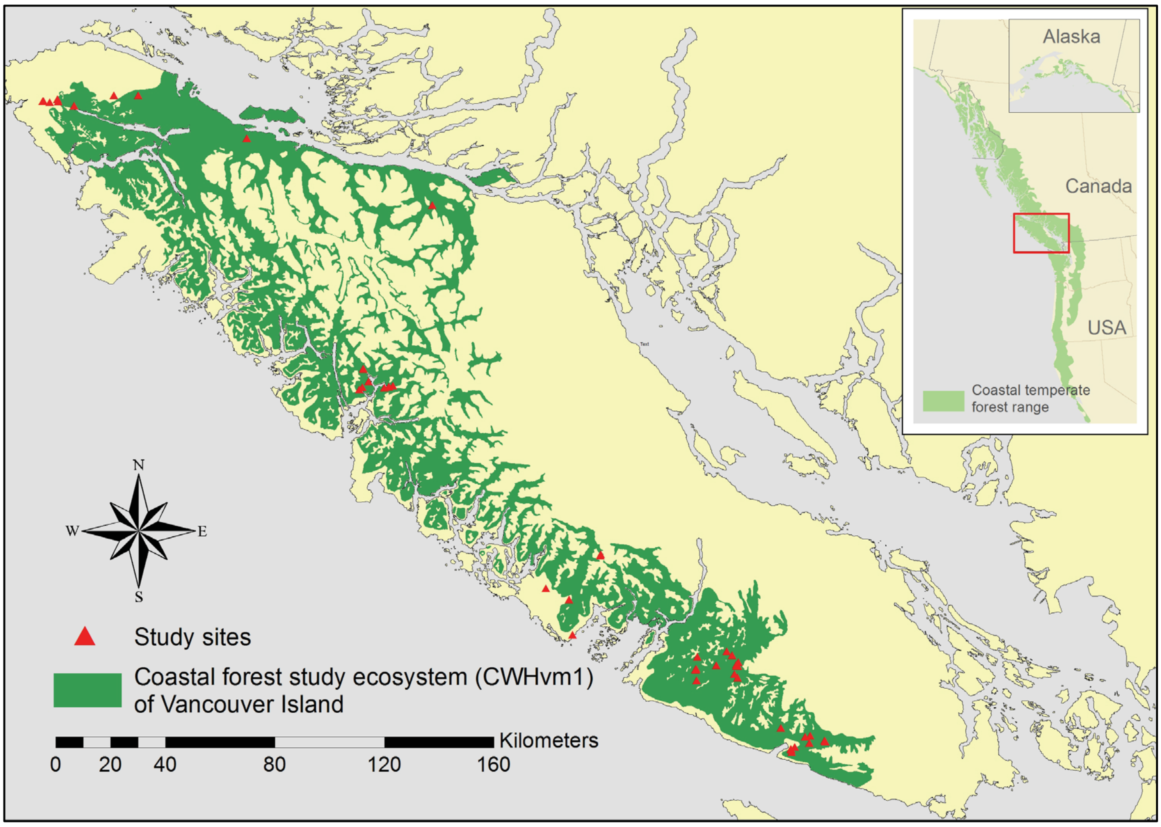

Figure 1-1. Extent of the coastal forests study area on Vancouver Island, BC, Canada, and location of study plots used in the analysis. Inset shows the approximate range of the North America coastal temperate forests.

Estimating ecosystem services

I used field data from two chronosequence studies on Vancouver Island, BC, Canada designed to track recovery of forest structure attributes across different forest ages (Figure 1-S1). Both studies used nested sampling techniques, which include overstory tree plots, understory vegetation plots, and line transect sampling following standards of either the BC Ministry of Forests or the Canadian Forest Service, which conducted the studies. Attributes examined in both studies included: understory plant species by percent cover; trees by species, size class and health; and coarse woody debris by size class species and decay state (for details see Trofymow et al. 1997 and Gerzon et al. 2011). I used these data as biophysical indicators to estimate provision of the eight ES at each plot (Table 1-1). I defined old-growth forests as those exceeding 250 years, based on the standard definition used on coastal BC (Gerzon et al. 2011).

Analysis of ES Recovery Trajectories

I used a flexible statistical modeling approach to best accommodate different response variable formats (e.g., proportional, presence/absence, continuous data), recovery trajectories, and heteroscedasticity. Also, use of transformations to linearize the data was deemed not appropriate since my primary research objective was to identify the shape of the recovery trajectories so I used generalized additive models (GAM). GAM's fit phenomenological smooth lines using regression splines, a fitting technique that divides the gradient of the x-axis into intervals, fits a cubic polynomial function to each interval, and then merges the intervals together to form a continuous smooth (Zuur et al. 2009). To fit GAM's I used the mgcv package in R, which uses cross-validation to control the number of intervals and hence the degree of smoothness in the model fits to avoid over fitting (Wood 2006).

When fitting GAM's, I selected a probability distribution to model each ES based on the type of response variable (continuous, proportional and presence-absence). I used a binomial logistic curve with a cloglog link to model presence-absence of large heritage trees, large redcedar and marbled murrelet nesting platforms. The cloglog link performs well for dependent variables with more zeros than ones, as was the case for these services (Zurr et al. 2009). I used a beta distribution with a logit link for wild edible berry-producing plants, which were recorded as proportional data with a minimum of zero and a maximum of one (Eskelson et al. 2011). Finally, I used gamma distribution with a square root link for wood volume, carbon storage, dead tree biomass and coarse woody debris because these are recorded as continuous variables. Also, in the gamma distribution negative values are not allowed, and the variance parameter increases in proportion to the mean, which helped accommodate heteroscedasticity. Using appropriate probability distributions improved model fits, which I validated by graphically assessing normality of the residuals as well as scatter plots of the residuals vs. the fitted values.

To represent the recovery trajectory of each ES towards baseline condition, I calculated and plotted the old-growth mean ES values for visual reference. I plotted 95% confidence intervals around both the recovery trajectories and the mean old-growth levels. To visualize recovery of ES bundles I standardized the predicted model fits for each ES relative to its old-growth mean and then displayed them on a polar plot. All analyses used R (R Core Team 2011).

RESULTS

ES recovered along varying non-linear trajectories and over markedly different timeframes, with incomplete recovery for some services at 212-years (Figure 1-2, Table 1-S1). Carbon storage (Figure 1-2, panel a), wood volume (Figure 1-2, panel b) and dead tree biomass (Figure 1-2, panel c) recovered along sigmoidal trajectories with maximum recovery rates, identified by inflection points, at around 65 years post-harvest. ES reached the old forest baseline at approximately 210 years (carbon storage), 160 years (wood volume), and 140 years (dead tree biomass). In contrast, wild edible berries (Figure 1-2, panel d) followed a U-shaped trajectory and achieved old-growth baseline levels nearly 212 years after harvest. Recovery of the marbled murrelet potential nesting platforms (Figure 1-2, panel f) and large heritage trees (Figure 1-2, panel g) also followed sigmoidal curves but with maximum recovery at approximately 166 years (marbled murrelet habitat) and 212 years (large heritage trees). In contrast, I detected no effect of forest age on coarse woody debris biomass (Figure 1-2, panel e; $p = >.10$) or large cedar used by First Nations (Figure 1-2, panel h; $p = >.10$). Despite being present in only 2 of the 37 recovering forest plots, large cedar was present in 7 of the 12 old forest baseline plots.

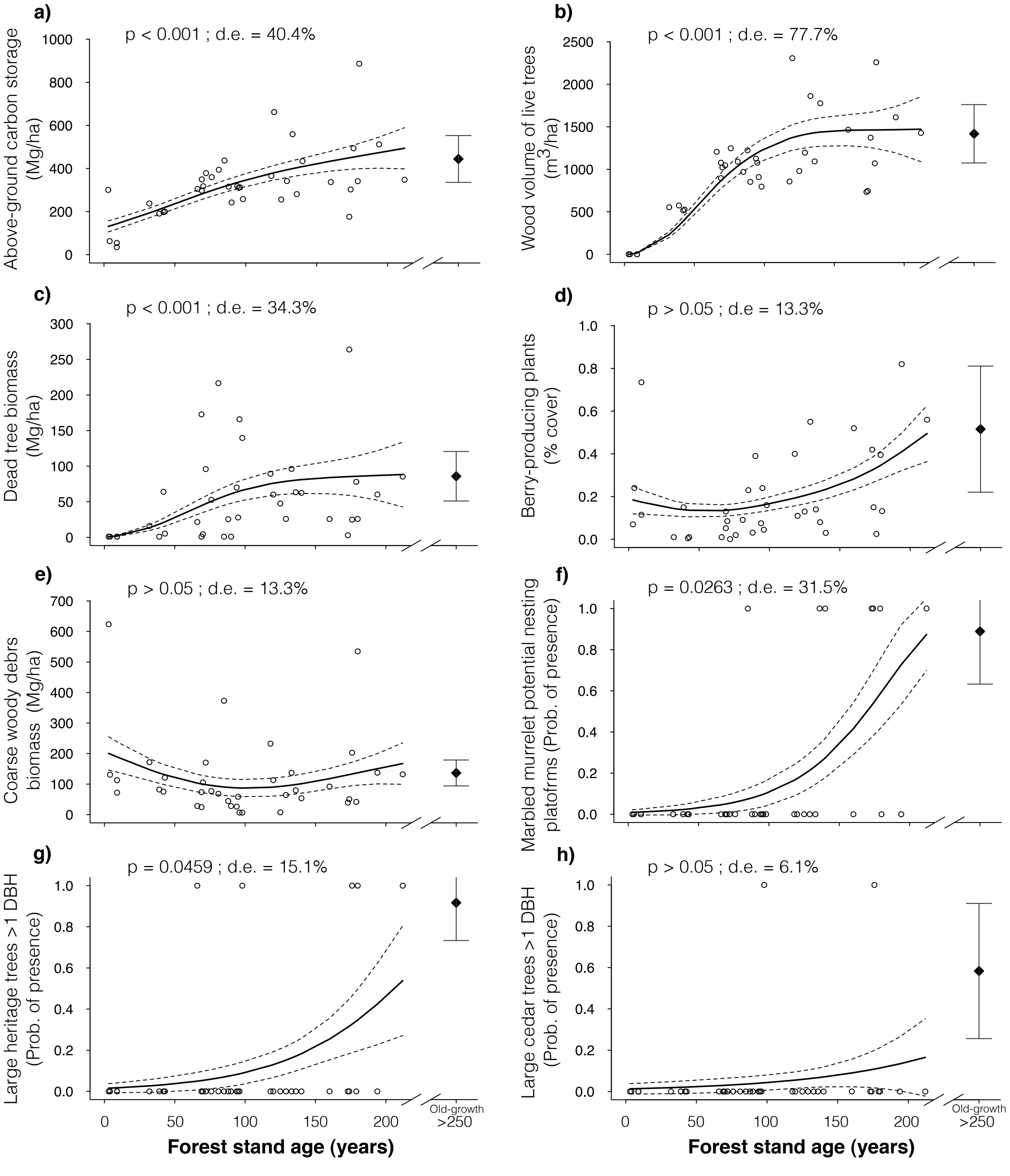

Figure 1-2. Forest ecosystem services (ES) recover along varying trajectories over 212 years towards a baseline of old-growth stands (>250 years age). Panels (a) through (e) estimate ES recovery using indicators in units relevant to each service (e.g., Mg carbon/ha). Panels (f) through (h) show recovery of ES defined as probability of occurrence. Confidence intervals (.95) are plotted as dashed bands around the fit line and as error bars around the old-growth mean.

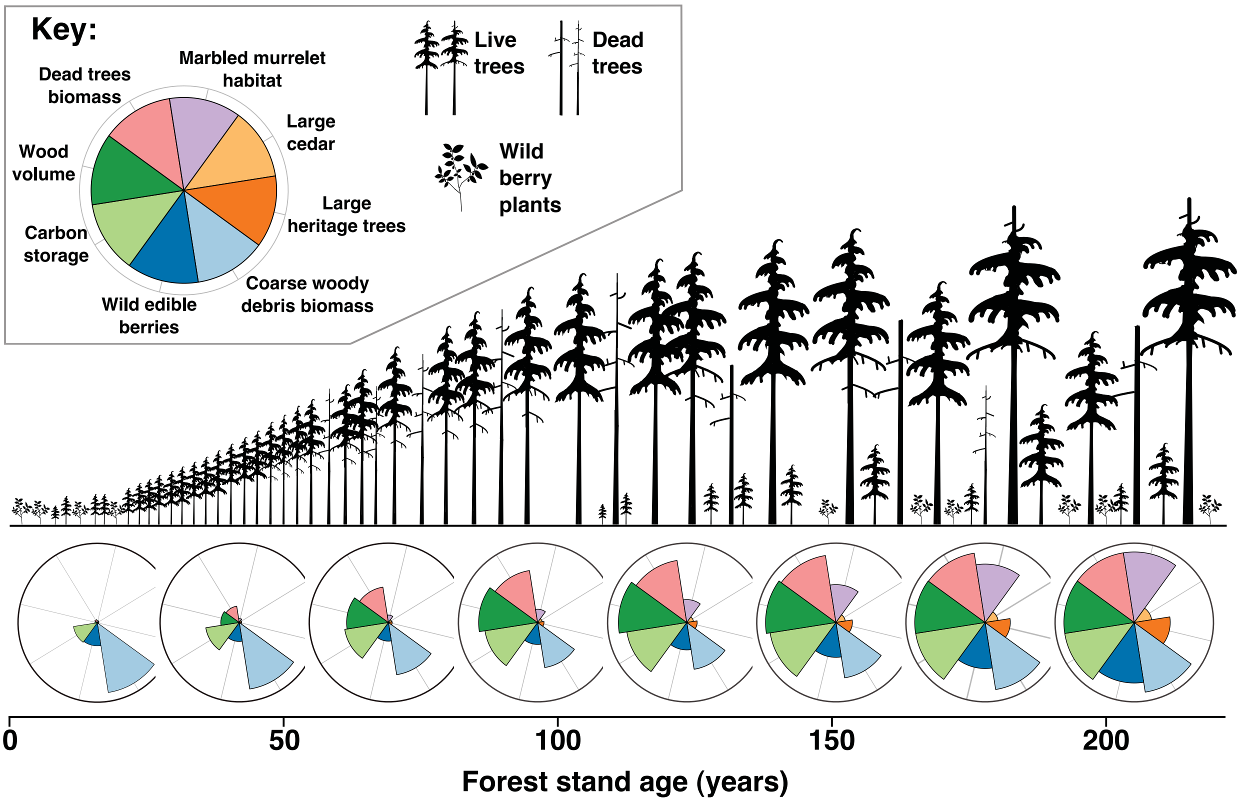

Figure 1-3. A bundle of ecosystem services recovers gradually following forest harvest driven by the recovery of forest structure. This figure was produced by extracting values from models fits of ES recovery trajectories then standardizing them relative to mean old-growth baseline value.

