

**EXAMINING THE IMPACT OF THE
NORTHWARD MIGRATION OF YELLOW
CEDAR ON ECOSYSTEM BIOGEOCHEMISTRY
AND THE NET CARBON EQUILIBRIUM**

A THESIS

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FULL BEANS AHEAD

Abstract: Yellow Cedar is an ecologically, culturally, and commercially important tree species; its habitat extends 20° in latitude from Southeast Alaska to the Northern California. It is experiencing extensive decline in areas of low elevation, latitude, and drainage capacity. This decline is due largely to climate change decreasing the snowpack, resulting in root-freezing injuries. Future climate change will place even the northernmost reaches of its range in conditions conducive to mortality by the end of the 21st century, putting Yellow Cedar on a path towards extinction. As vast areas of Yellow Cedar forest experience mortality, the species is also slowly migrating north to newly suitable habitat. Its northward migration is hampered by meager dispersal capability and its niche traits, which limit its competitiveness to marginal soils. The effects of Yellow Cedar's northward migration needs to be better understood to properly implement conservation strategies that can protect the longevity of the species. In particular, how does Yellow Cedar colonization alter soil conditions and forest ecosystem function? Soil biogeochemical analyses in pioneer stands indicate that the presence of Yellow Cedar improves the suitability of soils to many forest species; soils have higher N content and are less acidic. The results also illuminate a decrease in the bioavailability of soil carbon with the presence of Yellow Cedar, which suggests that the species increases carbon storage capacity of soils in temperate rainforests. This suggests an increase in soil respiration in areas of decline, a positive feedback cycle from global warming. Yellow Cedar is an important case study of the global impacts of climate change on our biosphere and a harbinger for many species as climate change intensifies.

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Peace, Love, and Yellow Cedar,

Patrick Journey

Introduction

The greatest problem that our biosphere faces is the magnitude of human-caused climate change. Fluctuations in temperature are an inherent part of climate over time, but taxa will be faced with environmental changes more rapid than ever experienced in global history (Jaskon and Overpeck 2000). In fact, the magnitude of predicted climate change over the next few centuries will be equivalent to the fluctuations of the last 25,000 years (Houghton et al. 1996). The forecasted changes necessitate range shifts of species at rates of 300 to 500 km per century (Davis and Shaw 2001), more than an order of magnitude faster than the velocity of range shifts seen since the Last Glacial Maximum (Neilson et al. 2005). The average species migration rates of 20-50 km per century falls far short of future shifts in suitable habitat, posing a unique and major challenge for nearly every species on earth (Davis and Shaw 2001). Taxa that fail to migrate to new suitable ranges or adapt to tolerate rapidly changing climate regimes will undergo major environmental stress or ultimately extinction (Neilson et al. 2005).

The response of biota to these changes will be far from uniform. Species with very specific climatic requirements are projected to decrease in range on average by 60% by the end of the 21st century (McKenney et al. 2007). It is predicted that these accelerated alterations to global climate will lead to a newly realized climate space with no prior equivalent (Hannang and Wang 2006). Entire plant communities will not shift en masse to favorable habitat; instead, new assemblages will appear as vulnerable species decline and new species dominate (Hennon et al. 2012). The global climate system runs along a multiplex trajectory and never returns precisely to a preexisting state, resulting in novel plant associations through time. These shifts in ecosystem and species composition

will alter the biogeochemistry and potentially form global climate feedbacks as carbon storage of the biosphere transforms in impactful ways. As the magnitude of environmental change increases, population responses will shift from tolerance to habitat shift to migration to extinction (Jaskon and Overpeck 2000).

Climate change specific to northwest North America

Climate change's impact on the globe is far from uniform, with certain regions much more vulnerable to harmful change. Biological response will be particularly substantial in the northernmost ecosystems where the warming signal is strongest (Zhou et al. 2001). Already, the 0.7 °C increase in mean annual temperature for British Columbia has had remarkable ecological consequences (Hamann and Wang 2006). A predicted warming trend of 0.5 °C per decade for British Columbia will place great pressure on its ecosystems and forest resources (Hamann and Wang 2006), which will lead to a marked reorganization of forest ecosystems (McKenney et al. 2007).

Specifically for British Columbia, predictions are of a potential movement of suitable habitat of up to 1000 km for tree species, a vast shift in latitude (Hamann and Wang 2006). Less than 15% of future potential habitat has even a meager probability of colonization within the next 100 years by tree species (McKenney et al. 2007). These local changes to the climate are especially concerning for the Mountain Hemlock zone, which consists of a narrow band on the east side of the coastal mountains where Yellow Cedar maintains a major presence (Hennon et al. 2012). By 2050, there is nearly no spatial overlap with the current climatic envelope for this zone, which will cause major loss to some of the most important conifer species (Hamman and Wang 2006).

Yellow Cedar's vulnerability as a niche species

Large swaths of temperate rainforest are dying off at alarming rates in Southeast Alaska. The casualty of this epidemic, Yellow Cedar (*Callitropsis nootkatensis*, (D. Don) Spach), is experiencing mortality at an unprecedented scale. Given this species' ecological, commercial, and cultural importance, it is critical to understand the cause for this decline and the greater implications of this trend. Furthermore, it is imperative to better understand the capacity, potential, and impact of Yellow Cedar's migration north to create conservation strategies to best promote its longevity.

Yellow Cedar is found largely along the coastal regions of Alaska and British Columbia, with disparate populations south of the Canadian border at high elevations (Hennon and Trummer 2001). In total, its range spans over 20° of latitude and Yellow Cedar is one of the central components of the region's temperate rainforests (Buma et al. 2016). In Alaska, Yellow Cedar can be found from sea level to treeline, whereas elsewhere in its range it is predominantly limited to high elevations (Harris 1990). Yellow Cedar is the most valuable tree in the region (Hennon and Trummer 2001), known for its strength and capacity to maintain its structure well after mortality (Hennon et al. 2012). Its heartwood resists decay for up to 100 years after dying (D'Amore and Wittwer 2008). It also has great importance for the indigenous people of the region. It is the predominant building resource for canoe, longhouse, and totem pole construction, and its bark is used as a material for weaving. Yellow Cedar is also deeply rooted in indigenous mythology and spirituality (Turner 1998).

This species is a defensive, slow growing tree, commonly living to more than 1000 years (Harris 1990). It is able to withstand a diverse array of natural pathogens

(D'Amore et al. 2009) and diverts considerable resources towards defense against a number of biotic stressors (Schaberg et al. 2011). These defenses allow Yellow Cedar to dominate forests over an extended period of time (Harris 1974), despite its very low reproductive capability (Hennon et al. 2008). Through gaps in the canopy and a variety of niche traits, Yellow Cedar can slowly outcompete other conifers and extend its reach out of areas of initial colonization (Krapek 2016).

Yellow Cedar is most competitive in low productivity forests. These sites are typically highly saturated, low in the availability of nitrogen, and maintain a slow turnover of nitrogen (D'Amore et al. 2009). It is able to thrive on these marginal soils due to its high concentration of fine root biomass in the shallow soil horizons (Schaberg et al. 2011). This allows for greater uptake of a form of nitrogen (NO_3^-) that other species lack sufficient access to (D'Amore et al. 2009). This greater concentration of roots in the upper soils also increases access to base cations found predominantly in higher soil horizons (Dahlgren et al. 1991).

Cold hardiness is of great importance in the fall before snow can insulate roots from freezing events (Sutinen et al. 1998), but historically snowpack has remained sufficient through spring to protect roots from temperatures that could cause damage (Schaberg et al. 2008). Another previously competitive trait for Yellow Cedar is that its roots de-harden in late winter and early spring before its competition. The shallow roots are 13 °C less cold tolerant in late winter (*Figure 1*) than Spruce or Hemlock (Schaberg et al. 2005). The roots are poised for uptake of nutrients during spring pulses of nitrogen while the other species' roots are still hardened to the extent of limited physiological activity (D'Amore et al. 2009). Thus, the susceptibility of Yellow Cedar in spring to cold

temperatures has not historically been a disadvantage, and in fact has given the species a competitive edge against its competition (D'Amore and Wittwer 2008).

Another competitive trait contributing to its niche is its unique accumulation of calcium in its plant tissues, which aids in the assimilation of nitrate (D'Amore et al. 2009). Yellow Cedar foliage on the forest floor increases the concentration of calcium and thus deacidifies the pH of the soil due to calcium's basic properties (Hennon et al. 2012). This is suggested to lead to higher rates of biological activity and decomposition compared to sites without Yellow Cedar. Calcium promotes higher bacterial biomass, which allows for greater nitrogen uptake relative to the low nitrogen concentrations of these highly

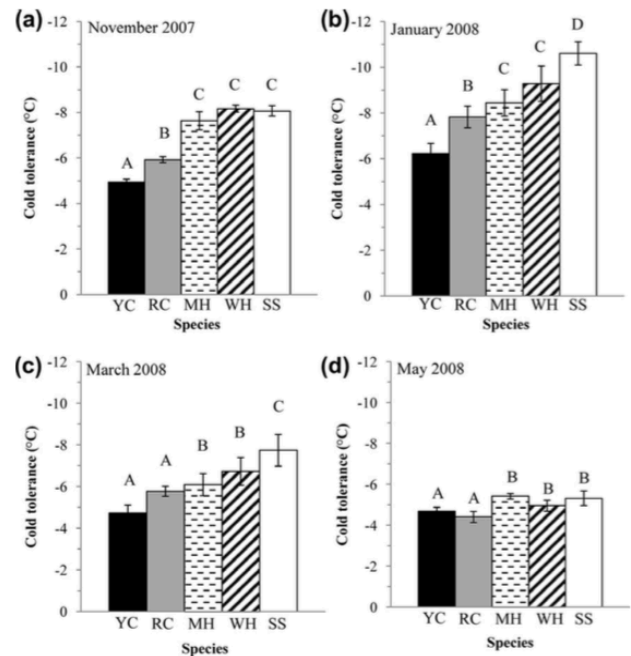


Figure 1 shows Yellow Cedar's cold tolerance compared to the other present species (western red cedar (RC), mountain hemlock (MH), western hemlock (WH) and Sitka spruce (SS)). The four graphs show cold tolerance varying throughout the seasons. Yellow Cedar is consistently the least cold tolerant. The greatest difference is apparent in late winter when snowpack has historically maintained insulation (Schaberg et al. 2011).

saturated sites (D'Amore et al. 2009). This is because a more neutral pH increases both the rates of mineralization and nitrification, creating additional availability of nitrate (Booth et al. 2005). Yellow Cedar utilizes the linked uptake of nitrate anions with calcium cations to better exploit nutrients in shallow soil horizons (Hennon et al. 2012).

These traits allow Yellow Cedar to occupy a niche of being highly adapted to colonize marginal soils.

Yellow Cedar's historic range shifts

Yellow Cedar's range has shifted considerably in recent history. During the Holocene, warmer climate in the region propelled the species into a northward migration, especially on areas of poor soil drainage. During this time, snowpack remained substantial enough to limit die-off in the southern extent of its range (Beier et al. 2008). In the period of the Little Ice Age, increased snowpack and cooler climate in Southeast Alaska promoted the colonization of Yellow Cedar into lower elevations, greatly expanding the local extent of its cover (Hennon et al. 2008). The spread was also largely centered on saturated and nitrogen limited soils where the species is the most competitive (D'Amore et al. 2009). These two expansionary periods led to the abundance of Yellow Cedar in the region. The culmination of the Little Ice Age in the mid 19th century marked the onset of Yellow Cedar decline. This decline is recorded to have commenced at approximately 1880-1900, although the original decline was limited in its extent of destruction and has since accelerated greatly (D'Amore and Wittwer 2008).

Factors of decline

What were once competitive traits for Yellow Cedar - shallow roots and early de-hardening to maximize nitrogen uptake in saturated and nitrogen-limited soil - have now become major factors of decline for the species. With a higher concentration of roots in the upper soil horizon (D'Amore et al. 2009), Yellow Cedar has a heightened risk of

mortal root freezing injury (Schaberg et al. 2011). Sufficient snowpack dramatically diminishes the likelihood of root freezing injury, and reductions in snowpack in the 20th century are now considered the leading cause for the unprecedented decline (D'Amore et al. 2009). A majority (78.8%) of the die-off of Yellow Cedar is located in regions of low snowpack and nearly all (94.3%) are in either low or moderate snow accumulation zones

(Beier et al. 2008). The regions of low snowpack are predominantly at low elevations in Southeast Alaska. Another impact of this decline is the finding that Yellow Cedar at higher elevations maintain higher cold hardiness of its roots later into the season (Beier et al. 2008), increasing the disparity of decline along an elevation gradient. This decreases the severity of damage during a thaw-freeze event at both higher elevations and higher latitudes (Davradou and Hawkins 1998).

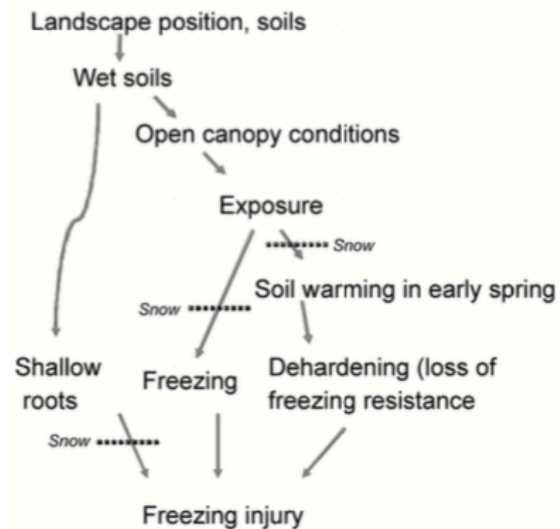


Figure 2 shows the cascading factors causing Yellow Cedar decline. The dotted lines indicate when snowpack disrupts this process by insulating roots (D'Amore and Wittwer 2008).

Another central factor of decline is the level of soil moisture. Highly saturated soils limit Yellow Cedar root depth, which increases the impact of a freeze-thaw cycle (Hennon et al. 2010). The spreading pattern of Yellow Cedar decline occurs along a gradient of soil saturation (Hennon et al. 1990): trees on sites of highest saturation are the first to die (D'Amore et al. 2009). After an initial die-off in a stand, an opened canopy induces much greater temperature fluctuation, which promotes further decline at

accelerated rates (Schaberg et al. 2011). Yellow Cedar has been found to be most susceptible to mortality when there are at least seven growing days in the spring followed by at least three freezing days (Beier et al. 2008). The spreading epidemic of Yellow Cedar decline has centered on sites with highly saturated soils in its southern range but continues to expand upwards in latitude and elevation as snowpack diminishes.

Current and future decline

The decline of Yellow Cedar since the end of the Little Ice Age has extended to more than 200,000 hectares (ha) of temperate rainforest in Southeast Alaska (Beier et al. 2008). An additional 50,000 ha of Yellow Cedar has experienced mortality along the coastal region of British Columbia (Westfall and Ebata 2009). Mapping the decline has been possible due to the decay resistance of the heartwood, with dead Yellow Cedar standing completely intact up to 100 years after mortality (Kelsey et al. 2005). Records show that snowfall has steadily decreased since 1950 at an increasing rate (Beier et al. 2008), and with continued warming the decline is predicted to escalate in magnitude and scale. The highest concentration of mortality causing thaw-freeze events have occurred in the last two decades (Beier et al. 2008).

Modest changes in climate can have a dramatic impact on total snow deposition and the duration of snowpack (D'Amore and Wittwer 2008). Temperatures in this region are increasing at the fastest rate in February, which is important both because this is when Yellow Cedar roots experience de-hardening and also because warming events in February can have significant impact on the seasonal extent of snow cover (Beier et al. 2008). The rainforests of Southeast Alaska are expected to experience the greatest

increase in frost-free days of any region in North America during the 21st century (Meehl et al. 2004). This will likely push the winter climate across the snow–rain threshold, a terrible scenario for the longevity of Yellow Cedar (Hennon et al. 2012). There are projections that even the most northern range of Yellow Cedar will be vulnerable to decline by the end of the 21st century, especially at lower elevations (Krapek 2016).

With the unprecedented pace of climate change due to the human production of greenhouse gases (Every Scientist 2017: IPCC 2007), climate is predicted to shift at a rate faster than vegetation is able to respond (Hamann and Wang 2006). Yellow Cedar's niche competitive traits and poor ability to migrate makes this species much more vulnerable to changes in climate than its competitors. There is high concern that its rate of migration will not keep pace with warming climate, a major threat to the survival of this species (Malcolm et al. 2002). This species is not unique in its response to warming climate; its response is simply at an accelerated and greater scale than its counterparts. Yellow Cedar decline also parallels a similar die-off of Yellow Birch and other northern hardwood species on the east coast of North America (Beier et al. 2008). Future warming will likely have far reaching impacts on nearly all plant species. The decline of Yellow Cedar across broad swaths of the region indicates the vulnerability of temperate rainforests to warming (Beier et al. 2008) and may be a harbinger of future changes on a much greater scale.

Effects of decline

The impacts of Yellow Cedar die-off are far reaching on both a local and global scale. In the regions experiencing this decline, there is potential for species conversion to

Western and Mountain Hemlock, but these species are not capable of tapping into the limited nitrogen sources in these saturated soils and do not thrive where Yellow Cedar previously dominated (D'Amore et al. 2009). This indicates an overall decline in the cover of temperate rainforest in the region. This impact is consequential both for the local ecosystem and also in its capacity for carbon storage. The marine temperate rainforests of North America have the carbon storage capacity (per unit area) of well over double any other ecosystem on the continent (Zhu et al. 2012). With potential for permanent transition from temperate rainforest to less carbon rich ecosystems, this decline will contribute to more carbon in the atmosphere and additional warming.

On a micro scale, areas of Yellow Cedar decline are correlated with greater magnitude of landslides, a major ecological disturbance. While prior to this decline the dominant disturbance of the region was wind throw, an emerging disturbance is the die-off of cedar itself, which not only leads to loss of rainforest cover but also an increase in landslides (Buma and Johnson 2015). The impacts on the local timber economy and the indigenous people who still rely on Yellow Cedar for their livelihood are significant as well, as Yellow Cedar is a major source of prosperity for the region (Hennon and Trummer 2001).

Species control on ecosystems

Individual species maintain important controls on ecosystem function. Plant species are dominant controllers of the activity of soil microbial communities, which impacts nutrient cycling (Knops et al. 2002). Alterations to plant community structure and composition - especially the loss of a major species such as Yellow Cedar - have

important consequences for how elements cycle through the soil (Hobbie 1996). Nitrogen, in particular, is heavily influenced by plant species. Different species compositions can lead to varying rates of nitrification and de-nitrification in an ecosystem, which is important due to nitrogen's limiting qualities for productivity (Knops et al. 2002). Plant species shifts can also alter carbon inputs, which can shift net carbon equilibrium and impact carbon fluxes (Hobbie 1996). It is important to understand the role specific species play in these processes to gain insight on the impact of species migrations and declines.

Certain species can be considered an ecosystem engineer or a keystone species due to their heightened importance for ecosystem function. Ecosystem engineers modify habitats, directly or indirectly control resource availability for other organisms, and oftentimes create more species diversity (Jones et al. 1997). A keystone species is the foundation of a community's structure, and the persistence of the ecosystem is determined by their activities and abundance. The loss of a keystone species entails a decline of overall ecosystem functions and can lead to a total ecosystem collapse as well (Mills et al. 1993). Yellow Cedar creates temperate rainforest on marginal soils that often would not be a rainforest ecosystem without its presence, which indicates its role as a keystone species for certain sites (D'Amore et al. 2009).

As a whole, greater species diversity is correlated with increased water quality, recovery potential, and ecosystem stability and productivity (Worm et al. 2006). Furthermore, soil N content can be more fully utilized with greater diversity of species, which leads to less leaching of nitrogen from these ecosystems (Tilman et al. 1996). The loss of species diversity can be a major threat to ecosystem functioning and can create

domino effects within the community. Species diversity maintains more than an inherent, anthropocentric value, but can also be critical in the overall functioning of an ecosystem (Worm et al. 2006). The loss of Yellow Cedar in temperate rainforests will have many implications as species diversity declines.