Overall, when recovery trajectories were standardized relative to old-growth baselines, it becomes evident that original old-growth ES bundles recovered gradually throughout the 212-year recovery period (Figure 1-3). Bundle recovery began with wood volume and carbon storage at about 40 years, followed by dead tree biomass after about 70 years. In contrast, other services such as marbled murrelet habitat, large heritage trees and wild edible berries begin to recover at varying time frames more than 100 years post-harvest such that the bundle continues to change throughout the 212 year period.

Along each ES recovery trajectory, I observed that variance increased with forest age (Figure 1-2). Variance increased with forest age for continuous variables such as carbon storage (Figure 1-2, panel a), wood volume (Figure 1-2, panel b), dead tree biomass (Figure 1-2, panel c), and wild edible berries (Figure 1-2, panel d). Variability of edible berries was also high in regenerating forests. Variability in recovery of presence/absence such as marbled murrelet potential nesting platforms (Figure 1-2, panel f), large heritage trees (Figure 1-2, panel g), and large cedar (Figure 1-2, panel h), were intermittent during the recovery period.

DISCUSSION

The temporal dimension of tradeoffs from forest harvest

The variable and prolonged rates of ES recovery that I observed indicate that some tradeoffs from harvesting old-growth forests persist for decades, if not centuries, but eventually dissipate, while others may continue indefinitely. Declines in the old forest associated ES, marbled murrelet habitat, large heritage trees, and edible berries, that result from timber harvesting persist for at least 100 years. The cultural ES of large cedar was mostly absent in recovering stands, suggesting that this tradeoff may persist for centuries or that specific conditions may be required for recovery (Kimmins 2008). Furthermore, old forest associated ES had recovered only partially or not at all by the time wood volume reached its maximum rate of increase, which indicates the biologically optimal timing for harvest rotation. Maximum rate of increase for wood volume occurred at around 65 years in my dataset, suggesting optimization of timber production would lead to repeated cyclical declines in other services and may preclude recovery of some ES. These results highlight that site-level tradeoffs depend not only on the immediate impacts caused by forest harvesting on multiple ES, but also they depend on the persistence of these impacts during forest recovery. To maintain the multiple ES provided in older forests would require either a larger landscape in which some area is not cut or a considerably longer rotation time (Lindenmayer et al. 2014). The persistence of tradeoffs in some ES that result from timber harvest highlights the importance of proactively identifying ES interactions before they cause potentially irreversible losses in some ES (Rodriguez et al. 2006, Lindenmayer et al. 2011).

Recovery of a bundle of ES as a multi-stage process, driven by changes in forest structure

My results show that recovery in a bundle of ES in coastal temperate forests is a multi-stage process that likely spans more than 212 years following forest harvest. In the initial stage of recovery, habitat ES (from coarse woody debris) provided by biotic legacy structures and provisioning ES (wild edible berry plant) are present but decline with time. Within decades, a subset of provisioning (wood volume), regulating (carbon storage), and habitat services (from dead trees) begin to recover rapidly due to biomass accumulation in growing trees. A third, much more prolonged, stage occurs as the mature forest structurally transforms into an old-growth forest ecosystem, thus initiating recovery of culturally important ES. For example, large heritage trees recover as tree diameters increase, and habitat for at-risk marbled murrelets recovers as large branches, required by murrelets for nesting habitat, develop (Ishii and McDowell 2002, Van pelt and Nalini 2004). Wild edible berries also recover during this prolonged third stage, likely due to tree blowdowns that open the canopy and create growth conditions for understory plants. These stages I describe reference known processes of structural development (e.g., Franklin et al. 2002, Bauhus et al. 2010, Lohbeck et al. 2014). Additional stages of recovery may continue well beyond the time period observed in my study, as trees in this area can be older than 1400 years (Parish and Antos 2004). For example, the presence of cultural ES (large cedar) appears largely limited to stands older than 212 years.

Lagged large cedar recovery warrants special management attention

The effects of long-lasting, persistent tradeoffs may be felt by some beneficiaries more than others, which may warrant special management attention (Howe et al. 2014). Of note, the absence of large redcedar in recovering stands suggests a potential dearth of large cedar for traditional purposes in areas of coastal BC where most old-growth has been harvested and converted to second-growth. Declines of redcedar observed along the north coast of BC have recently been highlighted as a salient concern for management due to the high economic, cultural and spiritual values associated with this species (Banner and LePage 2014). On northern Vancouver Island, the restocking of redcedar following clear-cut has been a long-term management challenge (Sajedi et al. 2012), perhaps in part because the successional niche of redcedar, and other factors needed to regenerate healthy stands of large redcedar, remain unclear (Daniels 2000, Kimmins 2008, Weber 2014). The persistence of tradeoffs that I found, combined with the cultural importance of this species, indicate that long-term large cedar planning might be an important next step for forest management in this region.

Variability in recovery trajectories increases with time

I observed that increasing variance of ES provision with forest age is a distinctive characteristic of ES recovery trajectories in BC coastal temperate forests, which has important management implications. The highly intermittent presence of cultural ES, such as large cedar in recovering stands, are likely caused by varying site conditions during initial forest establishment and stochasticity in seedling regeneration, which influence trajectories throughout a stands development (Swanson et al. 2010, LePage and Banner 2014, Weber et al. 2014). The overall pattern of increasing variance, which appears to be caused by increasing structural heterogeneity with forest age, suggests that forest age may be a reasonably accurate indicator of ES provision for young forests, but is a poor indicator in older forests. Efforts to steward ES through preserving old-growth (e.g., Lindenmayer et al. 2014) will be more successful if they select areas confirmed to have high levels of desired ES, rather than selecting areas based on age alone. My observations of natural variability highlight the value of long-term empirical datasets to empirically characterize variation in ES recovery and identify practical management solutions.

The limited potential of forest restoration to overcome long-term tradeoffs

Restoration can manipulate key structural development processes, such as tree seedling establishment, to promote ES recovery, but may have limited effectiveness for slowly recovering ES. Tree planting and other silvicultural treatments for stand establishment can promote rapid biomass accumulation and thus speed recovery of wood volume and carbon storage. Restoration actions aimed at increasing heterogeneity of mature forests, such as tree thinning and tree topping to create dead trees, could speed recovery of old-growth related ES (Pollock and Beechie 2014). However, this is costly and is generally only done in key habitat areas (Götmark 2013). Furthermore, care should be taken with restoration actions because silvicultural actions aimed to increase timber such as brushing (clearing understory plants), fertilization, or planting with exotic species could delay recovery of other services and lead to further tradeoffs among ES (Bauhus and Schmerbeck 2010). Conservation areas or retention of tree patches during harvest (Gustafsson et al. 2012) may be a more effective alternative to repairing damaged stands, in terms of maintenance of the provision of multiple services. Managers can reduce risk by conserving large areas rather than retaining small patches where isolated tree patches are subject to catastrophic wind blowdown, such as on northern Vancouver Island, BC, Canada (Mitchell 2012). The difficulty of restoration together with the long time frames of recovery emphasize that proactive policies in forest management are required to sustain bundles of ES in coastal temperate forests rather than retrospective ones that try to speed recovery in degraded forests.

CONCLUSION

I determined that ES recover at unique rates and along varying non-linear trajectories following timber harvest in coastal temperate forests. Old-growth forests had the highest capacity to provide most ES, while regenerating stands had the lowest capacity to provide all ES except for coarse woody debris. The immediate loss of some services following conversion of old-growth forests into recovering managed stands dissipated over time, but in a highly non-linear and uneven manner, affecting some services, and potentially some stakeholders, more than others. Forest managers can use knowledge of ES recovery trajectories and their variability to inform management decisions and maintain multifunctional forests. Compelling options for ES management include conserving older forests with their original bundles of ES, emphasizing inventory of particular services such as large redcedar, or lengthening harvest rotations. Uncovering long-term tradeoffs among ecosystem services can help define drivers of change to ES bundles and lead to better-informed ecosystem management.

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SUPPLEMENTARY INFORMATION

SI 1. Study area social ecological context

This study takes place on Vancouver Island, BC, Canada, where the slow and pronounced structural changes that occur during forest growth have been the subject of considerable forestry and conservation research (Clayoquot Sound Scientific Panel 1995, Trofymow et al. 1997). Multiple stakeholders, including First Nations, forestry licensees, and local communities with diverse forest-dependent livelihoods and values, make Vancouver Island an important region in which to evaluate multiple ES and their recovery from logging. Forest harvesting in the region initiated and became increasingly intensive during the 20th century, until legislation in the mid 1990's led to a diversification of management objectives (Hoberg and Morawski 1997).

SI 2. Study area ecosystem classification

My study of ecosystem services recovery focuses on the Coastal Western Hemlock Very Wet Maritime ecosystem (CWH vm1) as defined by the BC Biogeoclimatic Ecosystem Classification System. CWH vm1 roughly corresponds to the *Tsuga-heterophylla* ecosystem classification of Oregon and Washington (Mackinnon and Trofymow 1998). Forest fires are rare in the humid environment, and natural disturbances are typically caused by low-severity wind, fungal or insect disturbances. This lack of severe disturbance results in very old stands (>1000 years in age, Parish and Antos 2004), at which point forest-stands exhibit distinctive structural features including large trees, diverse understory plant communities, large pieces of woody debris, and a vertically complex canopy (Wells et al. 1998, Kimmins 2003). However, the areal extent of old-growth in this ecosystem has markedly declined as most productive forests have been logged and supplanted by second-growth forests less than 100 years old (Meidinger and Pojar 1991).

SI 3. Data sets

I obtained data from two previous studies on Vancouver Island, which surveyed the structure of forest stands with different ages (Figure 1-S1). The following forest structural variables were recorded: understory plant species by percent cover, trees by species and size class, and coarse

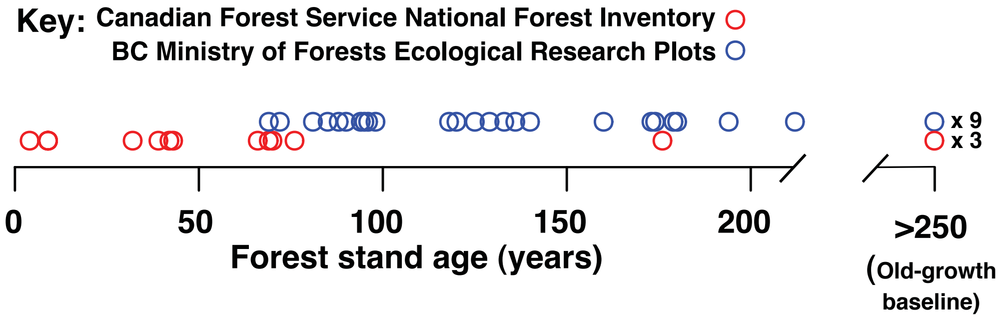

Figure 1-S1. Forest stand ages of field plots used in chronosequence analysis obtained from existing government databases.

woody debris (cwd) by size class, as well as species and decay state (for details see Trofymow et al. 1997, and Gerzon et al. 2011). Ecosystem classification was done using diagnostic vegetation, soil and site physiographic characteristics. Stand age was determined by tree ring counts of several dominant, non-residual trees in second-growth stands and based on qualitative indicators in the old-growth stands.

I merged the two studies, which collected the same data on forest structure, to create a continuous chronosequence of forest stands on Vancouver Island covering forest development over a 212-year period. All forest stands aged 4-76 years old (n=12) were derived from the Canadian National Forest Inventory (NFI) (Trofymow et al. 1997), which contrasted the structure of young forest stands (n =12) with that of old-growth forest stands (1 site is 176 years, 3 are >250 years). Data on older forest stands, aged 70-212 years (n=24), were derived from a ‘BC Ministry of Forests Ecological Research Plot’ study (Gerzon et al. 2011) which analyzed the structural transition from second-growth to old-growth forests (>250 years, n=9). The old-growth from both studies were pooled to represent a baseline condition of unlogged forests.

SI 4. Estimating locally important forest ecosystem services

Through literature review, I identified key forest structural features that determine the forests capacity to provide locally valued ecosystem services, including: trees by species size class and abundance, understory plants, and coarse woody debris by species, decay state, and abundance. These forest structural features were recorded in both data sets. I used them as biophysical indicators to estimate ES in units relevant to each ES for each study site within my chronosequence as follows (Table 1).

Large cedar as an ES were indicated by redcedar (*Thuja plicata*) trees > 1m diameter at breast height (DBH); diameter measured at 1.3 m above ground). The indicator calculated is the presence or absence of large cedar. I based this size threshold on the size criteria specified by the Haida First Nation (Haida Gwaii Strategic Land Use Agreement 2007). Large cedars are a sacred traditional resource used for traditional housing or totem poles and canoe carving by BC coastal First Nations. As a result of logging and reduced abundance of this resource, there is increasing efforts to manage large cedar as a sustainable resource to the north of Vancouver Island, BC, Canada, but relatively fewer efforts to date on the island.

Large trees as an ES were indicated by trees >1m DBH of any species. The indicator calculated is the presence or absence of large trees. I based this size threshold by adopting the size criteria specified by the Haida First for large redcedar (Haida Gwaii Strategic Land Use Agreement 2007). Large trees represent a more general case of cultural heritage ecosystem services than redcedar alone. Heritage trees are common in other regions around the world (Blicharska and Mikusinski 2014) including locally in BC (Kimmins 2003). Large diameter trees are likely to have the highest cultural value near population areas where more people can interact with them.

Coarse woody debris biomass was indicated by logs on the ground >7.5 cm in diameter. The indicator calculated is the cumulative biomass of fallen trees that intersected the line transects as estimated using equations developed for the line-transect method (eq 1-S1, Marshall 2003),

$$biomass\ ha^{-1} = \frac{\pi^2}{8 \times L} \Sigma \frac{d_k^2}{cos\lambda_k} \qquad \text{(eq. 1-S1)}$$

where L is the transect length, d is the diameter of log k at the point of crossing the transect, and $cos\lambda$ is the cosine of the angle of log k away from horizontal. Coarse woody debris supports the provision of numerous other ES. For example, they are a substantial store of carbon, and have numerous functions in regulating flows of water and soil, especially in riparian zones and cwd provides habitat for a range of aquatic and terrestrial wildlife, including rare species (Pollock and Beechie 2014).