Modes of migration

Migration is a multiplex process with great variance for different species and ecosystems. There are four generally supported ecological responses to climate change. Populations can (1) continue to occupy the same range as before, (2) shift locally along habitat gradients such as elevation and soil, (3) undergo migration, often disappearing from former territory and colonizing previously unsuitable regions, or (4) undergo local or complete extinction due to failure to colonize new territory (Jaskon and Overpeck 2000). Future distributions are not only determined by changes in climate, but also dispersal ability and important microbial and inter-species relations (McKenney et al. 2007). Furthermore, climate change will not solely impact the northern and southern limits of a species' range, but also affects taxa throughout (Davis and Shaw 2001), with shifts in population mass, density, and genetic structure (Jaskon and Overpeck 2000).

Analysis of species over the last 100,000 years of climatic oscillations has seen extinctions of large parts of species' ranges, dispersal to new locations, survival in refugia, and varied expansions and contractions of ranges (Hewitt 2000). These individualistic patterns are due to differences among species in the tolerance to climate variables (Davis and Shaw 2001). To survive in the face of environmental change requires the continuance of a potential niche in the realized world and the capacity to

disperse at a sufficient rate over a sufficient distance (Jaskon and Overpeck 2000). A novel barrier for the biosphere is human-altered landscapes, which is a major obstacle to natural migration patterns (Huntley 1991). These altered landscapes will not only impede range shifts, but also stymie gene flow among populations (Davis and Shaw 2001). These constraints will further slow the migration of ecosystems in response to climate change. For Yellow Cedar, both the prospect of the continuance of its niche and its migratory capacity is poor, which will likely lead to either genetic bottlenecking or extinction (McKenney et al. 2007). With such unprecedented magnitude of predicted climate change, many species will follow Yellow Cedar's pattern of decline and acceleration towards extinction (Jaskon and Overpeck 2000).

Adaptation to climate change

While migration is the dominant response to climate change, genetic adaption cannot be ignored for a cohesive understanding of the complexities of the biosphere's response to change. Different species have varying potentials to respond to changes with genetic adaptation due to differing evolutionary response times (Rehfeldt et al. 2001). This interplay of adaptation and migration is central to the biotic response to climate change (Davis and Shaw 2001). It has been found that greater genetic diversity allows for heightened robustness to change and capacity for genetic adaptation (Hewitt 2000). Allozyme studies of tree species in the Northern Hemisphere indicate a decline in genetic variability from south to north, which in turn leads to less potential for adaptation for northern species (Davis and Shaw 2001). However, many northern species are specially evolved for colonization and dispersal as they contain genotypes successful in expansion

after the last ice age (McLachlan et al. 2006). Yellow Cedar's low migratory capacity largely limits its resilience to climate change to genetic adaptation, which is generally poor for species at such latitudes.

Genetic structure of a specific species also varies within its range, with the reproductive biology of many plants suited to different temperature and light regimes across their range (Hewitt 2000). These distinct genetic structures are important factors in migration, as transplanted trees from lower latitudes often perform much worse in the northern range (Davis and Shaw 2001). Evolutionary response times are an important factor in a species' response to climate change, with longer response times requiring greater spatial displacement in light of climate change (Jaskon and Overpeck 2000). If Yellow Cedar were capable of genetic adaptation to the changing climate variables currently influencing the decline, migration would not need be as extensive to prevent extinction.

Tree-specific migration

The Little Ice Age saw a regional decrease of nearly 2°C in the mean annual temperature from 1200-1850 AD. During its entire span, forests remained in disequilibrium with the prevailing climate (Campbell 1993). Even with suitable soils and the presence of all relevant species, it can take several centuries for a forest ecosystem to equilibrate due to lags inherent in serial succession (Hennon et al. 2012). Seedling establishment in mature ecosystems is especially difficult and a major obstacle for Yellow Cedar migration (Neilson et al. 2005). Forest's responses to climate change are multivariate: some experience major forest declines or insect outbreaks, while others may

be subtler, such as a gradual transformation in a forest's species composition (Hennon et al. 2012). Results have shown that in response to the 20th century climate change, 58.7% of the tree species show a pattern of range contraction instead of expansion at both the northern and southern extent of the historic range (Kaizhu et al. 2012). This contrasts with model predictions of populations shifting to higher latitudes, which are often based on past range shifts that neglect the possibility of tree species spreading from refugia. These overestimates hinder our understanding of the environment and changes in taxa since the Last Glacial Maximum (Buma et al. 2014), and analysis of responses to the present climate change contrast with these models.

The center of suitable habitats for 134 US tree species are predicted to shift up to 800 km north based on the average climate projections, while the most common tree species analyzed are expected to shift

no more than 20 km beyond their current northern range in the next century (Iverson et al. 2008). Yellow Cedar's unprecedented decline is likely a harbinger for many other tree species to follow. The predominant pattern observed for tree species (*Figure 3*) has actually been contraction at both the northern and southern boundaries (Kaizhu et al. 2012). These observations bode poorly for the success of most of our forest ecosystems

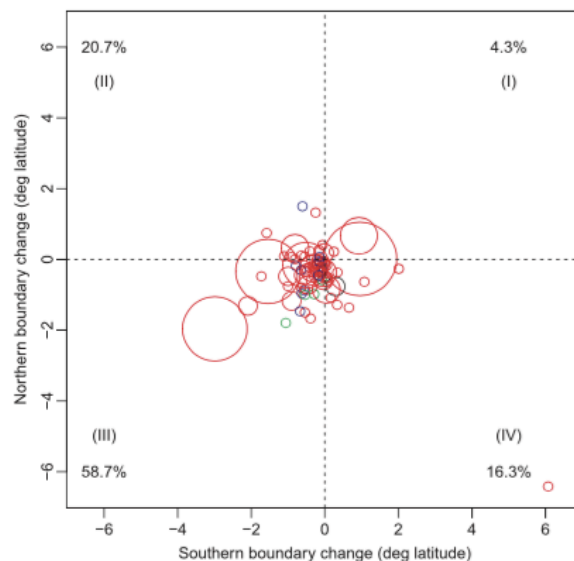


Figure 3 shows different species as a circle, scaled to seed size, with the different quadrants indicating shifts in latitudinal range. A majority of species (58.7%) experience range contraction for both the northern and southern boundary (Kaizhu et al. 2012).

and illuminates major shifts in the make-up of our biosphere. Forest contraction will alter total ecosystem function and induce an overall flux of carbon into the atmosphere, further exacerbating climate change (Zhu et al. 2012).

The Migration of Yellow Cedar

As the southern range of Yellow Cedar shrinks at a rapid pace, the species is also pushing northwards and into higher elevations as regions previously inhospitable become suitable for colonization (*Figure 4*) (Hennon et al. 2006). Yellow Cedar has been discovered as far north as Prince William Sound, substantially northwest of Juneau (Hennon and Trummer 2001). It is unclear whether this remote population has expanded from local refugia or from more recent patchy migration (Hennon and Trummer 2001).

Stands along the Alaskan and British Columbian coasts have migrated to higher elevations since the initiation of decline (Hennon 2006). The Holocene northward migration slowed as glaciers expanded once more in the Little Ice Age, but Yellow Cedar has slowly pushed north since the end of the Last Glacial Maximum (Hennon et al. 2008, Hennon et al. 2006). This

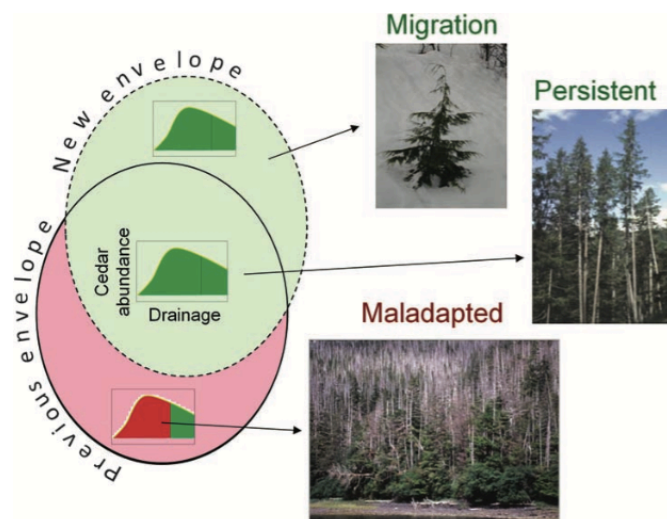


Figure 4 is a diagram depicting range shifts of the species in response to changing climate. Each envelope includes a graph of soil drainage, with the poorly drained soils an important factor of decline (Hennon et al. 2012).

movement is considered segmented, with episodic infillings during opportune openings or on landscapes with low nitrogen and high saturation exposed by glacial retreat (Krapek 2016, Harris 1990).

Yellow Cedar's potential for migration

Stands discovered north of the traditional Yellow Cedar range are increasing in abundance. These pioneer stands are maintaining substantial levels of growth and reproduction, an indication that Yellow Cedar is thriving past the northern extent of its traditional range (Hennon and Trummer 2001). Research has found that Yellow Cedar has only colonized 0.8 % of area suitable for success in the Juneau region (Krapek 2016), indicating an extremely high potential for expansion farther north. This potential for migration and colonization of Yellow Cedar is greatly increased when open growing conditions are present (Hennon and Trummer 2001). It is most common for Yellow Cedar to establish under open canopy conditions or to colonize bog ecosystems where they are the most competitive, and then to slowly expand into existing forests when canopy gaps occur (Krapek 2016). The principal forest disturbance of the Pacific Northwest rainforests is wind (Nowaki and Kramer 1998), with estimates of wind causing approximately 25% of tree mortality in Southeast Alaska (Buma and Johnson 2015). This disturbance is the primary catalyst for canopy gaps that aid in the colonization of Yellow Cedar.

While there is great opportunity for expansion of Yellow Cedar in regions now suitable for its success, the species is slowed by its meager migratory capacity. Without a disturbance, Yellow Cedar saplings have difficulty competing with other species, as they

are relatively shade intolerant compared to Western Hemlock (Harris 1974). Another major limit to their establishment is the presence of deer, which preferentially eat the saplings (Hennon and Shaw 1997). Few seedlings in the Juneau study area are observed to reach maturity both inside and outside existing pioneer stands (Krapek 2016). These barriers for establishment, paired with a weak reproductive capacity, severely diminish the migratory potential of this species.

Adaptive Strategies for Yellow Cedar

Due to Yellow Cedar's economic and cultural importance as a tree species, there is much interest in implementing conservation strategies to maintain its abundance. With vast areas suitable for colonization due to warming climate, yet meager migratory capacity, Yellow Cedar will require adaptive strategies to continue thriving in the region. One strategy for conservation is salvage harvesting: instead of logging healthy and living stands this strategy would limit the collection of timber to the dead stands (D'Amore and Wittwer 2008). Salvage harvesting is economically viable up to 100 years after death due to Yellow Cedar's impressive decay resistance (Kelsey et al. 2005). This would thus eliminate the killing of healthy trees while satiating the timber demand and maintaining the livelihoods of the local timber economy and indigenous groups.

Another adaptive strategy would be to favor Yellow Cedar on sites with better drainage, as this makes them much less vulnerable to freeze events in the spring. This would entail active planning and thinning to help the species compete with other faster growing conifers (D'Amore et al. 2009). While these strategies will slow the demise of the species in its current range, it is important to realize the futility of sustaining this tree

where it is maladapted (Hennon et al. 2012), which by the end of the 21st century could be its entire current range (Krapek 2016).

Thus, a conservation plan that could best ensure the longevity of Yellow Cedar survival is assisted migration north of its current range (Warren et al. 2001). With vast potential habitat (Krapek 2016) and successful planting initiatives (Hennon 1992), this strategy has a high likelihood of success. Studies have found that the survival rate of seedlings when planted is over 90% (Hennon et al. 2012). Rooted cuttings and seedlings have both been recorded to succeed in establishment (Hennon 1992) despite the considerable barriers to success such as deer and competing vegetation (D'Amore and Wittwer 2008).

Yellow Cedar has already experienced massive declines predicted to accelerate with continued warming, and to maintain this valuable species, adaptive management strategies should be implemented, especially assisted migration. However, a human movement of any species can be interpreted as the introduction of an invasive species and furthermore can have unanticipated consequences (Hennon et al. 2012). To properly aid in the migration of Yellow Cedar, research must be done to better understand these implications. Furthermore, the conservation strategy must be dynamic, as climate change will continue changing in velocity and the success of the species will be a moving target (Iverson et al. 2008).

Gaining insight on Yellow Cedar migration

Research is being done on Yellow Cedar pioneer stands to better understand the potential for migration and its impact on the existing ecosystem. A research team from

the University of Alaska - Southeast is the first to quantify the northward range expansion of Yellow Cedar (Krapek 2016). They have characterized the pioneer stands and examined the biotic interactions within them. In collaboration with both the team at the University of Alaska - Southeast and Dr. Rebecca Barnes at Colorado College, I conducted research to better understand the impact this migration has on ecosystem biogeochemistry. This is important to understand the biological complexities of Yellow Cedar, its potential for range shift, and to gain insight into the impact this species has on ecosystem function, in particular nutrient cycling and carbon storage.

It is imperative to have a complete understanding of the impacts of introducing a new species when considering conservation strategies. Expansions and contractions of species have the potential to alter the net ecosystem carbon balance, which is an important global feedback given that rainforests are a major carbon sink with the greatest capacity for storage on the North American continent (Zhu et al. 2012). A better understanding of the expanding northward envelope's effects can be extrapolated to the impacts of the declining southern envelope as well.

Methods

Field methods

Eleven pioneer stands of Yellow Cedar have been discovered north of their historic range near Juneau, Alaska. These stands were located using community knowledge, exploration, and targeted helicopter surveys, and it is expected that additional pioneer stands may exist given limited ability to survey vast areas of forest. Forest stands were fully stem-mapped in Geographic Information Systems (GIS) by other members of the research team, led by Dr. Brian Buma (University of Alaska - Southeast). They also cataloged the biomass

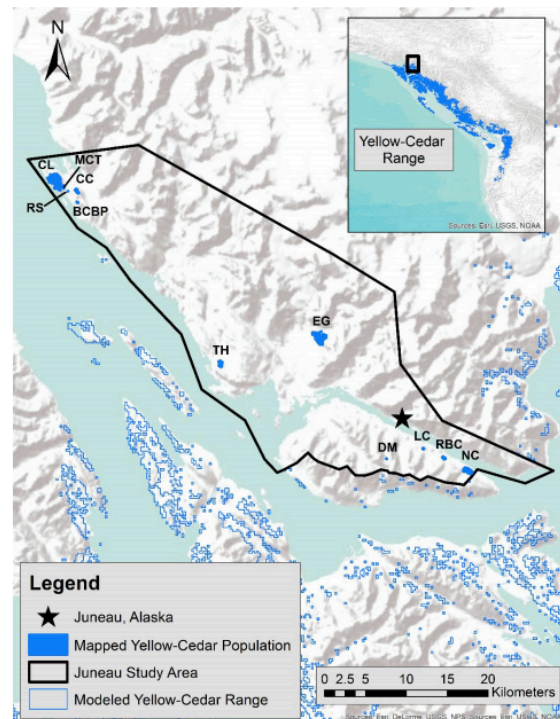


Figure 5: Mapped Yellow Cedar populations in study area near Juneau, Alaska. Map inset shows study area location in context of Yellow Cedar's traditional range (Krapek 2016).

and compared topographic, snow cover, and disturbance exposure metrics. Spatio-topographic trends of the establishment of Yellow Cedar were analyzed, shedding light upon the species dynamics over time (Krapek 2016). Ages of the stands were averaged and growth rates were also estimated with tree core samples. Previous research by

Buma's group provides information and analysis of seedling development, canopy cover, and rates of establishment (for more details, see: Krapek 2016).

Using GIS, transects were randomly placed along the stand boundaries perpendicular to the stand edge. Soil samples were taken from 10 of these transects (n=18 per transect). Soil was sampled three times at each point 8 m, 9 m, and 10 m from the stand boundary, in and out of the stand using a soil corer (343 cm³) (Figure 6). This was made difficult by the woody consistency of much of the soil. For each sample, soil pH and temperature were measured with the Hanna Instruments direct soil pH kit. The dominant undergrowth and overgrowth species and the slope were characterized for each point along the transect. Slope was determined at each sampling location between Flat (0), Shallow (1), Moderate (2), and Steep (3).

After collection, soil samples were stored at 5°C to limit microbial activity. Upon returning from the field, one soil sample from each set of three was weighed and then placed in a drying oven at 60°

C for 24-48 hours to remove all moisture. The samples were re-weighed to determine percent moisture and bulk density. The dried soil samples were sieved through a 2 mm sieve to separate coarse and fine soil fractions. These fractions were

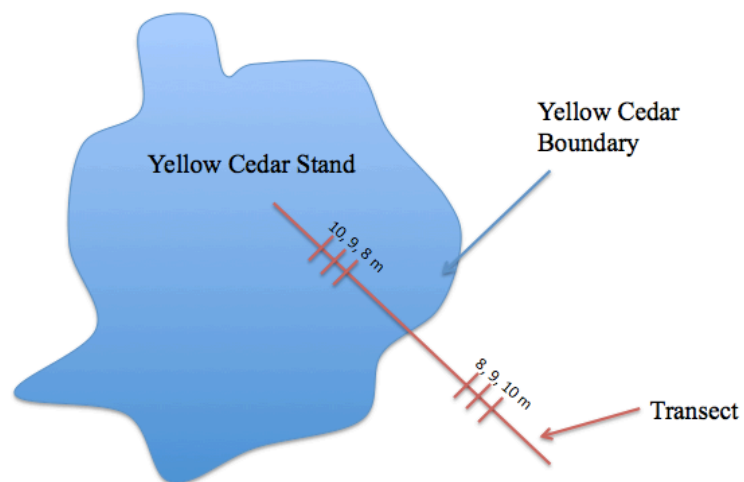


Figure 6 is a visual of field collection of soil samples from within and without the Yellow Cedar stands. Three samples were taken at 8, 9, and 10 meters from the Yellow Cedar boundary, inside and outside the stand (n=18 samples per transect).

quantified by mass.

Lab methods

The remaining soil samples - two from each set collected (120 total) - were used to characterize the soil biogeochemistry. Roots and woody material were removed and quantified from one half of these samples. The percent moisture for the roots and woody material was obtained by comparing their wet and dry weight. A sample of soil was placed in a drying oven at 60° C for 24 hours to determine the dry weight of the soil, which is used to compute percent moisture. Percent moisture was measured immediately following collection and two weeks later in the lab to determine loss of moisture over time and with travel. There was no significant difference between the two percent moisture measurements.

The bioavailability of the soil organic matter was measured using laboratory bioassays. These bioassays occurred at ~5°C and utilized mason jars fitted with gas tight caps that were left off between weekly respiration experiments that typically lasted 2-3 hours. The bioassays used approximately 30-40 grams of root and woody material-free soils and were incubated for a total of eight weeks. Before commencing the weekly respiration measurements, bioassay jars were re-weighed to determine moisture loss and the appropriate amount of MilliQ water was added to restore the soils to field moisture conditions. Jars were then sealed and returned to the refrigerator to incubate at 5°C for 2 to 3 hours. After incubation, 5 mL of headspace was sampled and CO₂ concentrations

were measured on a SRI 8610C Gas Chromatograph. The SRI GC was calibrated daily with three gas standards (101 ppm, 1,020 ppm, and 10,020 ppm CO₂) and lab air was tested (minimum of 3 times) for background CO₂ concentrations. These measurements were taken over a total of eight weeks to record changes in the respiration of soil over time.