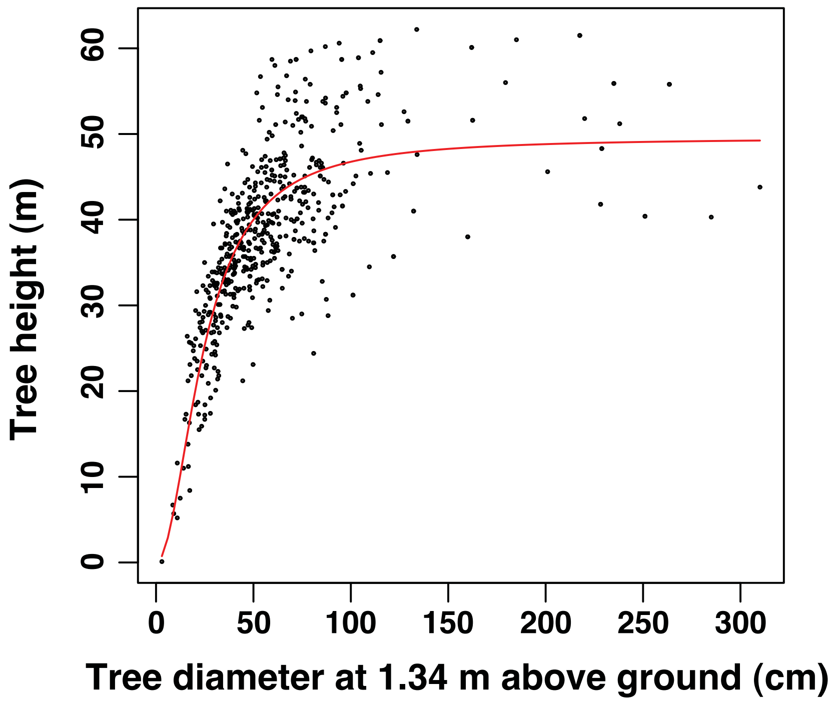

Figure 1-S2. A regression of tree height on DBH based on all live trees with intact tops (n = 534). I used this to calculate the biomass of dead trees with missing tops by estimating their theoretical height and biomass then subtracting the missing component biomass.

Dead tree biomass was indicated by dead standing trees >9cm DBH. The indicator calculated is the cumulative biomass of dead standing trees. I estimated biomass using species-specific regression equations developed for the forests of Canada (Ung et al. 2008). From these equations I calculated snag biomass of the tree compartments stem wood and stem bark, based on the parameters tree height and DBH as exemplified by the following equation for stemwood (eq. 1-S2).

$$\Upsilon wood = \beta wood1 \cdot dbh^{\beta wood2} \cdot H^{\beta wood3} + \varepsilon_{wood} \qquad \text{(eq. 1-S2)}$$

where $\Upsilon wood$ is the biomass of a single tree's stemwood, $\beta woodi$ are species specific regression parameters, dbh is the diameter of the tree at 1.34m above ground, H is the tree's height, and ε is the error term. For dead tree biomass I used stemwood and bark compartments, because most branches and all foliage were assumed to be absent from the dead trees. I calculated the biomass of dead trees with missing tops by estimating their theoretical height and biomass using a DBH-height regression equation derived from my own data then subtracted the missing component biomass (eq. 1-S3; Figure 1-S2).

$$Height = \frac{(\beta 1 \cdot dbh^2)}{(\beta 2^2 + dbh^2)} + \varepsilon \qquad \text{(eq. 1-S3)}$$

where dbh is tree diameter at 1.34m above ground, ε is a normally distributed random error term, and the regression parameters $\beta 1$ $\beta 2$ I optimized to: $\beta 1$= 49.54213, and $\beta 2$ = 24.40817. Dead trees store carbon, nutrients and water, and provide critical habitat for cavity nesters as well as foraging and shelter habitat for numerous species (Pollock and Beechie 2014).

Wild edible berries were indicated by the cumulative percent cover of five common understory plants that provide wild edible fruits: *Gaultheria shallon, Rubus spectabilis, Vaccinium parvifolium, Vaccinium ovalifolium,* and *Vaccinium alaskense*. Wild edible berries are abundant and available for harvest during much of the summer on the coast of BC. They have high nutritional value and are a significant traditional food source in First Nations cultures, but are rarely harvested for economic purposes.

Above-ground carbon storage was indicated as total above ground carbon store of trees >9cm DBH, dead trees >9cm DBH and coarse woody debris >7.5 cm in diameter. The indicator calculated is the sum of the carbon pools: live trees, dead trees and coarse woody debris (cwd). I first estimated the biomass of each of these pools, and then multiplied biomass by a locally-derived conversion factor of .48 to calculate carbon Mg ha^{-1} (Preston et al. 1998). Live tree and dead tree biomass were estimated for each tree >9cm DBH using species-specific regression equations developed for the forests of Canada, which calculate biomass of several tree compartments based on the parameters tree height and DBH (e.g., eq. 1-S2; Ung et al. 2008). For live trees I used the tree compartments: stemwood, bark, branches and foliage. Coarse woody debris biomass was calculated using equations developed specifically for the cwd line-transect sampling method (eq. 1-S3; Marshall et al. 2003). Above-ground carbon storage benefits people globally by providing regulation of the global climate.

Wood volume was indicated by volume of all live trees, calculated based on the abundance and size of all live trees >9cm. Individual tree volumes are estimated using species-specific volume equations derived for the province of BC. An example is given in eq. 1-S4 (BC Ministry of Forests 1976).

$$\log(v) = \beta 1 + \beta 2 \cdot \log(dbh) + c \cdot \log(H) \qquad \text{(eq. 1-S4)}$$

where v is a tree's volume, $\beta 1$ and $\beta 2$ are species-specific regression parameters (given in BC Ministry of Forests 1976), dbh is tree diameter (cm) at 1.34m above ground level, c is a species specific constant and H is tree height (m). Timber harvesting generates jobs for local communities and cash-flow from tax for the government. Redcedar is the most valuable timber crop, but all local conifers are harvested.

Habitat for iconic species as a cultural ecosystem services, was indicated by the presence of potential nesting sites available for an endangered seabird, the marbled murrelet (*Brachyramphus marmoratus*). The indicator calculated is the presence or absence of thick branches in the tree canopy (>15cm diameter, >10 m above ground), which marbled murrelets require for nesting, and these were recorded in my data set for forest ages 76 and up. Below this forest age, marbled murrelet habitat is unlikely to occur so I extrapolated zeros below this, which did not alter the trajectory of recovery above 76 years. The existence value of endangered species is high among local residents and I used marbled murrelets because their habitat is an important management objective across their entire range along western North America (including in the US).

Table 1-S1. Summary of generalized additive model fits for each ecosystem service.

Ecosystem service indicator	Recovery trajectory	Forest age at inflection point*	Deviance explained (%)	Test statistic	P-value
Gamma distribution (square root link) for continuous data				F value	
Coarse woody debris biomass	u-shaped	NA	13.3	1.708	0.187
Dead tree biomass	Sigmoidal with asymptote	65	34.3	28.3	<0.001**
AG carbon storage	Sigmoidal no asymptote	65	67.6	42.62	<0.001**
Wood volume	Sigmoidal with asymptote	65	77.7	179.1	<0.001**
Binomial distribution (cloglog link) for presence/absence data				Z value	
Marbled Murrelet habitat	Sigmoidal with delay	166	31.5	2.851	0.0263*
Large heritage trees	Sigmoidal with delay	Not reached	15.1	1.996	0.0459*
Large redcedar	unknown	NA	6.1	0.929	> 0.05
Beta Distribution (logit link) for proportional data				Z value	
Wild edible berries	u-shaped	Not reached	30.2	11.39	0.009*

*Inflection points are approximate, and only identified for curves with sigmoidal shape.

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CHAPTER 2 CONNECTING STATEMENT

While Chapter 1 provides a generalized understanding of the long-term recovery trajectories of multiple ES, there are likely strong differences in ES recovery caused by varying site conditions, which I did not capture in Chapter 1. For example, it ignores potentially important differences in ES between productive riparian sites and less productive upland sites. Local factors such as site productivity, disturbance regimes, and topographic position shape the unique structures found among forest ecosystems on Vancouver Island, and different forest ecosystems likely support different suites of ES (LePage and Banner 2014). Therefore, in Chapter 2, I aim to build understanding of how ES in old-growth and recovering forests differ across two local site conditions. I use fieldwork, located near Clayoquot Sound, Vancouver Island, BC, Canada, set in two forest types: a productive riparian forest and an upland forest of intermediate productivity. These forest types are classified according to the BC Biogeoclimatic Ecosystem Classification System, which is used in nearly all aspects of research and land-use planning in BC (Thompson and Gergel 2008, Price et al. 2009, Clason et al. 2008, Cocksedge and Titus 2006, Meidinger and Pojar 1991).

Additionally, in this chapter I am able to develop a more precise set of indicators for collecting data on ES through fieldwork. For example, I harvest and directly weigh ES provided by the understory plant salal. Also, by working in the field with a First Nations carver I gain insights into size and qualities of cedar trees needed for traditional First Nations use.

CHAPTER 2: SEEING THE FOREST FOR ITS MULTIPLE ECOSYSTEM SERVICES: INDICATORS FOR THE CULTURAL SERVICES PROVIDED BY TREES, UNDERSTORY PLANTS AND WOODY DEBRIS

ABSTRACT

The ecosystem service (ES) framework is gaining traction in forest management as a means to recognize the multiple benefits that forests provide, as well as the different forest attributes (trees, understory plants and woody debris) that provide those benefits. However, application of ES in management is challenged by knowledge gaps in how to measure and compare multiple ES at the stand scale. Indicators can help bridge the ES approach into forest management by providing a means for accurate ES inventory and mapping. I measured 10 forest ES in contrasting forest types to investigate the effects of past forest harvesting in the coastal temperate rainforest of Vancouver Island, BC, Canada. Specifically, my objectives were to 1) build a systematic set of ES indicators for coastal temperate forests based on forest structural features, including trees, coarse woody debris, and understory plants; 2) collect field data to compare the effects of forest age (old-growth vs. second-growth) and ecological site conditions (riparian vs. upland forest) on the bundle of ES provided by different types of forests. To identify cultural services, such as the large cedar traditionally carved by First Nations, I surveyed the forest with help from a local First Nations artist and wood carver. Forest age and forest type had significant and major effects on bundles of ES. Old-growth forests provided significantly higher carbon storage, habitat services, and wood volume than recovering forests. Within old-growth forests, the proportion of trees suitable for First Nations traditional carving was significantly higher in riparian stands. In general, old-growth riparian forests were a hotspot of ES, providing for example nearly three times as much carbon storage as old-growth forests on upland sites and 12 times the amount of carbon storage as found in second-growth forests on upland sites. These results indicate that the coarse-filter (or broad-scale inventories) of forest ES often used may generalize across dramatic variations in ES bundles in forested landscapes. The novel set of

stand-level ES indicators I developed can be useful for improved accuracy in ES assessment, including cultural ES, and addresses the role of landscape heterogeneity in influencing ES.

INTRODUCTION

A steady shift is occurring away from an industrial model of forestry towards managing for multiple values (Bunnell and Dunsworth 2010, Oliver 2014). Both sustainable forest management and ecosystem-based management paradigms seek to maintain ecosystem integrity while preserving opportunities for humans to derive benefits from forests (Higman et al. 1999, Price et al. 2009). Ecosystem service (ES) frameworks are gaining traction to assist such efforts as they help managers recognize and measure the multiple benefits provided by forested landscapes (De Groot and Van der Meer 2010). Recent advances in ES mapping now form the basis of much landscape inventory of ES and analyses of tradeoffs (Willemen et al. 2010, Raudseppe-Hearne et al. 2010, Grêt-Regamey et al. 2013, Qiu and Turner 2013). As a result, policy and management tools are rapidly being developed to implement ES management on broad spatial scales, through the US Forest Service, European Environmental Agency, and United Nations programs, among others (Patterson 2014, Schaefer et al. 2015, Diaz et al. 2015).

Despite the momentum for using an ES approach in forest management, major data and methods gaps in how to measure, monitor and assess ES in heterogeneous forests remain roadblocks to implementation (Syrbe and Walz 2012, van Oudenhoven et al. 2012). In general, inventory and mapping studies of forest ecosystem services (ES) have relied on coarse scale, generalized land cover classes as spatial proxies for ecosystem services (Andrew et al. 2015). While efficient for large areas, applying generalized ES measures across large areas of forest can result in major errors and uncertainty (Plummer 2009, Eigenrod et al. 2010, Mitchell et al. 2013). ES can vary dramatically among forest stands for reasons not typically considered in such broad-scale land-cover-based ES assessment. For example, forest stands of differing ages, species composition, or tree density may provide different amounts of carbon storage, habitat, and wild edible foods (Trofymow et al. 2008, Clason et al. 2008, Pollock et al. 2012). Broad-scale land cover based methods may also entirely disregard key forest types (such as riparian corridors or sacred forests), which may be smaller than the resolution of the geodata used in assessment, yet contain locally important ES (Gergel et al. in review). Thus, broad-scale ES assessment methods may be too imprecise to detect subtle nuances among forest stands that occur at fine resolution.

Indicators capable of distinguishing differences in the provision of ES within and among heterogeneous forest stands are needed to support effective planning and decision-making (van Oudenhoven et al. 2012, Burkhard et al. 2012). To date, no ES study has examined how the nuanced architecture of forest stands influences forest stand capacity to provide ES. Forest stands are composed of numerous biophysical structures, which have unique roles in providing ES. For example, understory plants species provide wild edible foods (Clason et al. 2008), accumulations of woody debris (i.e. dead fallen trees) store carbon, and dead trees provide habitat for culturally important cavity-nesting bird species (Pollock and Beechie 2014). Trees, depending on their shape, size and species, may be valuable as timber or fuelwood, provide critical habitat for rare species, or act as a cultural resource to Indigenous people who gather their fruits and nuts, carve them into canoes, or strip their bark for use in weaving (Turner et al. 2009, Blicharska and Mikusinski 2014).