To determine headspace volume in the bioassays, the soil fine fraction density was estimated using a graduated cylinder and mass difference. This density estimate was then applied to the mass of soil added to each bioassay jar to determine the soil volume, and thus the headspace volume. The 2-3 hour measurements of CO₂ produced were extrapolated to a week and summed to an eight-week period for a total respiration rate. The relative bioavailability of soil organic matter was calculated by normalizing the total amount of CO₂ produced via respiration to the total soil organic carbon of each soil sample.

To determine the easily accessible organic matter and ions within the soil, approximately 10 grams of each of the sixty soil samples were mixed with 200 mL of MilliQ water. These samples were put on the VWR Advanced Digital Shaker table for 24 hours. The resulting solution was then filtered through pre-combusted glass fiber filters (Whatman GF/F, nominal pore size 0.7 µm). Solutions were stored in the freezer until the samples were run for analysis of dissolved organic matter and cation and anion analysis. Dissolved organic carbon (DOC) and total dissolved N (TDN) were determined on the Total Organic Carbon Analyzer + Total Nitrogen Measuring Unit Shimadzu (Model: TOC-LCPlt). Each sample was run three times and then averaged to improve precision. Cations and anions were determined using the Dionex Aquion Ion Chromatographer

System. A subset of samples had duplicates to check precision of the instrument. The anion and cation measurements were normalized to the dry weight of soil (mg cation/g soil).

The elemental content (% C, % N) and stable isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the soil were determined in the Yale Analytical and Stable Isotope Center (YASIC) using a Costech ECS 4010 Elemental Analyzer with ConFlo III interfaced with a Thermo DeltaPlus Advantage mass spectrometer. Finely ground soil samples were weighed into aluminum tins and sent to the YASIC to be run. The YASIC ran the soil samples against CN2, YGA, and Beech standard reference materials for $\delta^{13}\text{C}_{\text{PDB}}$ and $\delta^{15}\text{N}_{\text{AIR}}$ to measure %N, %C, and the C:N ratio.

Statistical analyses

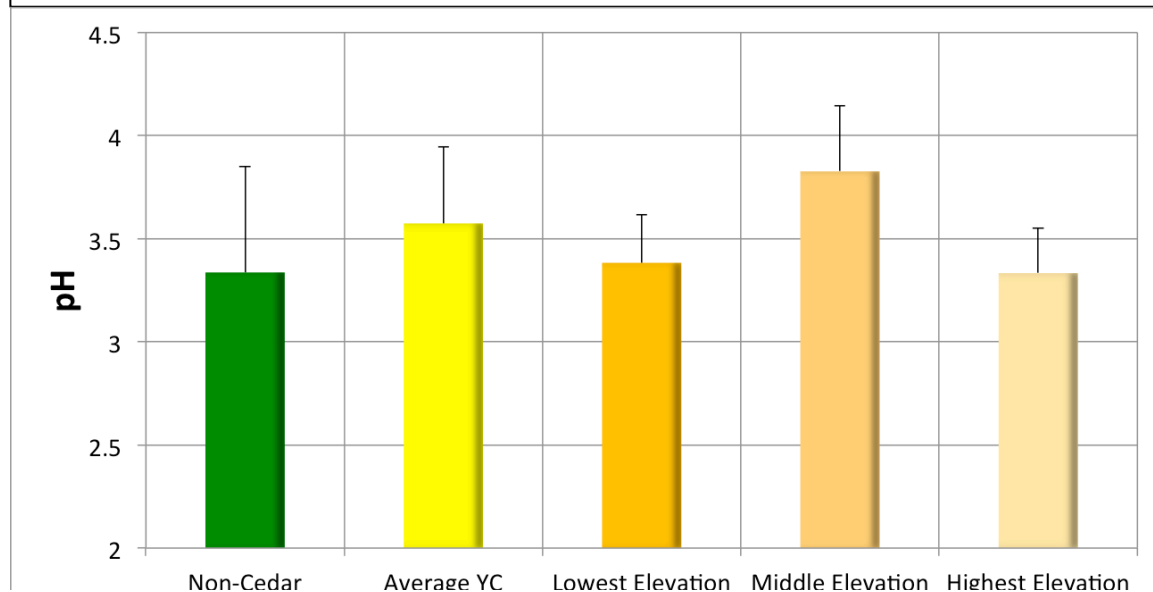
Using the statistical program *Minitab* (Version 17), Yellow Cedar and non-Cedar stand soils were statistically compared using Student's t-test and stand soils were compared across binned age (age = 1, 2, 3) and elevation (elevation= 1, 2, 3) groups using ANOVA. Pearson's correlation (r) was used to examine relationships between continuous variables. Statistical significance was determined when p-value < 0.05.

Results

Soil pH differences between stands

There is strong evidence ($p = 0.002$) that soil pH differs between Yellow Cedar and non-cedar stands. Soil pH is higher in the presence of Yellow Cedar (3.57) compared to non-cedar species (3.36). Soil pH also increases ($p < 0.001$) with Yellow Cedar basal ratio, indicating that the increased presence of the species has a positive relationship with pH. Soil pH is positively correlated ($p < 0.0001$) with Mg^{2+} and Ca^{2+} soil concentrations. pH is also positively correlated ($p < 0.0001$) to species diversity. Another correlation ($p < 0.0001$) was found between slope and pH, with greater slope correlated to a decrease in pH. However, more saturated soils (poorer drainage) are typically more acidic (Thomas et al. 1984) and saturated soils are more likely to occur in shallow slopes, so this relationship is likely spurious.

Figure 7 shows soil pH differences between Yellow Cedar and non-cedar stands. Yellow Cedar stands are also binned between different elevations, with a peak in pH at the middle elevation. Binned Elevation: 0 - 100 m // 100 - 300 m // 300+ m.



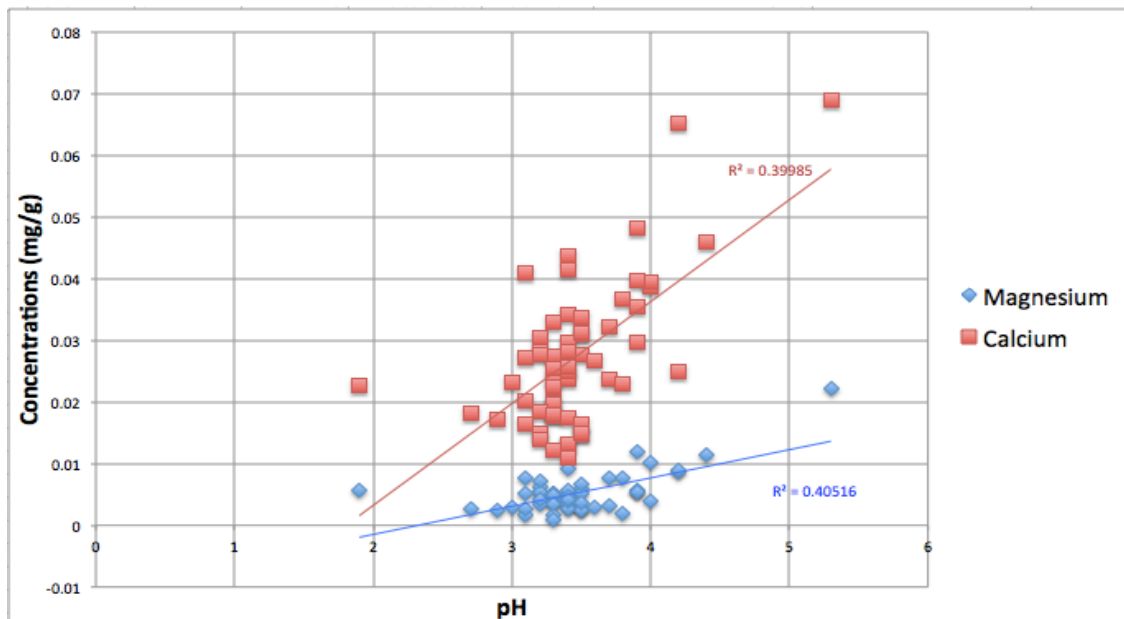


Figure 8 shows correlations between the base cations magnesium and calcium and pH in the soils. Both increase with an increase in pH. Calcium maintains a greater response to changes in soil pH.