Biophysical indicators for cultural ES (the ES class linked to non-material, intangible benefits) are generally lacking worldwide (Daniels et al. 2012, Hernández-Morcillo et al. 2013). However, many biophysical attributes of forests are fundamentally linked to culture, such as the harvesting and processing of tree and plant materials by indigenous people (Turner 1988, Blicharska and Mikusinski 2014). Identifying the cultural role of particular plants and their specific traits, with help of traditional ecological knowledge, can assist efforts now underway to create indicators for tracking sustainability of cultural ES (e.g., through the Intergovernmental Panel on Biodiversity and Ecosystem Services; Hernández-Morcillo et al. 2013).

On the coast of British Columbia (BC), Canada, there is an ongoing shift towards management for multiple forest values motivated, in part, by concern over the impacts of forest harvesting on cultural ES (Tuner and Bitonti 2011). First Nations (the common term used in Canada to describe people of indigenous ancestry) are now key actors in BC forest policy (Hoberg and Morawski 1997). First Nations have mandated sustenance of their traditional cultural forest resources including large cedar used for building canoes, carving ceremonial poles, and stripping cedar bark for use in weaving (Haida Gwaii Strategic Landuse Agreement 2007). However, the indicators needed for responsible stewardship of these cultural resources are lacking.

Old-growth (late seral stands >250 years old) cedar forests on the coast of BC, Canada, are potential ES hotspots. Because they have large old cedar trees, productive growing conditions, and diverse understory plant communities, I hypothesize that these old growth forests may provide large cedar for traditional use and other socially valued ES such as carbon storage, wild edible berries, botanical forest products, soil erosion control, and habitat for iconic rare wildlife species (Green 2007, Burger et al. 2010). Low-elevation riparian cedar forests are likely to produce the largest cedar trees and associated First Nations cultural resources (Gergel et al. 2007). Additionally, they help regulate environmental quality for spawning salmon. However, cedar is a valuable timber species, and many productive riparian old-growth cedar forests have already been harvested (Green 2007). It remains unclear whether remaining old-growth cedar forests, located at less productive upland sites, provide equivalent ES, as logged riparian forests once did.

To improve our ability to measure and predict ES across heterogenous landscapes, I used fieldwork at Clayoquot Sound, Vancouver Island, BC, Canada, to assess how ecosystem services are recovering in two distinct coastal forest types —a productive riparian forest and an upland forest of intermediate productivity. My three primary objectives were to:

1. build a systematic set of ES indicators for coastal temperate forests based on structural features, including trees, coarse woody debris and understory plants;
2. collect field data to analyze the effects of forest age (old-growth vs. second-growth) and ecological site conditions (riparian vs. upland forest) on a bundle of ES, and
3. assess the influence of canopy shading on understory plant ES.

METHODS

I collected field data from 12 forest stands at Clayoquot Sound, Vancouver Island, BC, Canada, (Aug 2014) to contrast ES among different forest types (riparian vs. upland) as well as between older, late seral forests >250 years age (herein referred to as *old-growth*) and second-growth forest ~35 years age. I measured elements of forest stand structure (e.g., trees, understory plants, and coarse woody debris) for use as biophysical indicators of ES then compared differences in ES provision among forest stands using mixed effect models. To explore ES recovery, I determined whether canopy cover influenced ES from understory plants, and the extent to which coarse woody debris underpinned tree regeneration.

Study system

In Clayoquot Sound on Vancouver Island, BC, Canada (figure 2-1), the social and ecological effects of forest harvest have received considerable research and management attention (Clayoquot Sound Scientific Panel 1995). The diverse forest-dependent livelihoods of multiple stakeholders, including forestry licensees, national park operators, local communities, as well as three First Nations (*Tla-o-qui-aht*, *Ucluelet* and *Ahousaht* First Nations), make it an important region in which to evaluate multiple ES and their recovery following forest harvest. Forest harvesting, primarily using the clear-cut method of harvest, was widespread in the 1960's through the 1980's. In the early 1990's, intense landuse debates centered in this area resulted in new provincial forest management guidelines, which slowed the rate of old-growth harvesting (Clayoquot Sound Scientific Panel 1995, Hoberg and Morowski 1997). A new era began, emphasizing management for broader social, ecological and economic forest values, with First Nations recognized as core actors in the policy and management of the forest (van Kooten and Bult 1999, Hoberg and Morowski 1997).

Both old-growth (>250 year age) and young second-growth (30-40 years) stands in this region are dominated by long-lived, shade tolerant conifers, mainly western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), yellow cedar (*Chameacyparis nootkatensis*) amabilis fir (*Abies amabilis*), Sitka spruce (*Pices sitchensis*) and Douglas-fir (*Psuedotsuga menziesii*). While small trees comprise dense second-growth stands, old-growth tree canopies

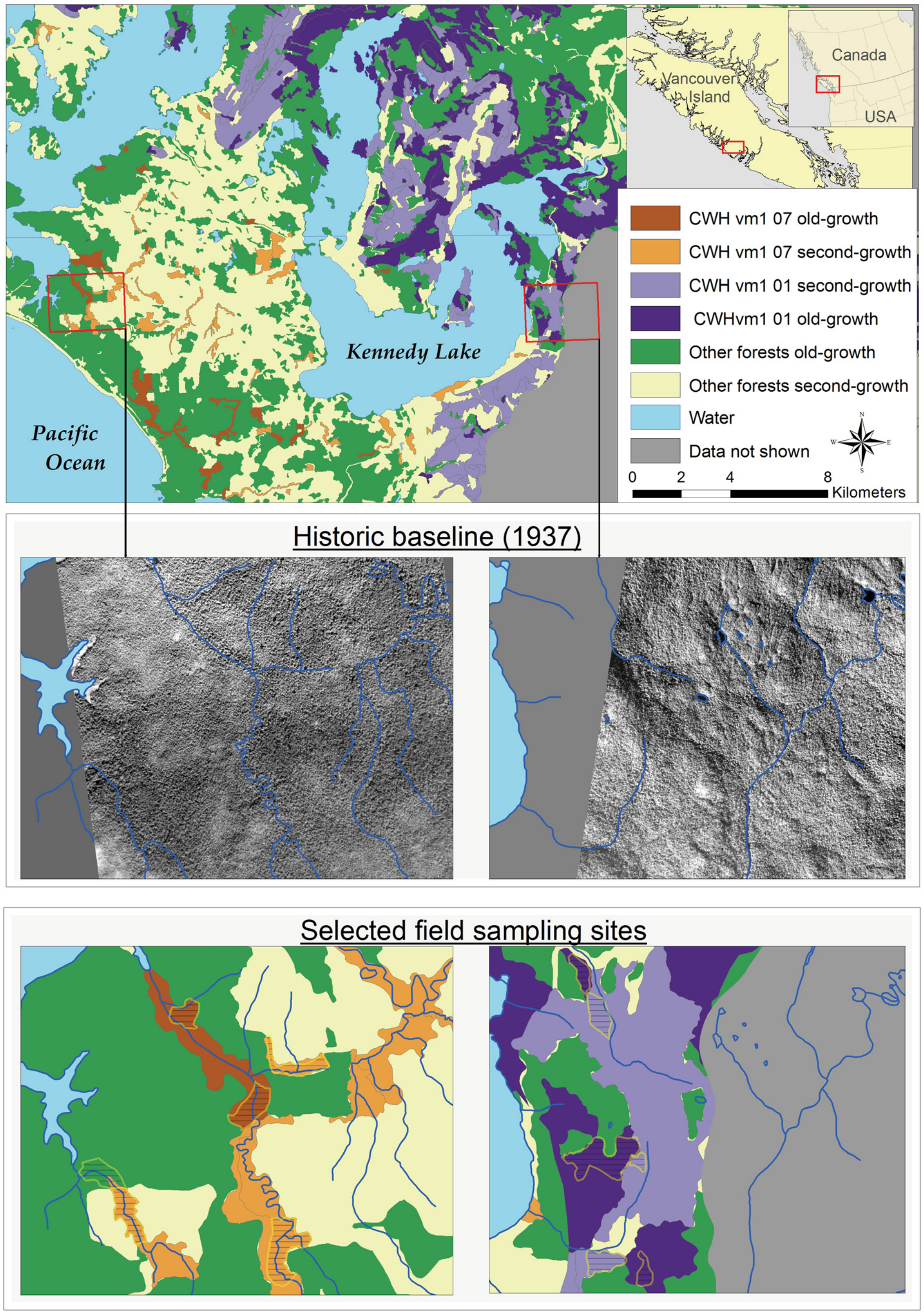

Figure 2-1. Study area and field sampling sites selected by geospatial analysis. Panel A) For the comparison, I first selected a productive riparian forest and a medium productivity sloped forests and two forest ages: baseline old-growth stands >250 years age and recovering stands ~35 years age. Panel B) I used historical aerial photos to ensure that second-growth and old-growth sites shared a common historic baseline. Panel C) I selected forest stands representative of the regional conditions for the sampling plots to be used in the comparison.

can exceed 70m in height and contain attributes such as dead standing trees important to wildlife and wide mossy branches used as nesting sites by an at-risk bird species the marbled murrelet (*Brachyramphus marmoratus*) (Burger et al. 2010). Canopies are more open in old-growth allowing greater understory plant growth. Ericaceous shrubs such as salal (*Gaultheria shallon*) are particularly common. Coarse woody debris (cwd; dead wood that is not self-supporting) volumes accumulate over time becoming abundant in old-growth forests, while cwd volume varies in second-growth stands according to the amount of residual cwd left following forest harvest (Feller 2003). Natural large-scale disturbances, such as forest fires, are rare. However, since the 1960's substantial areas have been logged and converted to second-growth.

Overall, forest structure and growth patterns differ by ecological site conditions, which are characterized for research and management purposes according to the BC Biogeoclimatic Ecosystem Classification (BEC) System (Meidinger and Pojar 1991, Lertzman et al. 1996). Most forests in the area are classified as the Coastal Western Hemlock very wet maritime zone (CWH vm1) or the foggier hypermaritime variant (CWH vh1). I focus on the forests of the CWH vm1 <20km from the coastal margin, <250m above mean sea level with a cool, humid maritime climate (mean annual precipitation = 2787mm, Meidinger and Pojar 1991). Within this region, diverse forest types occur among a complex network of islands, fjords, flat plains and mountain ridges. In the BEC system, *site series* are fine-scale classifications based on the integrated influences of local disturbance, climate, and relative soil moisture and soil nutrient regimes, which together drive site productivity and niche differentiation of plant species. Old-growth forests are defined as >250 years old in this region by the BC Ministry of Forests.

Study site selection using geospatial datasets

I used a stratified systematic approach based on both contemporary and historical geospatial data to select representative forest stands within four experimental levels (herein referred to as *forest classes*) based on unique combinations of forest age and forest type with (figure 2-1). First, I selected two distinct forest types as per the BC Biogeoclimatic Ecosystem Classification (BEC) system, which were accessible in the field and important for ES. Provincial Terrestrial Ecosystem Mapping (TEM, Madrone Consultants 2001) was used to identify productive riparian forest (BEC: CWH vm1 07 site series) and upland forests of intermediate productivity (BEC: CWH vm1 01 site series). This upland forest type is regionally widespread on an areal basis and thus representative of much of the forests in the vicinity; whereas riparian forests were examined because they were expected to provide First Nations large cedar and other ES associated with the productive growing conditions of riparian zones. Within these two forest types, I stratified stands by age using forest inventory data (Vegetation Resources Inventory, BC Ministry of Forests 1998). Old-growth forests (>250 years old) were selected to represent ES baseline conditions and second-growth forest ~35 years age [specifically, mean age of upland stands was 32.5 years (sd = 0.5 years) and mean age of riparian stands was 37.5 years (sd = 1.0 year)] were selected to represent stands recovering from harvest forests because this is a stand age common in the study area. Interpretation of historic air photos (circa 1930s) (Morgan and Gergel 2010; Morgan and Gergel 2013) were used to ensure stand characteristics of contemporary young stands (prior to harvest) were originally similar to old growth stands. To further ensure fair comparisons between second growth and old-growth stands, I sampled adjacent young/old stands, which were also along the same stream or adjacent tributary for riparian stands.

Within these four forest classes, I selected stands representative of the regional averages of their respective forest classes by controlling for forest inventory variables such as: percent canopy openness (indicates understory plant abundance), tree basal area in m^2/ha, stand density in number of trees/ha, and leading and second tree species (indicates values of trees for wood and traditional First Nations use). Thus the final factorial design 2x2x3 examined two forest ecosystem types, two stand ages, and three replicates of each for a total of 12 forest stands.

Measuring forest stand structure

Through literature review, I identified forest structural features that determine the forest's capacity to provide ecosystem services then used a combination of field plots and line-transect sampling to measure those structural features (figure 2-2). Because few studies existed as a source of reference, to assess and develop indicators for cultural ES of large cedar, I worked with a First Nations carver with decades of familiarity with the characteristics of trees useful for traditional aboriginal arts.