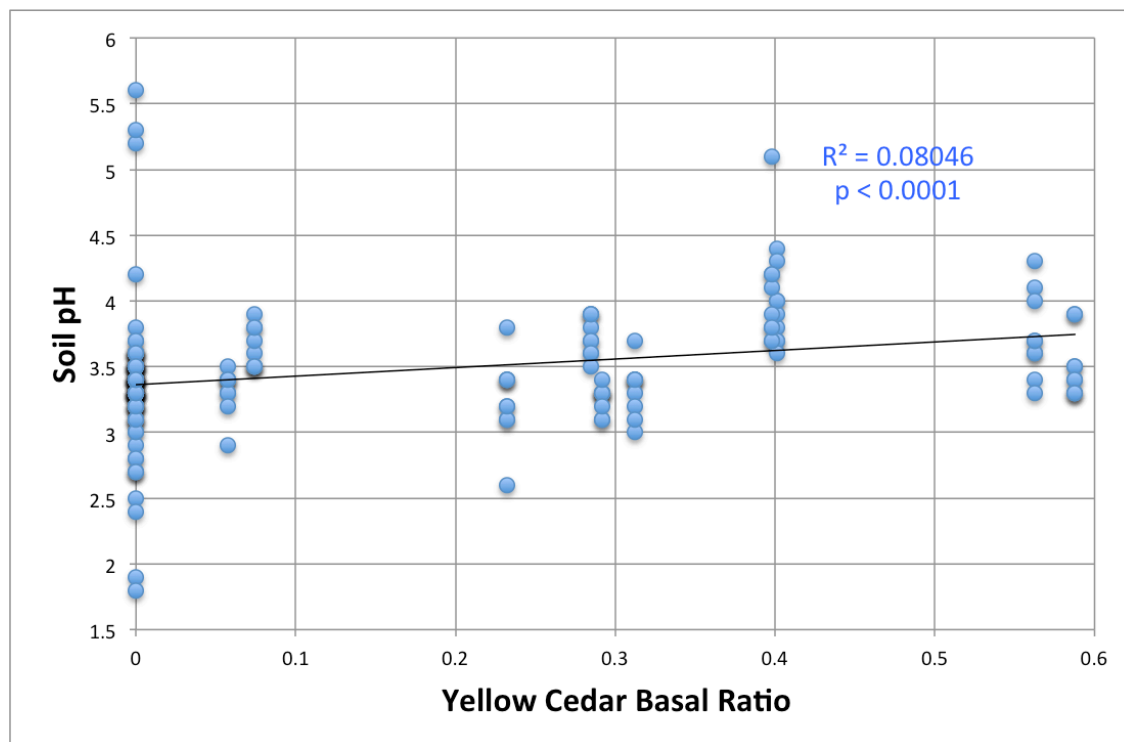
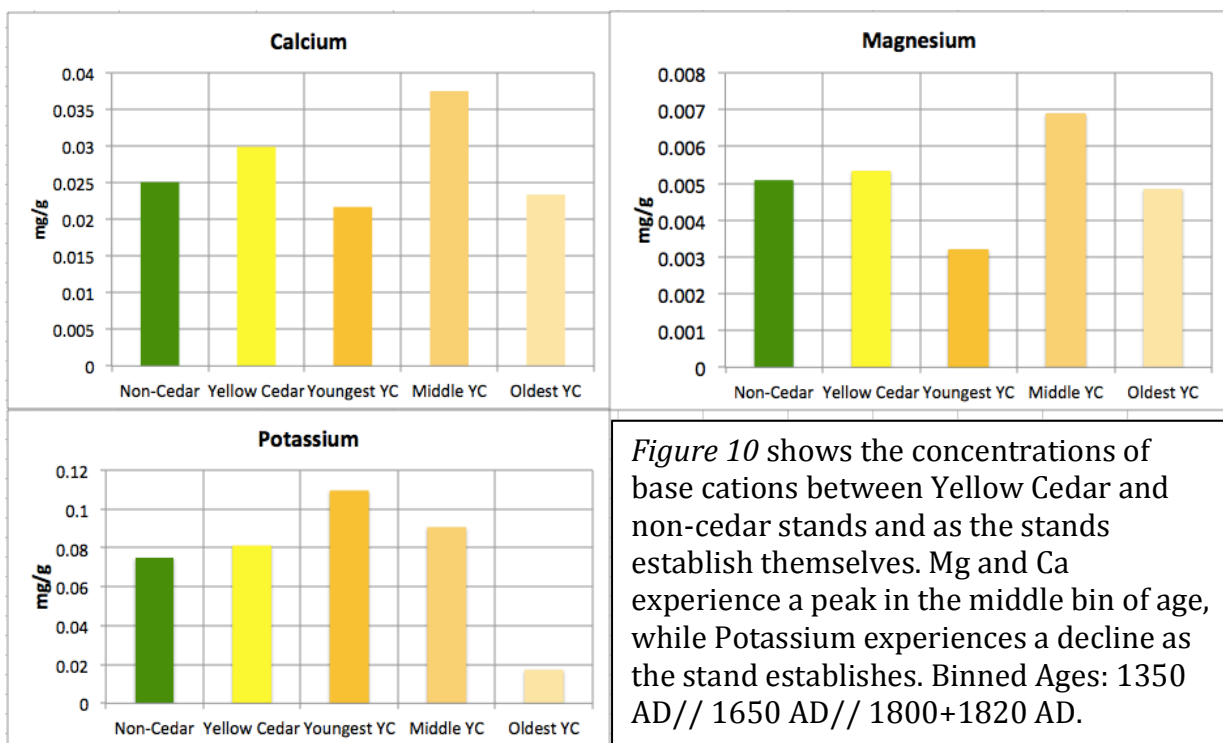


Figure 9 shows the correlation between soil pH and Yellow Cedar Basal Ratio, which positively increases as the ratio of Yellow Cedar increases in the stand. This indicates that the presence of Yellow Cedar decreases acidity of soil.

Trends of base cations

There are higher quantities of the base cations magnesium and calcium in Yellow Cedar soils, although this difference was not statistically significant. Magnesium ($p = 0.059$), potassium ($p = 0.002$), and calcium ($p = 0.001$) all show statistical differences across elevation. Potassium concentrations decrease with elevation, whereas magnesium and calcium are greatest in the middle elevation bin. Magnesium ($p = 0.052$) and calcium ($p = 0.001$) both show strong evidence of this bell curve with the age bins as well. Potassium ($p = 0.0045$), however, shows a strong trend of decreasing with the age of the cedar stands (*Figure 10*).



Soil saturation of Yellow Cedar and non-cedar stands

Percent soil moisture is used as an indicator of overall saturation of the environment. There was no difference between soil moisture measurements made immediately following sample collection and those made two weeks later, prior to the start of the bioassays (*Figure 11*). Soil moisture is statistically greater (3% more) in non-cedar stands as

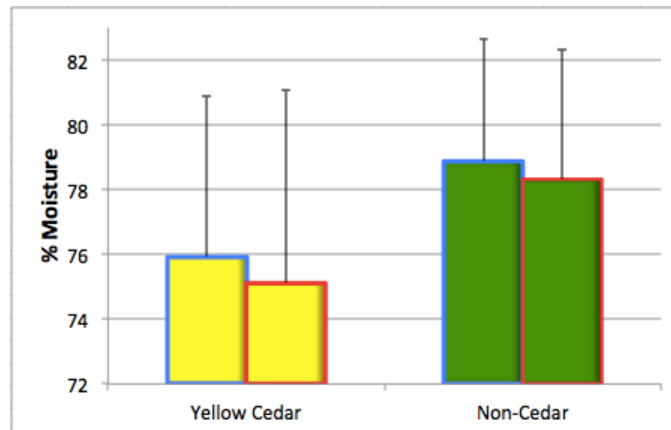


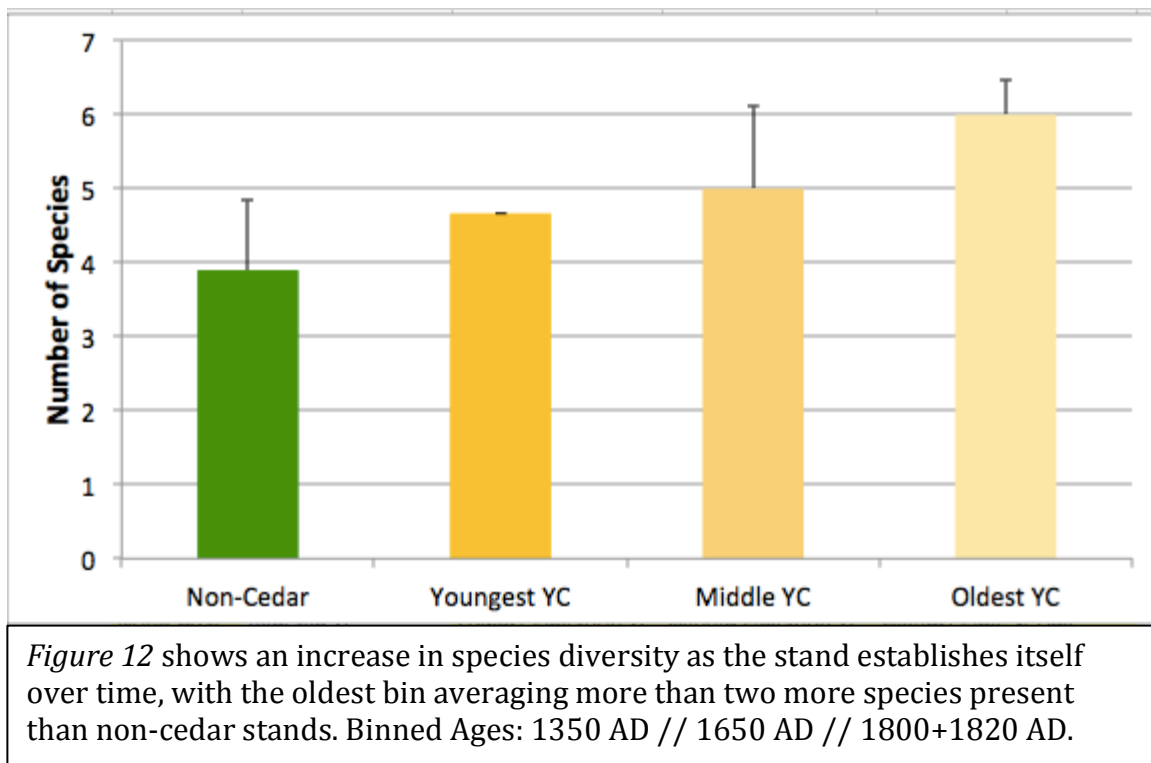
Figure 11 shows percent moisture 1 (blue outline) and percent moisture 2 (red outline) of Yellow Cedar and Non-Cedar soils. Non-cedar stands maintain significantly higher saturation for both measurements.

compared to Cedar stands ($p = 0.012$). Yellow Cedar basal ratio and percent moisture ($p < 0.05$) are negatively correlated, indicating a decrease in saturation with the increased presence of Yellow Cedar. This conclusion contrasts the consensus of literature that Yellow Cedar stands predominantly colonize highly saturated soils (D'Amore et al. 2009).