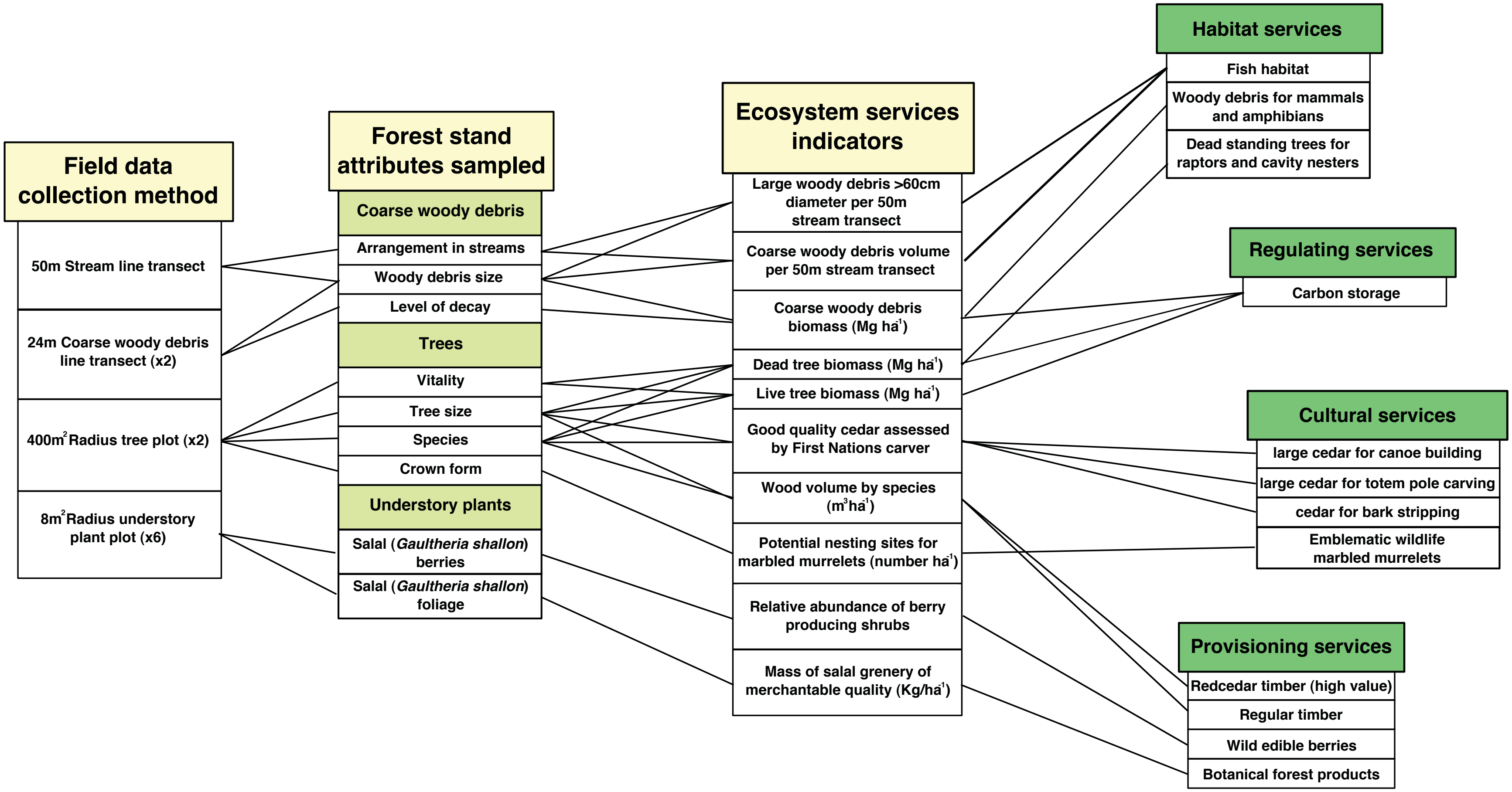

Figure 2-2. Estimating forest stand ecosystem services based on field measurements, as follows: (seen in left column) I used various field sampling plots and transects to measure (left-center column) forest stand biophysical attributes, which I then used to calculate (right-center column) ecosystem service indicators for estimation of (right column) habitat, regulating, cultural, and provisioning ecosystem services.

At each forest stand, I measured several biophysical indicators to assess the following ES provided by trees: wood volume, tree carbon storage, cultural First Nations uses of cedar, potential nesting platforms of an at-risk bird species the marbled murrelet (*Brachyramphus marmoratus*), and biomass of dead standing trees. To sample trees I used two 400m^2 circular plots within each forest stand. In riparian stands, I placed tree plots within the hydro-riparian zone as much as possible. In each tree plot, I recorded tree species, vitality (live vs. dead), height and diameter, as well as quality defects that might influence First Nations cultural use of cedar. Furthermore, I recorded tree growing substrate, the presence of potential First Nations cultural uses of cedar trees, and the number of large canopy branches defined as those >15cm diameter, the size used to classify potential nesting platforms for marbled murrelets (Burger et al. 2010).

I measured the relative abundance of edible berries and mass of salal, an economically important species used in the floral industry, within 8m^2 circular understory plots. Specifically, three understory plots were placed within each of the two tree plots per stand (thus 6 understory plots total per stand). Understory plots were placed 6m from the tree plot's center, 90 degrees apart, beginning at a randomized azimuth. In each harvest plot I picked and weighed the merchantable salal greenery and qualitatively assessed abundance of edible berries using the BC Non-timber Forest Product Code (BC Ministry of Forests 2010). Only edible berries species in green fruit to ripe stage of phenology across the two-week study period were used in the analysis.

To measure ES associated with coarse woody debris, I established two 24m line transects at each forest stand, oriented perpendicular to each other, traversing between the two tree plots. Along each transect I measured diameter, decay class, angle from horizontal and species of each piece of debris greater than 7.5cm diameter to estimate biomass and carbon storage (BC Ministry of Forests 2010). Additionally, at the riparian stands I used one 50m transect placed along the stream bank to measure pieces of instream woody debris by species, decay class, diameter (at both sides of channel) and instream piece length. I recorded debris positions as either 'instream' or 'spanning.' Also, I measured bankfull stream channel width at 5m intervals.

Sampling of interactions among ecosystem services

To examine the effects of canopy shading on understory plant ES, I measured canopy openness using a spherical densitometer at the center of each understory plot. To examine the role of coarse woody debris as substrate for tree growth, I recorded whether or not trees were growing on woody debris.

Overview of estimating ecosystem services using biophysical indicators

Based on the biophysical information collected, I developed indicators (figure 2-2) to estimate forest capacity to provide ten different ES, including, provisioning, regulating, habitat, and cultural services. Services examined include both intermediate services and final services (De Groot and Van der Meer 2010, Wong et al. 2014). Intermediate services are defined as the biophysical structures and processes of forests with indirect links to human benefits, but that underlie provisioning of final services. Intermediate services examined include coarse woody debris, dead trees, fish habitat by instream logs, and carbon storage. Final services are the characteristics of ecosystems with explicit links to human well-being and that are directly valued by identifiable beneficiary groups. They include wood volume, First Nations traditional use of cedar, botanical forest products and edible berries.

Estimation of ecosystem services provided by trees

A First Nations cedar carver assessed all cedar trees, including redcedar (*Thuja plicata*) and yellow cedar (*Chameacypris nootkatensis*) for their potential use. Based solely on the observations of the carver, I recorded whether or not the tree had potential use in the following ways: First Nations bark stripping, ceremonial pole carving, or canoe building. The carver used visual inspection of the tree, such as looking at branchiness, trunk diameter, and crown health (as an indicator to gauge potential inner rot). Cedar is a sacred traditional resource for BC coastal First Nations, and is known as ‘the tree of life.’ Cedar bark, most often of redcedar, is traditionally stripped from trees then woven for making baskets, clothing, hats and crafts. Large cedar are used for carving ceremonial pools (also known as totem poles) and the finest quality logs are carved out to build ocean-going canoes. Recent changes in BC forest policy have stimulated interest to develop indicators and methods for managing cultural cedar (BC Ministry of Natural Resource Operations 2011).

Habitat for iconic species as a cultural ecosystem services was indicated by the presence of potential nesting platforms available for an endangered bird, the marbled murrelet. Based on observations from the ground, I counted the number of thick canopy branches, defined as >15cm diameter and >10 m above the ground (Burger et al. 2010), that may potentially be used by murrelets for nesting. For data analysis, I later converted these counts to a simple presence absence of whether or not each tree contained nesting platforms. Endangered species have emblematic and cultural value on coastal BC (De Groot and Van der Meer 2010) and I examined murrelets because managing their habitat is mandated along the Pacific coast.

Habitat services provided by dead trees were indicated by the biomass of dead trees >12.5cm DBH (Diameter measured at breast height, or 1.3m above ground) using species-specific regression equations for Canada (Ung et al. 2008). Using tree height and DBH, tree biomass compartments were determined then summed to calculate total tree biomass. Assuming most branches and all foliage were absent from dead trees, I only used the tree stem and stem bark compartments for dead trees. Fifteen dead trees with broken tops meant I could not calculate their biomass using standard methods. For such trees I used DBH-height relationships for my measured intact trees (n=445 intact trees) to predict the theoretical heights and biomass of the broken top trees had they been intact. Then I subtracted the height and biomass of the missing broken top component from the tree's theoretical biomass. Dead trees provide habitat for numerous wildlife species including emblematic species such as raptors and cavity nesting birds (Lofroth 1998).

Above-ground carbon storage was estimated as the sum of the carbon pools for live trees, dead trees and coarse woody debris. I first estimated the biomass of each of these pools, and then multiplied biomass by a locally-derived conversion factor of 0.48 to calculate Mg/ha carbon (Preston et al. 1998). Live tree biomass was estimated for each tree >12.5cm DBH as per Ung et al. (2008) for tree compartments: stemwood, bark, branches and foliage. Above-ground carbon storage benefits people globally by regulating the global climate.

I assessed wood volume for all live trees >12.5cm DBH using species-specific Provincial equations (BC Ministry of Forests 1976). In characterizing ES of wood volume, I analyzed redcedar separately because it is among the most valuable of local timber species and thus a key consideration in forest harvest planning. Timber volumes of other important species were grouped (western hemlock and lesser amounts of yellow cedar, Sitka spruce, amabilis fir and Douglas-fir). Most wood harvested locally is for export, and the industry generates primary jobs for local rural communities as well as tax for the government (Green 2007).

Estimating ecosystem services provided by understory plants

To assess mass (kg ha^{-1}) of salal greenery of merchantable quality in understory plots, I picked all merchantable stems, defined as visually attractive branchlets >60cm length with a minimum of four fully green leaves formed within the past two years (Cocksedge and Schroeder 2006). Older leaves were stripped off prior to weighing. Salal dominates BC's floral greenery industry, which generates $55-60 million per year (Hobby et al. 2010). Local beneficiaries of this ES are the harvesters who tend to be youth or migrant workers (Ballard and Huntsinger 2006) due to the relatively hard physical labour and seasonality of salal collecting (Cocksedge and Schroeder 2006).

I assessed relative abundance of edible berries in each harvest plot using the BC Ministry of Forests non-timber-forest products abundance codes (BC Ministry of Forests 2010). Using this protocol I assigned an abundance code (from 0-5) based on the level of harvesting effort that would be justifiable given the amount and quality of berries present. For example, a "0" means that the plant is absent and no harvest attempt would be made, where as a "5" means there is enough fruit of high enough quality to warrant significant collection efforts. Wild edible berries are a seasonally abundant food source traditionally harvested in large volumes by the coastal First Nations (Clayoquot Sound Scientific Panel 1995) and are also consumed by visiting tourists and hikers.

Estimating ecosystem services provided by coarse woody debris

To estimate aquatic services important for fish habitat I measured the frequency of instream woody debris, defined as the volume of instream woody debris exceeding 10cm diameter per 50m riparian transects. Debris volume was calculated based on the length and diameter at both ends of each woody debris piece using a conic-paraboloid equation developed for estimating woody debris volume (Fraver et al. 2007). To permit comparison among stands with different sized streams, the total volume of a stand's woody debris was standardized according to mean stream width found in that stand. The variable used in analysis was thus volume of woody debris per 50m transect standardized according to stream width. I also counted the number of larger woody debris, >60cm diameter, to test for a forest age effect specifically on the largest pieces of wood. Instream woody debris, especially larger pieces, support many functions that create and maintain habitat for salmonids including stabilizing stream banks, forming habitat pools, trapping sediment, storing nutrients, providing substrate for primary producers, and increasing hyporheic exchange (Moore and Wondzell 2005, Melina and Hinch 2009).

Ecosystem services associated with woody debris not in the stream were indicated using the biomass of cwd (kg ha^{-1}) estimated based on field measurements and line transect sampling equations designed for calculating woody debris volume on a per area basis (Marshall et al. 2003). I adapted these volume equations to estimate biomass by adding a wood density variable based on decay class and species-specific wood density (following Holub et al. 2001). Biomass estimates along two transects at each stand were averaged for analysis. Coarse woody debris provides critical habitat for amphibians and small mammals (Pollock and Beechie 2014), stores carbon and nutrients, and provides substrates or "nurse logs" for regenerating tree seedlings (Haeussler et al. 2013).

Statistical Analyses

To visualize the differences among the four forest classes, I plotted the mean ES values from each forest class on multi-axis flower diagrams (figure 2-3). I used mixed effect models to test for the effects of forest age and forest ecosystem type on each ES individually. To account for the adjacent pairing of second-growth and old-growth baseline stands in my design, I specified the pairs as random effects. I estimated significance of the fixed effects using 95% confidence intervals. For ES represented as continuous variables [wood volume (M^3 ha^{-1}), carbon storage (Mg ha^{-1}), coarse woody debris biomass (Mg ha^{-1}), dead tree biomass (Mg ha^{-1})], I used a standard mixed effects model assuming normal distributions (n=12). However, due to the nested layout of multiple understory plots within each stand, I was able to increase sample size by analyzing the continuous variables [ornamental salal greenery (Kg ha^{-1}) and salal berries (relative abundance)] using a measure from each of the two tree plots within each stand by specifying forest stand as a random effect (n=24). To meet assumptions of normality and homoscedasticity of residuals, I used log, cube root, or square root transformations, as best suited for each ES (Table 2-1).

I could not analyze count data as a normally distributed variable. Instead, I analyzed trees found within old-growth stands using logistic regression to test for effects of forest type in the proportion of trees that were large cedar, useful as bark-stripping trees or had potential marbled murrelet nesting platforms. Also, because instream woody debris was only measured in the riparian forest types, I analyzed the effect of forest age using a paired t-test.

I also analyzed several plant interactions hypothesized to influence ES abundance and recovery. I used linear and non-linear regression analyses (generalized additive models) to analyze the effect of canopy cover on understory plant ES. Finally, I used mixed effect logistic regression to test for differences among forest classes in the proportion of trees visually identified as growing on coarse woody debris (cwd) substrate (or having previously grown on cwd) vs. those growing on a soil substrate.

All analysis was done in R (R Core Team 2013), with lme4 (Bates et al. 2014) and mgcv packages (Wood 2006).

Table 2-1. Calculations of ecosystem services mean abundance (and standard deviation) of the four forest classes examined. Significant effects of forest age (>250 year old vs. ~35 year old forest) and forest type (riparian forest vs. upland forest) on ecosystem services abundance are highlighted in bold, where a positive significance is determined based on whether 95% confidence intervals from mixed model do not cross zero.