Species diversity between Yellow Cedar and non-cedar

Yellow Cedar stands contain greater species diversity ($p < 0.0001$). The average dominant understory and overstory species total count for the Yellow Cedar stands is 5.1 species, whereas for non-cedar stands the count is 3.9 species. Accounting for the addition of Yellow Cedar for species diversity, this difference loses its significance. However, there is still an apparent increase in species diversity as stands age ($p <$

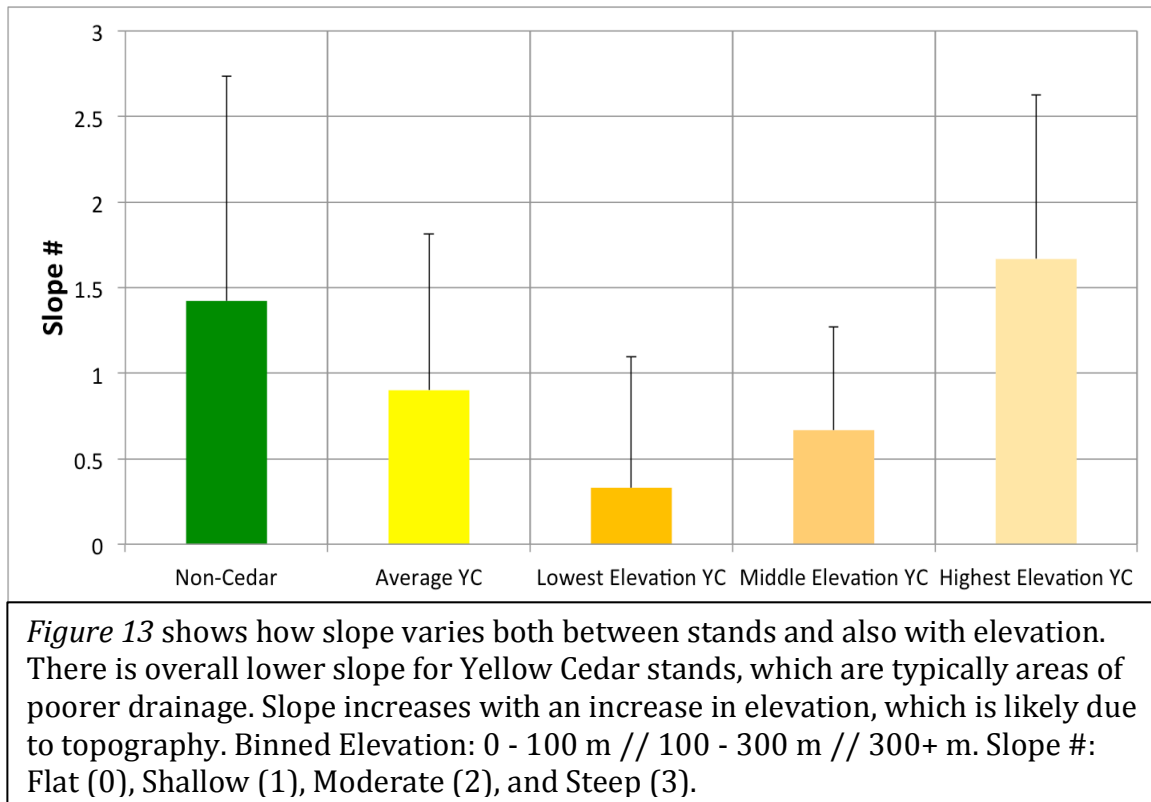
0.0001). The oldest binned Yellow Cedar stands have an average diversity of 6 species, while the youngest stands average only 4.7 species, suggesting that as a Yellow Cedar stand establishes itself over time, species diversity increases. Yellow Cedar basal ratio and species diversity are also positively correlated ($p < 0.0001$), strengthening this observed relationship (*Figure 12*).



Difference in slope

There is strong evidence ($p = 0.003$) that non-cedar stands occupy landscapes with greater slopes (1.42) on average than Yellow Cedar stands (0.9). This finding is consistent with the consensus that Yellow Cedar preferentially colonizes flatter areas, as these soils are often of greater saturation. There is a gradient of slope between Yellow Cedar stands at different elevations, with the highest elevation stands averaging a slope of 1.67 and the lowest averaging a slope of 0.33 (*Figure 13*). This is likely due to the

topography of the region. This is important to note because correlations due to elevation or slope could be a product of both or one variables.



Nitrogen differences in soils

There is no statistical difference in the elemental nitrogen content of the soil between Yellow Cedar and non-cedar stands. Total Dissolved Nitrogen (TDN) does differ between the Yellow Cedar (2.89 mg/g of soil) and non-cedar (3.49 mg/g soil) stands. There is evidence ($p = 0.04$) of an increase in N content over time, with the oldest stands having soils with significantly greater soil %N than the youngest. Furthermore, there is an accumulation of nitrite, ammonium, and TDN as the stands establish themselves over time, indicating a general increase in N content with increasing Yellow Cedar age. This is reflected in a greater presence of ammonium and nitrite in the older

Yellow Cedar soils (0.0073 mg/g compared to 0.0032 mg/g in youngest soils for ammonium). Nitrate, however, experiences a decline in concentration as the stands establish themselves. Higher elevations also maintain higher averages of %N for Yellow Cedar soils, with greater ammonium in the stands at higher elevations.

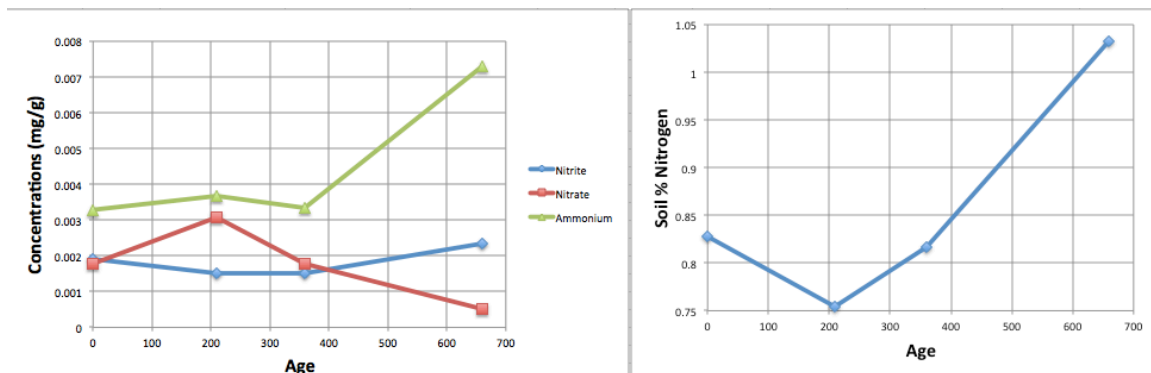


Figure 14 shows how nitrogen varies with Yellow Cedar stands through age. The data for age zero comes from the non-cedar stands. The graph on the left shows nitrate decreasing over time as nitrite concentrations show slight increases and a significant spike in ammonium in the oldest stand. The graph on the right shows a distinct increase in Soil % Nitrogen over time for Yellow Cedar stands.

Carbon differences in soils

There is no statistical difference in % carbon between Yellow Cedar and non-cedar soils. Bioassay data ultimately shows greater CO₂ respiration per gram of carbon in the soil for non-cedar stands. The mean for the Yellow Cedar soils is

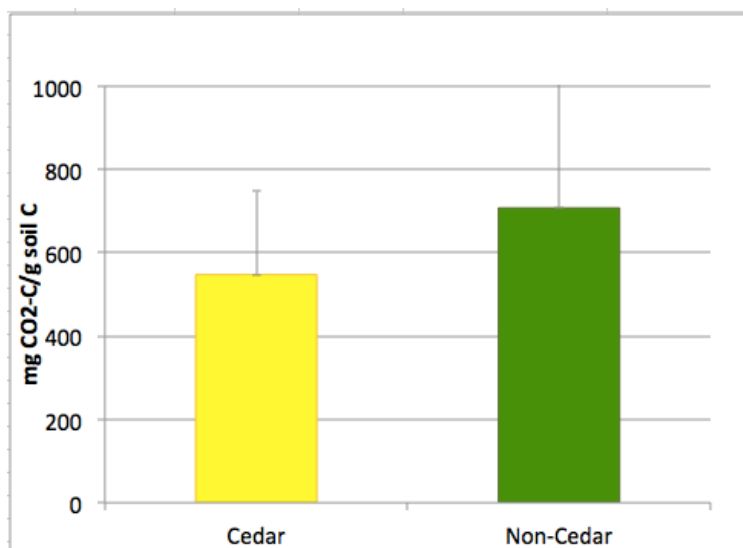


Figure 15 shows that there is greater bioavailability in the soils of non-cedar stands as well as a greater coefficient of variation.

547.1 mg C-CO₂/g soil C compared to 707.2 mg C-CO₂/g soil C ($p = 0.019$). The coefficient of variation (standard deviation/average) for non-cedar CO₂ respiration is 42.675 compared to 37.031 for the Yellow Cedar soils, indicating greater variability for non-cedar stands as well. The youngest Yellow Cedar bin maintains the highest bioavailability ($p = 0.024$), indicating that as the stand establishes itself, this difference becomes greater over time. There is also a negative correlation ($p = 0.003$) between the Yellow Cedar basal ratio and bioavailability, indicating that the higher presence of Yellow Cedar further decreases the bioavailability of the soils.