		Observed means (and standard deviations)				**Test statistics for significant effects**		
Ecosystem service (measurement units)	**Sample size used in analysis**	**Upland old-growth**	**Upland second-growth**	**Riparian old-growth**	**Riparian second-growth**	**Response variable transformation**	**Forest age 95% confidence intervals**	**Forest type 95% confidence intervals**
Merchantable salal greenery (Kg/ha)	24	260.49 (115.)	232.99 (59.17)	139.58 (118.60)	28.13 (38.40)	square root	-5.565, 0.746	**4.323, 12.813 ***
Wild edible berries (relative abundance)	24	1.33 (1.09)	1.28 (0.59)	1.00 (0.73)	1.17 (1.88)	square root	-0.682, 0.613	-0.505, 0.867
Coarse woody debris biomass (Mg/ha)	12	91.87 (59.6)	79.51 (20.22)	257.67 (230.18)	209.94 (240.6)	log + 1	-0.329, 0.320	-0.922, 0.372
Dead tree biomass (Mg/ha)	12	67.45 (27.2)	0.23 (0.39)	82.05 (78.75)	7.86 (13.67)	cube root	**-4.570, -2.240 ***	-1.509, 0.820
Above ground carbon storage (Mg/ha)	12	192.34 (118.)	51.41 (7.05)	590.31 (308.53)	153.48 (84.95)	log + 1	**-0.772, -0.303 ***	**-0.781, -0.181 ***
Hemlock timber (M^3/ha)	12	487.50 (361.)	30.74 (28.12)	470.48 (574.92)	89.52 (96.03)	log + 1	**-1.470, -0.438 ***	-0.701 0.467
Cedar timber (M^3/ha)	12	39.79 (55.5)	19.95 (25.65)	1266.09 (411.26)	102.03 (116.6)	cube root	**-5.988, -1.052 ***	**-7.394, -2.460 ***

*Significant at $p < 0.05$

Table 2-2. Site descriptions of forest stands surveyed during fieldwork. Descriptions are based on protocol of the BC Land Management Handbook (BC Ministry of Forests and Range 2010).

Site ID	Disturbance history	Regeneration	Meso slope position	Microtopography	Surface shape	Drainage	Soil depth (cm)	Slope	Aspect
Upland second-growth 1	harvest	planted	mid	slightly gullied	flat	moderate	>30	35	27
Upland second-growth 2	harvest	natural	mid	slightly undulating	concave	rapid	>30	21	330
Upland second-growth 3	harvest	natural	mid	moderately gullied	convex	rapid	~30	28	155
Upland old-growth 1	NA	NA	mid	moderately gullied	concave	rapid	~30	17	20
Upland old-growth 2	NA	NA	mid (lower)	slightly hummocky	concave	imperfect	>30	26	320
Upland old-growth 3	NA	NA	mid	slightly gullied	concave	rapid	>30	30	235
Riparian second-growth 1	harvest/wind	natural	bottom	moderately hummocky	concave	imperfect	>50	3	285
Riparian second-growth 2	harvest	natural	toe (mid)	moderately hummocky	concave/level	poor	>50	3	20
Riparian second-growth 3	harvest	natural	lower	moderately hummocky	level	imperfect	>50	4	128
Riparian old-growth 1	NA	NA	level (toe)	moderately hummocky	concave	moderate	>50	2	290
Riparian old-growth 2	NA	NA	level	severely hummocky	flat	imperfect	>50	5	20
Riparian old-growth 3	NA	NA	toe	moderately hummocky	concave	imperfect	>50	9	155

RESULTS

Among the 12 stands sampled, I measured 456 trees, of which 17 trees had potential use for traditional First Nations carving or bark stripping. By tree volume, western redcedar was more abundant than all other species combined. Secondary species included western hemlock, yellow cedar and lesser amounts of amabilis fir, Sitka spruce and Douglas-fir. All second-growth stands had a history of clear-cutting but wind had caused substantial blow down at one second-growth stand prior to harvest (Table 2-2). The upland stands were on moderate slopes (mean = 26%, sd= 6%) with thin (30-50 cm depth), rapidly draining soils on rocky gullied microtopography. The riparian stands were on flat terrain with deeper (>50cm depth), imperfectly drained soils on hummocky microtopography (Table 2-2).

Each unique combination of forest age and forest type provided a distinct bundle of ecosystem services (Figure 2-3). Old-growth forests had significantly higher levels of dead tree biomass, carbon storage, redcedar wood volume, and non-redcedar wood volume than second-growth forests (Table 2-1). Both cedar cultural resources and marbled murrelet potential nesting platforms were entirely absent in second-growth sites. Forest type affected fewer ES, but riparian forests had significantly higher redcedar wood volume and carbon storage than upland forests. Also, the proportion of trees observed to have marbled murrelet nesting platforms in each forest type was significantly higher in riparian forests than in the upland forests ($p < 0.001$). In contrast, mass of harvested salal merchantable greenery was higher in upland forests. I did not detect significant differences among forest classes for coarse woody debris biomass or salal edible berries.

Cedar trees with potential for First Nations traditional uses were absent in recovering stands. Within old-growth stands, the proportion of trees observed to be large cedar suitable for First Nations carving was significantly higher in riparian stands (figure 2-4; $p = 0.032$). Nine large trees [mean DBH = 112 (+/-38) cm] were identified as suitable for totem poles, of which 2 were yellow cedar and 7 were redcedars. Three large redcedar trees (DBH's of 109.0cm, 152.0cm, and 161.1cm) were identified as suitable for canoe carving. Trees identified by the carver as useful

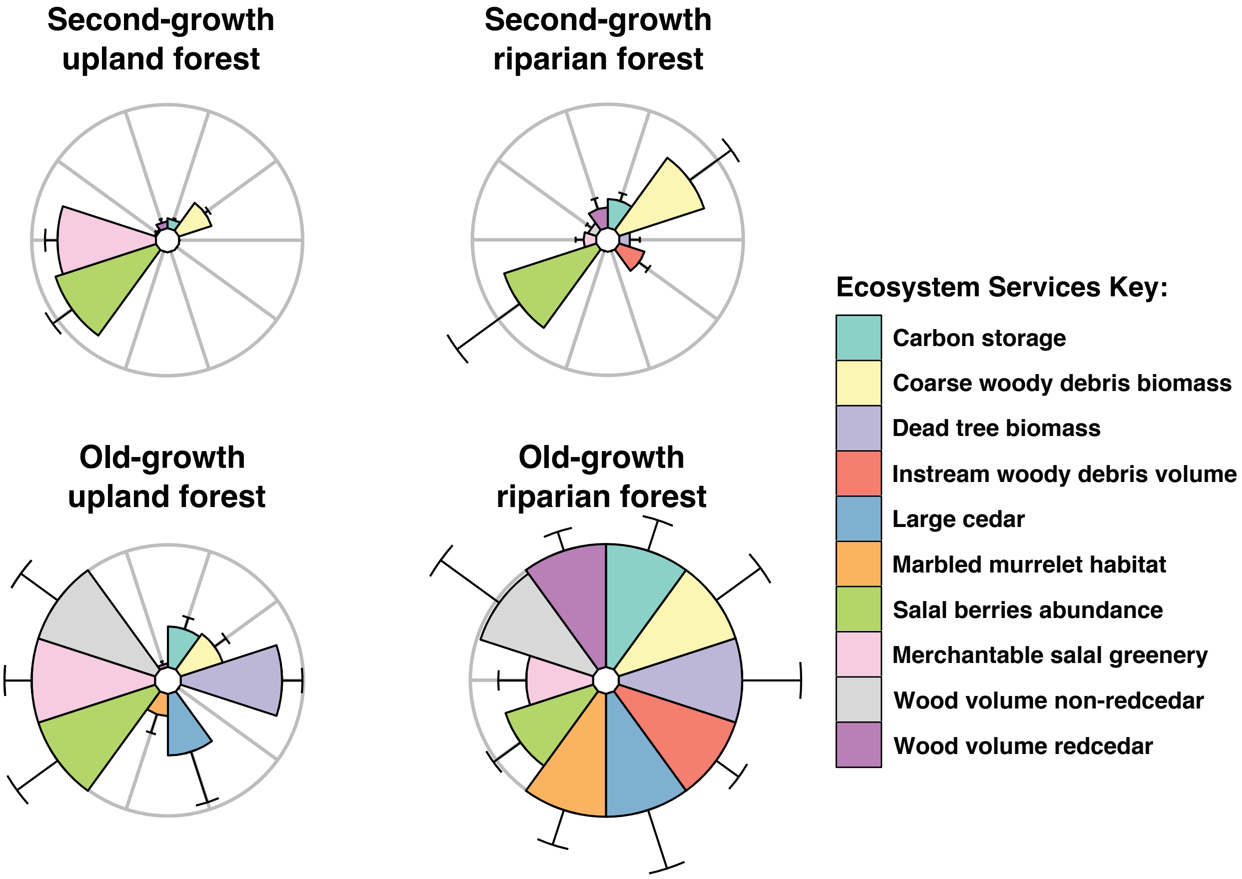

Figure 2-3. Each forest class, a unique combination of forest type and forest age, provided a distinct bundle of ecosystem services. Ecosystem service measures were averaged among the three sites of each forest class then standardized against the maximum average ecosystem service value. Error bars show a measure of relative variation calculated as half the standard deviation of each forest class divided by maximum ES of any forest class.

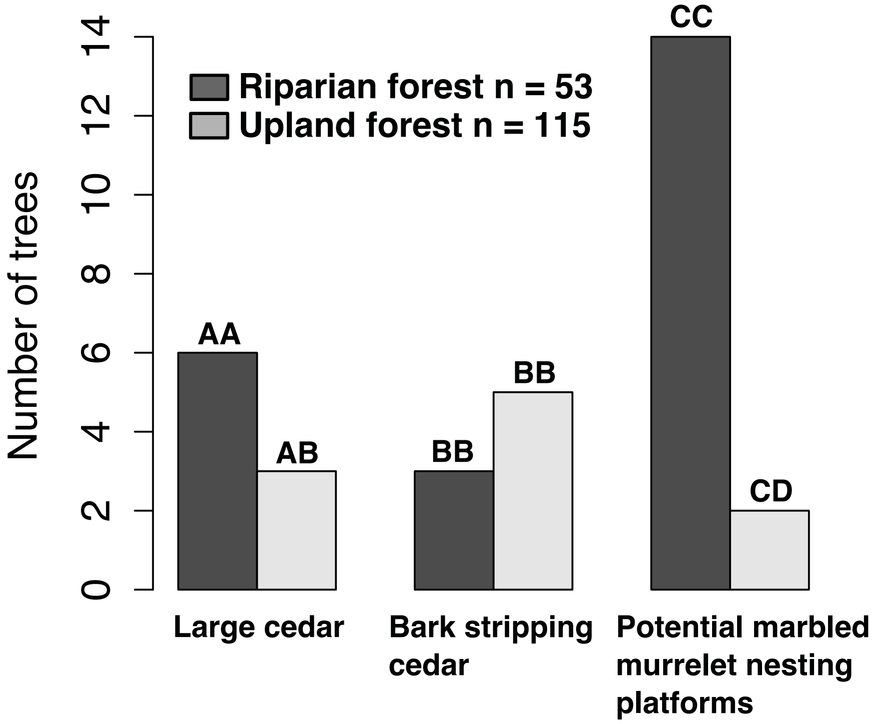

Figure 2-4. Differences between forest types in the counts of large cedar, bark-stripping trees or trees with potential marbled murrelet nesting platforms among old-growth sites (n = 53 trees in the riparian old-growth and n = 115 trees in the upland old-growth).

For canoe or totem pole carving had no defects located below the uppermost portion (top 1/6th) of the tree. Eight trees were identified as suitable for cedar bark stripping, including 5 yellow cedar and 3 redcedar. The mean DBH of bark stripping trees was 99.0cm (+/-40.1cm). Three bark stripping yellow cedar trees with relatively small diameters (45.0, 57.0, and 68.0cm DBH) were identified as trees that would be used primarily for bark stripping rather than carving. I detected no significant differences between riparian and upland forest types in the proportion of trees observed to be suitable for bark stripping (p= 0.711).

Old-growth stands had significantly more large instream logs (defined as instream logs >60cm diameter) than second-growth stands (t = 5, df = 2, p-value = 0.038) (figure 2-5). Also, old-growth riparian forests had more than 4 times the mean volume of instream woody debris than second growth forests (30.33 m^3 compared to 4.96m^3 per 50 m transect), but this difference was not statistically significant (t = 1.524, df = 2, p-value = 0.267), and neither was it when standardized according to stream width (t = 2.864, df = 2, p = 0.103).

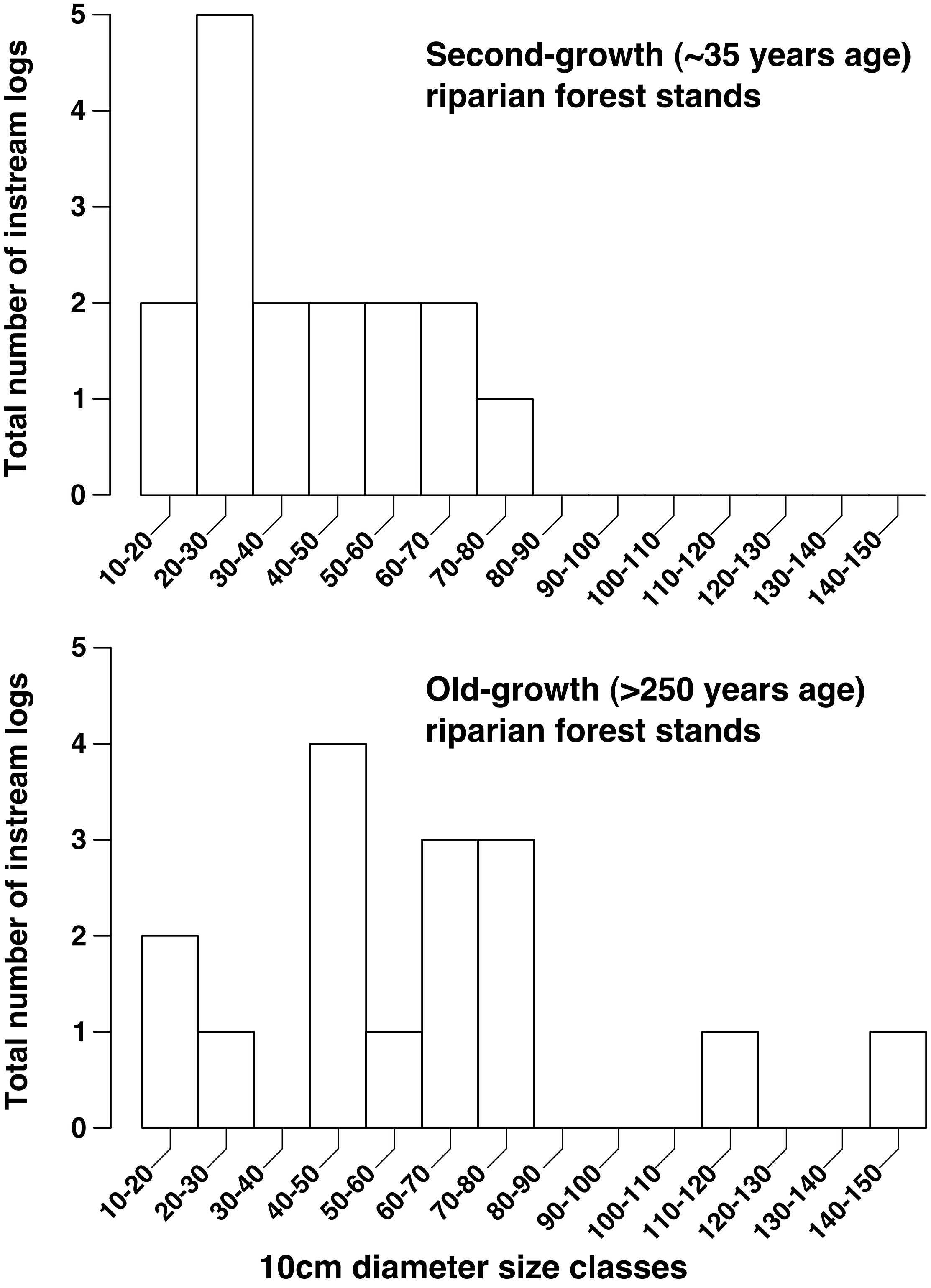

Figure 2-5. Size class distribution of instream woody debris (fully within the course of the stream) measured along 50m stream transect at all riparian forest stands. Overall, old-growth stands had significantly more instream logs >60cm diameter (t = 5, df = 2, p-value = 0.038).

Canopy openness was positively related to abundance of salal berries, but this was only significant at the $p < 0.10$ level ($F_{(1-10)} = 3.611$, $p = .0866$, $R^2 = 19.18$) (figure 2-6). Increasing canopy openness explained 36.4% variation in merchantable salal greenery when fit with a non-linear smooth line, but this relationship was not significant ($p = 0.222$; figure 2-7). Of the 456 trees I measured during fieldwork, 192 were growing on a substrate of a visible fallen tree, or nurse log, as opposed to the soil substrate. Of these, the proportion of trees growing on nurse logs was significantly higher in riparian forests than it was in upland forests ($p = 0.0353$, figure 2-8) whereas forest age had no effect ($p = 0.8136$).

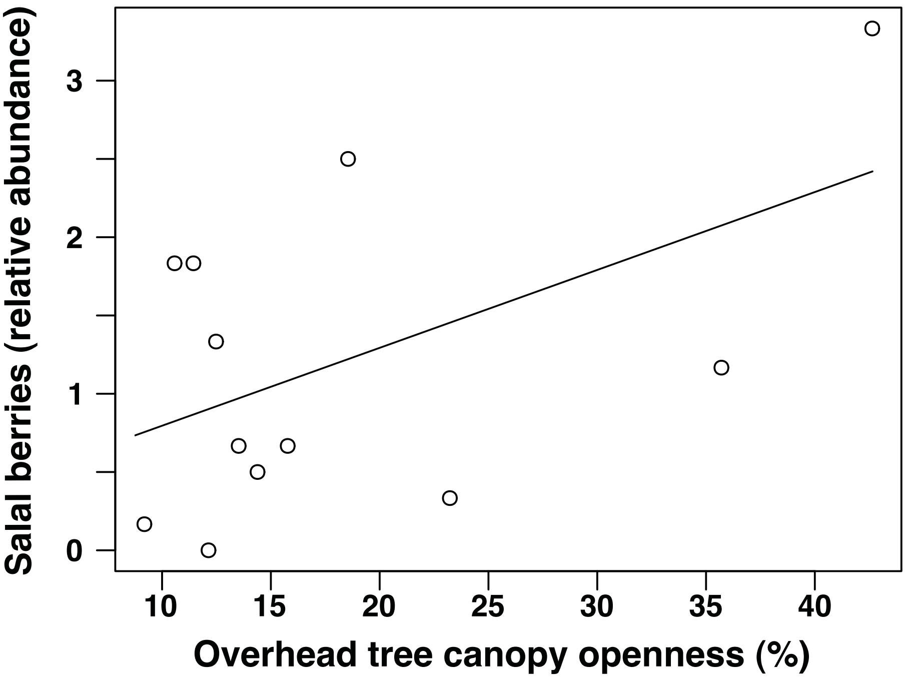

Figure 2-6. Relationship between salal berries and overhead canopy openness ($F_{(1-10)} = 3.611$, $p = .0866$, $R^2 = 19.18$). Both the explanatory and response variables (a measure of relative abundance) are calculated based on the average of 6 understroy plots.

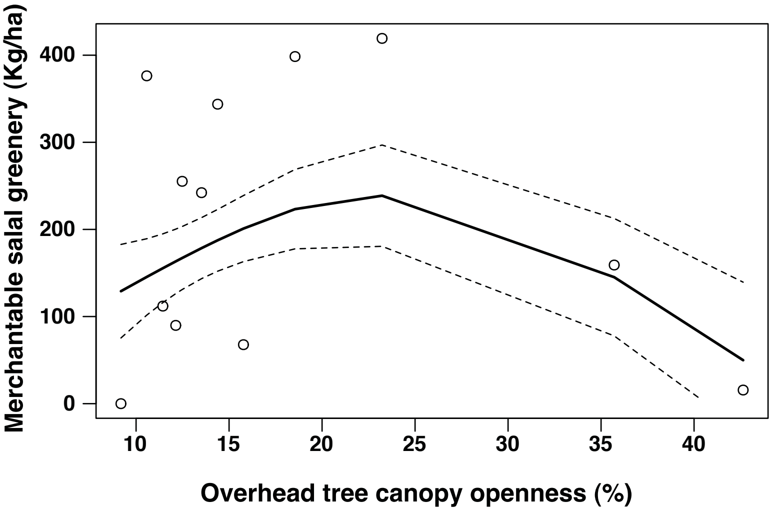

Figure 2-7. Relationship between overhead canopy openness and merchantable salal greenery. Canopy openness explains 36.4% of the variation in merchantable salal greenery, but this relationship is not significant (p = 0.222). Dashed lines represent 95% Bayesian confidence intervals.

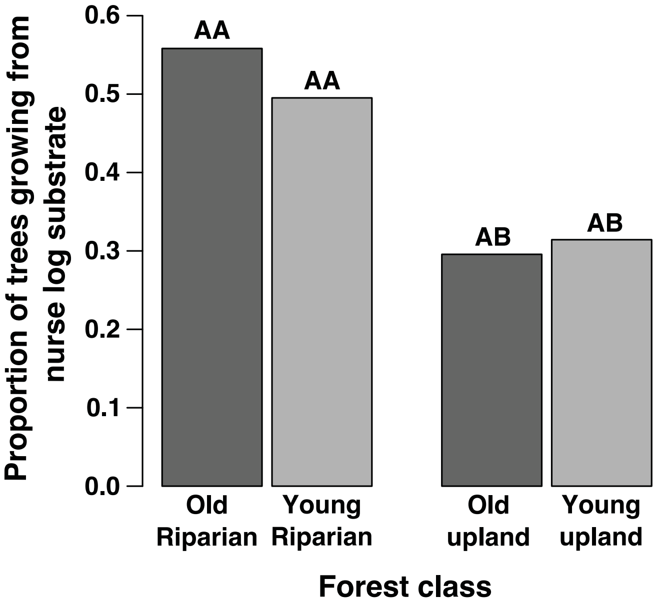

Figure 2-8. The proportion of trees growing on nurse logs compared to ground substrate is higher in riparian sites than it is in upland sites (p = .0318). Forest age had no significant effect (p = .7266). Nurse log trees are classified as trees either visibly growing on large woody debris >30 cm diameter or, in the case of older trees, trees with root structures evidently formed due to past growth on nurse logs. Analyzed using a generalized linear mixed model and binomial distribution (n = 456 trees).

DISCUSSION

Effects of forest age and forest type on multiple ecosystem services

ES bundles were influenced more by forest age than forest type, suggesting that the history of management is a key variable determining forest ES. In second-growth forests, the cultural ES (large cedar and habitat for at-risk marbled murrelets) were absent and several provisioning (redcedar wood, non-redcedar wood), regulating (carbon storage) and habitat services (from dead trees) were significantly lower than in old-growth forests. These services, impacted by forest harvest, likely have recovery times substantially longer than 35 years time span since harvest (see Chapter 1). Forest management history is thus a key variable that drives ES bundles.

The substantial and significant differences in ES bundles among forest classes highlights the importance of incorporating heterogeneity among forest stands when assessing ES. In particular, riparian old-growth forests were a hotspot of ES provision, providing, for instance, more than three times the carbon storage as old-growth forests on upland terrain, and nearly 12 times the carbon storage as upland second-growth stands. Assuming uniformity of ES provision across large extents of forest risks generalization errors in assessment and may lead to misplaced management efforts to conserve or restore ES (Plummer 2009, Eigenbrod et al. 2010).

While the differences in ES among forest classes I observed caution against using forest cover as a general proxy in ES assessment, they do lend support for using a fine-scale benefits transfer approach (Plummer 2009). Benefits transfer extrapolates known measures of ES (in monetary or biophysical units) for a given mapping unit across a study extent. Estimates of ES provided by a given forest class, such as those derived from my study, could be linked to fine-scale spatial data that is already widely available. For example, while mapping of few ES has been done on the BC coast, similar historical datasets, forest inventory and ecosystem classification as used in my stratification are widely available (Thompson and Gergel 2008, Price et al. 2009, Morgan and Gergel 2013). Making use of existing data, familiar to local forest managers and planners, may help bridge ES assessments into existing resource management frameworks. Thus it may help reduce extensive data gaps that impede management of forest ES.

Indicators for management of First Nations cultural ecosystem services

The rarity of cultural cedar in all forest stands suggests that careful management, supported by accurate indicators, is needed to sustain this important resource. Cultural cedar trees were rare everywhere, and absent altogether in recovering forests, which corroborates the observation of Gergel et al. (in review) that large cedar may be substantially reduced from baseline levels in this heavily harvested region. I observed that riparian old-growth forests were the only forest class containing large cedar suitable for canoe carving, suggesting that this forest class may be a priority for establishing cultural cedar stewardship areas. In many circumstances, a coarse filter approach to identify stands dominated by good quality cedar (especially redcedar) of various sizes may be an appropriate stewardship strategy, especially over larger areas. Stewardship of diverse age and sizes is furthermore integral to ensure long term supply of cedar to meet prevailing and future needs of this slowly developing resource (BC Ministry of Natural Resource Operations 2011).

Through working with a local carver I identified characteristic tree sizes and traits for different types of cedar cultural uses. Cedar for canoe building appear to require the most particular traits; namely, sound large redcedar of exceptional quality, devoid of defects or branches in lower part of the tree. The mean sizes of large cedar identified by the carver (ceremonial poles = 112cm DBH and canoe building = 141cm DBH) were comparable with those found in archaeological studies of tree stumps from historic aboriginal logging (143cm Stryd and Eldridge 1993), but slightly larger than recommended size thresholds for management of cedar on the north coast of BC (>100cm DBH; Hadia Gwaii Strategic Landuse Agreement 2007). The mean DBH of bark stripping trees identified by the carver (99cm) was slightly larger than the mean DBH by identified for living trees historically stripped for cedar bark (74cm; Stryd and Eldridge 1993). While cultural ES are generally classified as non-material goods (MA 2005, Hernández-Morcillo et al. 2013), these trees are concrete tangible objects harvested in quantity in the past and still valued today as an important cultural ES to account for in management. Through working with a carver I've identified biophysical indicators for their management. Acknowledging traditional aboriginal use of trees as a form of cultural ES, and identifying indicators for their management, may lead to improved incorporation of cultural ES into the ES management framework. An important limitation of this work, and likely of any work related to aboriginal use of culturally integral plants species, is that I have only investigated a small subset of the diverse benefits aboriginal people derive from cedar and I have only based my observations on the fieldwork assistance of one carver.

The effects of canopy shading on understory plant ecosystem services

The high variation in understory ES within any given forest class is likely due to the interacting effects of canopy openness, ecological conditions and site-specific interactions among forest vegetation. The hump-shaped response of merchantable salal greenery to increasing canopy openness, although not significant, may be a trend to note for future investigation. It corroborates quantitatively with qualitative data collected from salal pickers in Washington State, which is that salal plants under open canopy have little merchantable quality foliage because they are sun-scorched or in reproductive mode (Ballard and Huntsinger 2006). Similar to the effect of forest type on salal ornamental greenery, forest type likely affects other understory plant ES due to the limited edaphic range of many plant species, which are restricted to certain soil conditions or topographic locations (Clason et al. 2008). For example, the upland ecosystem classification I examined (the CWH vm 1 01) has characteristically thick growth of Ericaceous shrubs (Meidinger and Pojar 1991) including salal (Madrone Consultants 2001). Predictive models that take into account the effect of forest type, canopy openness, and potentially other variables are likely needed to provide the most accurate estimates of understory plant ES.

Indicators for predicting understory ES based on canopy openness could be improved in future work by using a similar nested design as I did but instead taking multiple canopy openness estimates per understory plot (ideally 3-5). Low patchy tree canopies in both old-growth and second-growth stands interfered with the accuracy of my canopy openness measurements, which invalidates an assumption of using this as an explanatory variable in regression. I was able to compensate for this by averaging the understory plots across each tree plot. This provided an accurate measure of canopy openness but caused a three-fold reduction in the sample size.

The higher likelihood I observed for trees to grow on nurse logs in riparian stands compared to upland stands may be due to riparian stands having wetter soils or more intense vegetation competition. Identifying the role of woody debris as a habitat service for sustainable forest management may depend on local site conditions and ecological processes (Wang and Fu 2013). While woody debris was abundant in most recovering stands, further reductions in woody debris in third-growth forests (Feller 2003), may effect tree regeneration in riparian forest stands more than in upland stands. For example, in flood bench riparian ecosystems of the Skeena River on the north coast of BC, a reduction in nurse logs due to historic logging and large flooding events, has contributed to a regime shift whereby old-growth Sitka spruce forests have converted into resilient pioneer forests dominated by black cottonwood (*Populus trichocarpa*), red alder (*Alnus* rubra) and salmonberry (*Rubus* spectabilis) (Haussler et al. 2013). Future development of indicators and criteria related to woody debris should explore additional interactions between site conditions, recovery and multiple ES.

CONCLUSION

Bundles of ES differed significantly across forest stands of varying ages and site conditions, which suggests that age and site conditions are both important variables for assessing ES in forested landscapes. The effect of forest age was most pronounced, implying that site management history is a key variable affecting ES on coastal BC. Old-growth riparian forests were ES hotspots, providing higher levels of cultural, regulating, provisioning and habitat services, suggesting the importance of safeguarding these ecosystem types in particular. High variability both among and within forest classes in understory plant ES are partly attributable to the effect of canopy cover suggesting a need for close examination of forest stand structure in managing multiple ES and predicting change in some ES through time. In this work, I have developed indicators for multiple ES linked to stand-scale forest structural features and also to spatial data sources widely available throughout the coast of BC, Canada. Linking local knowledge with empirical measures of biophysical ES capacity has a promising future to overcome data gaps and support implementation of policies that sustain multiple ES.

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SYNTHESIS, FUTURE DIRECTIONS AND CONTRIBUTIONS TO KNOWLEDGE

SYNTHESIS

The fundamental aim of this thesis was to improve our understanding of forest ES recovery, using the highly valued, but heavily harvested, forests of western Vancouver Island, BC, Canada as a study site. In Chapter 1, my aim was to build a general empirical understanding of the long-term post-harvest recovery trajectories of multiple ES, which I accomplished using a 212 year chronosequence. In Chapter 2, my goal was to test whether local site conditions (riparian forest vs. upland forest) have an effect on a bundle of ES. I did this using field work and with help from a First Nations carver, was able to gain insight into the rarely studied cultural ES of large cedar. Throughout this thesis, I have sought complimentary links between the ES framework and forest ecological understanding, and, in doing so, have managed to systematically build a set of biophysical indicators to track changes in the goods and services people value from forests.

Overall, the empirical results from this thesis establish that forest age and ecosystem classification are two key variables for inventorying, mapping and managing multiple ES in heterogeneous, forested landscapes. The regression models from chapter 1, which show recovery trajectories of eight ES, can directly assist management by establishing ecological production functions —formulas that link key variables of interest for management, in this case forest age, to predict marginal differences in a bundle of multiple ES (Polasky 2008). Ecological production functions are increasingly cited as models needed for accurate ES mapping (Andrew et al. 2015), predicting tradeoffs (Kline and Mazzotta 2012), and informing policy of the marginal costs and benefits of alternative decisions (Wong et al. 2014). The ecological production functions developed in Chapter 1 can be improved in future work by incorporating the effects of site conditions as I have conceptualized in Figure 3-1.

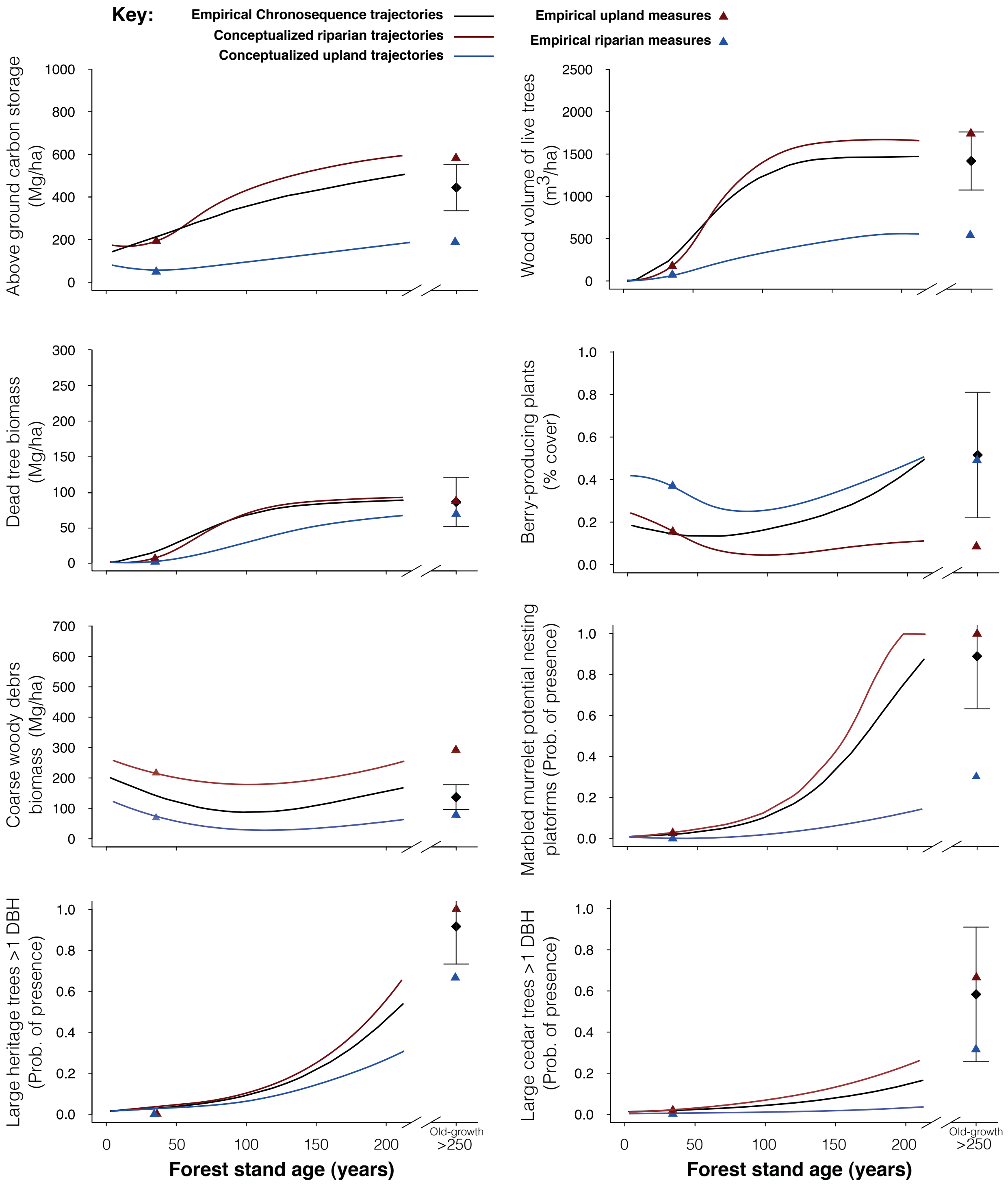
Key:
Empirical Chronosequence trajectories
Conceptualized riparian trajectories
Conceptualized upland trajectories
Empirical upland measures ▲
Empirical riparian measures ▲
Above ground carbon storage (Mg/ha)
0
200
400
600
800
1000
Wood volume of live trees (m^3/ha)
0
500
1000
1500
2000
2500
Dead tree biomass (Mg/ha)
0
50
100
150
200
250
300
Berry-producing plants (% cover)
0.0
0.2
0.4
0.6
0.8
1.0
Coarse woody debrs biomass (Mg/ha)
0
100
200
300
400
500
600
700
Marbled murrelet potential nesting platofrms (Prob. of presence)
0.0
0.2
0.4
0.6
0.8
1.0
Large heritage trees >1 DBH (Prob. of presence)
0.0
0.2
0.4
0.6
0.8
1.0
Large cedar trees >1 DBH (Prob. of presence)
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
200
Old-growth
>250
Forest stand age (years)
0
50
100
150
200
Old-growth
>250
Forest stand age (years)

Figure 3-1. Conceptualized ES recovery trajectories for upland and riparian stands. (Previous page) Predictions shown are based on my Chapter 2 observations for ES in ~35 year age and >250 year age stands. Panel A). Carbon storage in uplands stands will recover along a flatter s-shaped trajectory, beyond the 212 year period due to slow tree carbon increase only slightly exceeding woody debris carbon decomposition. Panels B and C) wood volume and dead tree biomass inflection points are likely to occur earlier in riparian stands, later in upland sites. Panel D) Edible berry producing plants are likely to more abundant in upland sites across all ages (Meidinger and Pojar (1991). Note, percent cover of berry-producing plants shown above was recorded in field but is otherwise not analyzed in rest of thesis. Panel E) in upland sites delayed woody debris recruitment (from slow tree maturation) slows woody debris recovery, compared to faster recruitment in more productive riparian stands. Panel F, G, and H) Marbled murrelet platforms, heritage trees and large cedar recovery inflection points likely to occur earlier in riparian stands, later in upland sites where tree maturation is slower.

Long ES recovery timeframes emphasize the need for proactive planning to mitigate tradeoffs at the landscape scale, for example, by establishing special use conservancy areas (Turner and Bitonti 2011, Bunnell and Kremaster et al. 2010). Conservancies are now being established on the north coast of BC, Canada, for stewardship of biodiversity and First Nations resources (Price et al. 2009, Turner and Bitonti 2011). My results suggest that candidate sites for conservancy should be identified using high-resolution information and indicators to determine that ES levels are indeed high, as opposed to selecting areas based on age alone. Results from Chapter 2 corroborate that local site conditions as well as effects of canopy shading on understory plants can be significant determinants of ES.

I hypothesize that some patterns of ES recovery I observed can be deduced as general patterns likely to be seen in other recovering forests worldwide. Recovery trajectories of some ES (e.g., wood volume and carbon storage) likely follow forest biomass recovery, which can be extremely rapid in tropical areas (Marin-Spiotta et al. 2007, Lohbeck et al. 2014). In contrast, recovery of other ES, such as those linked to specific habitat niches, may be reliant on the slower development of nuanced structural features restricted to old forests, such as large branches, decadent trees with inner rot for cavity nesting birds, and instream large woody debris (Franklin et al. 2002). Further successional processes, such as understory establishment of shade tolerant species, may be required for recovery of valuable timber species or culturally important plant ES (Chazdon 2008). My empirical results add specificity to the long held assumption that different aged forests provide varying levels of ES; they suggest that recovery of a bundle of ES is a multi-staged process and some ES may remain absent for long periods, or indefinitely, in recovering forests.

The rarity of ES such as large cedar in recovering stands is cause for special management attention. Large redcedar trees are culturally sacred to First Nations on the coast of BC, just as the Kaori trees (*Agathis australis*) are for the Maori Indigenous of New Zealand, and the monkey puzzle trees (*Araucaria araucana*) are for the Mapuche Indigenous of Patagonia. However, the cultural importance of large trees remains largely absent from policy (Turner et al. 2009, Blicharska and Mikusiński 2014, Lindenmayer et al. 2014). Bridging traditional values for large trees into the ecosystem services approach, through development of indicators, can help bring these rare resources into policy and management. For example, developing indicators informed by a carver with local knowledge, as I have done in this thesis, provides a means to identify large cedar and establish management criteria to ensure their sustainability (Lindenmayer et al. 2014). Local Indigenous people should be included throughout efforts to conserve cultural forests. Instances where the legacy effects of harvesting may impact some services, and thus some stakeholders, more than others, is a special type of tradeoff demanding greater research and management attention.

FUTURE DIRECTIONS

Towards synthesizing a comprehensive definition of timber harvesting tradeoffs

In this thesis I have improved understanding of the temporal component of ES tradeoffs, which I define as the severity of service-specific impacts to ES from forest harvesting, as well as the persistence of these impacts as forests recover. Future work can integrate these temporal dimensions with spatial analysis. Spatial-temporal models such as ARIES (Bagstad et al. 2014) are capable to model ES at the landscape scales thus being able to identify potential ES shortfalls where ES demand exceeds supply (Bagstad et al. 2014, Howe et al. 2014). For services that require access routes (e.g., for harvest of wild foods) or have other specific spatial configurations (e.g., habitat near the sea for marbled murrelets and viewsheds for landscape aesthetics), the tradeoffs of timber harvest in terms of inducing shortfalls also depend on the location of forests impacted relative to the people that desire them (Wolff et al. 2015, Mitchell et al. 2015).

Variability in successional pathways may also be important in predicting the recovery of ES and hence the persistence of tradeoffs following forest harvest. Thus, one way to account for the unpredictability of vegetation interactions would be to incorporate a measure of the likelihood of poor recovery into predicting tradeoffs from proposed harvest plans (Hearn et al. 2008). A wide literature in coastal forests of BC, Canada, suggests that recovery problems are often limited to identifiable ecosystem classifications, making this an appropriate variable for assessing and managing the likelihood of poor ES recovery (Messier and Kimmins 1991, Madrone Consultants

2001, Poulin and Simmons 2001, Haeussler et al. 2013). Thus, the potential tradeoffs of harvesting a forest stand could be comprehensively predicted on a site-by-site basis according to the expected immediate impact to occur for multiple ES, the persistence of the impacts to multiple ES during forest recovery, and the likelihood of whether or not ES on a given site conditions would recover as expected.

Using forest ecology to build understanding of social-ecological systems

While chronosequences have fundamentally improved our understanding of how vegetation changes through time, they have yet to be applied to build improved understanding of social-ecological system dynamics. Existing chronosequence data are potentially rich sources for developing empirical knowledge to help conceptualize how the role of succession in combination with human drivers can change ES through time.

CONTRIBUTIONS TO KNOWLEDGE

I have shown that forest age and forest type have significant and major effects on bundles of ES, and are thus two key variables for inventorying, mapping and planning for ES in forested landscapes. Furthermore, I have provided empirical insight into the effects of forest harvesting on multiple ES and I have characterized the tradeoffs from harvesting old-growth forests in consideration of impacts to multiple ES and also whether or not these impacts will dissipate during forest recovery.

Through extensive literature review and fieldwork, I have built and refined a novel set of ES indicators (e.g., Table 1-1 and Chapter 2 methods) based on the specific architecture of forest stands as well as readily available geodata. A notable contribution of this work are the indicators I have developed for incorporating First Nations cultural use of cedar into management. Future research can utilize these indicators to incorporate precise measures of ES into field sampling and spatial analysis.

In addition to the knowledge contributions this thesis makes towards sustainable management of forest ES, my empirical tracking of ES recovery forms an improved theoretical understanding of how ES interactions can change through time. In particular, I address a key ES interaction affecting forests worldwide —the tradeoffs caused by timber harvesting on multiple other ES. Together these knowledge contributions set an empirical foundation to steer forest policy and management away from the most persistent tradeoffs of timber harvesting, and closer towards sustainable management for the diverse values that society has for forests.

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