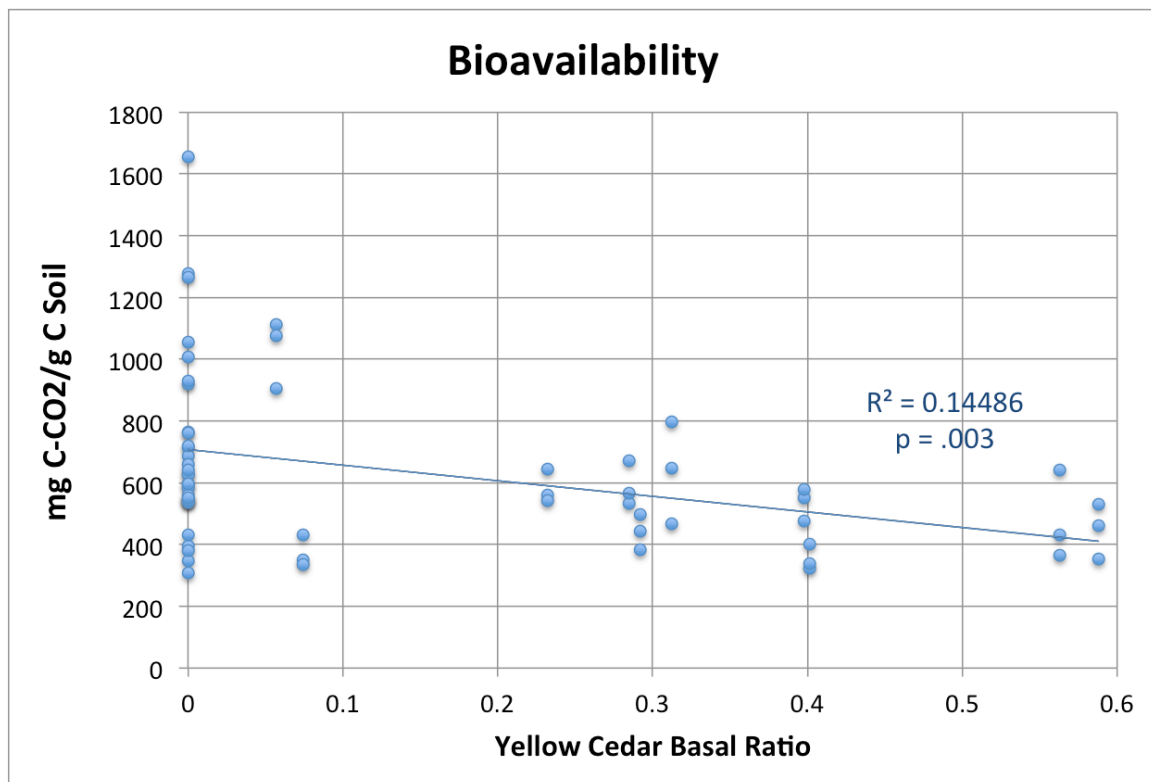


Figure 16 indicates a decrease in the bioavailability of the soils as the basal ratio of Yellow Cedar in the stand increases. Yellow Cedar Basal Ratio data from: Krapek 2016.

Discussion

Climate change's impact on the biosphere

The changes in climate during the 20th century have had a significant impact on species vulnerable to variance in climate such as Yellow Cedar, but the extent has been limited in both scale and magnitude on the biosphere as a whole. Estimates place the total increase in global mean temperature between 2.4 and 6.4 °C by the end of the 21st century (IPCC 2007), with significant alterations to the hydrologic cycle (Trenberth et al. 2003). Even the most conservative forecasts for climate change will have immense impacts on our biosphere. Across all scales, the mean temperature and the balance between precipitation and evapotranspiration are essential for biota because these factors predominantly control the rates of biological reactions (Lafleur 2010). Temperature and precipitation are especially important for microbial activity and net primary productivity (Nemani et al. 2003), which impact total ecosystem function. Yellow Cedar's decline is a harbinger for nearly every species as the impacts of climate change increase, and the future alterations on the ecosystem biogeochemistry and capacity for carbon storage will have significant global consequences.

Constraints to migration

Yellow Cedar's pattern of southern decline paired with insufficient expansion northward will likely be replicated by many other species across the globe as climate change intensifies. Even with a capacity for dispersal to new suitable habitats, there are significant obstacles to successful migration. There are major lags in the serial succession of mature ecosystems (Hennon et al. 2012), which will slow the migratory capacity for

many species. Furthermore, soil properties are a major constraint for species migration (Lafleur 2010). Species are often adapted to very specific soil conditions, which vary greatly both locally and regionally. Species with narrower tolerance to soil conditions will see their migration greatly constrained. With Yellow Cedar adapted to colonize marginal soils low in nitrogen and high in soil moisture, the species struggles to compete on more optimal soils (D'Amore et al. 2009). Other species that are also most competitive with specific soil conditions will experience major obstacles to successful migration.

The lack of fertile soil in the northernmost regions will limit the front line of ecosystem expansion, as certain species must alter soil character for others to follow and thrive (McKenney et al. 2007). For example, Yellow Cedar's capacity to increase soil pH (*Figure 9*) and N content in the soil (*Figure 14*) corresponds with increased species diversity, indicating that Yellow Cedar is a keystone species for the presence of greater diversity (*Figure 12*). Yellow Cedar's slow migratory capacity has the potential to stymie other migrations of species that rely on Yellow Cedar.

Yellow Cedar's migration across a complex landscape

While at the continental scale, climate is the predominant factor in determining plant distribution, locally and regionally edaphic and topographic factors are more powerful influencers in vegetation patterns (Lafleur 2010). The results indicate that Yellow Cedar's migration is influenced by important landscape characteristics, which parallels the consensus of literature (Beier et al. 2008, D'Amore et al. 2009). My findings show that Yellow Cedar is predominantly located on areas of lower slope, which

indicates that they are better able to establish on these flatter sites (*Figure 13*). There is a trend of increasing slope with higher elevation. This factor - likely topographical - furthers the disparity of vulnerability to decline, as the stands in the Juneau region of greatest elevation will maintain both the highest snowpack and best drainage capability. Yellow Cedar on sites with higher snowpack and lower soil saturation will continue to thrive far longer than their counterparts (Beier et al. 2008, Hennon et al. 2010).

Percent soil moisture and Yellow Cedar basal ratio were negatively related, suggesting Yellow Cedar prefer better drained soils, which runs counter to the literature (*Figure 11*) (D'Amore et al. 2009). This is likely due the supersaturated environment of the Juneau study region. All soil is of such high saturation (>75%) that percent moisture loses its importance as a controlling landscape variable, despite the fact that soil saturation is generally a very important factor in the success of species colonization (Lafleur 2010). This result also indicates that Yellow Cedar has not reached a limit of expansion and can continue to compete with the other present tree species. If expansion were excluded to sites of greater soil saturation, we would see Yellow Cedar predominantly colonizing soil of higher percent moisture, which is not the case (Krapek 2016).

The results also indicate that Yellow Cedar plays a role in altering ecosystem function. As the stands increase in basal ratio and in age, there is a significant rise in species diversity (*Figure 12*). This result implies that Yellow Cedar is an ecosystem engineer for greater species diversity, which is likely due to its impact on the biogeochemistry discussed below. Increased species diversity has inherent value for the ecosystem on both the local and regional scale by inducing greater robustness to change

and capacity for genetic adaptation (Hewitt 2000), and Yellow Cedar's positive relationship with species diversity strengthens its ecological importance.

Yellow Cedar's impacts on ecosystem biogeochemistry

Tree species play an important role in the ecological functions of the biosphere, with certain species having distinct influence on these functions. My findings indicate that Yellow Cedar is an ecosystem engineer due to its particular impact on the ecosystem biogeochemistry by altering soil pH and N content. Along with soil saturation, soil pH and nitrogen are both important factors for ecosystem function (Lafleur 2010). My results show that as Yellow Cedar establishes itself over time and becomes a more dominant component of the forest stand, soil pH increases significantly (*Figure 9*). This is important because a less acidic pH promotes higher rates of mineralization and nitrification (Booth et al. 2005) as well as increased biological activity and decomposition (D'Amore et al. 2009).

Soil pH is the net effect of all the chemistry in the soil, and thus understanding why Yellow Cedar is seen to increase soil pH is difficult and complex. One potential causal for this trend is that Yellow Cedar is unique in its increased accumulation of calcium, which promotes higher concentrations of calcium in the upper soil horizons (D'Amore et al. 2009). My results found higher concentrations of calcium as the stands establish themselves over time and a positive correlation between soil pH and Ca^{2+} concentrations (*Figure 8*). These findings are concurrent with the consensus of literature that calcium decreases the acidity of soils (Hennon et al. 2012). Increased pH also promotes better retention of base cations such as calcium, making it difficult to discern

which variable is controlling the other (Driscoll et al. 2001). While Yellow Cedar could be preferentially colonizing sites of greater pH and calcium concentrations, the trends of accumulation as stands age and with a higher Yellow Cedar basal ratio suggest that the presence of this species is altering soil chemistry.

Along with increasing the soil pH, the results show that Yellow Cedar increases soil nitrogen, a limiting nutrient in temperate rainforest ecosystems (Buma et al. 2016). On average the soil of these pioneer stands has a C:N ratio of 54.9, confirming nitrogen as a very limited nutrient. As the stands establish themselves over time, soil N content increases from 0.82% to 1.03%, a small but significant change due to such low nitrogen concentrations (*Figure 14*). Soil N also significantly increases as Yellow Cedar becomes a more dominant component of the forest stand, providing more evidence that the presence of this species changes soil conditions rather than Yellow Cedar preferentially colonizing sites with more soil N. Specifically, ammonium (NH_4^+) and nitrite (NO_2^-) concentrations increase over time, while nitrate (NO_3^-) decreases as the stands establish themselves. This is likely due to the fact that Yellow Cedar is able to uptake greater concentrations of nitrate than its competitors due to assimilation with calcium (Hennon et al. 2012). This increase in soil N could be another potential cause for Yellow Cedar's positive impact on species diversity.

Overall, my findings indicate that the presence of Yellow Cedar in the Juneau study region improves the ecosystem biogeochemistry by de-acidifying the soil and increasing the soil N content, both of which are seen to aid in the overall productivity and diversity of the ecosystem. As climate change causes species composition and ecosystem type to transform on a global basis, major changes will occur to ecosystem

biogeochemistry. It is impossible to understand the future global impact on nutrient cycling, productivity, and ecosystem robustness, but Yellow Cedar's impacts on soil pH, N content, and species diversity are an important case study of a singular species' role on ecosystem biogeochemistry and function.

Yellow Cedar's impacts on net carbon equilibrium

There are important feedbacks between forests and climate, including accompanying shifts in albedo and carbon cycling associated with forest decline (Cox et al. 2000). These feedbacks have the potential to ameliorate or exacerbate climate change, depending on what ways the biosphere is impacted by fluctuations in climate (Neilson et al. 2005). Through the burning of fossil fuels and land use change, humans add 9-10 gigatons yr^{-1} of carbon into the atmosphere, and the observed and predicted impacts of this flux are immense (IPCC 2007). The carbon flux from soils (i.e. soil respiration) is approximately 90 gigatons yr^{-1} (IPCC 2007), and therefore even a small adjustment in this flux can have significant impacts on the global carbon cycle. An increase in the carbon flux from soil respiration would be a major positive feedback for climate change, inducing further warming of the globe.

Already, major impacts on the biosphere have occurred due to climate change, such as the decline of Yellow Cedar across more than 400,000 ha in Southeast Alaska and British Columbia. It is predicted that approximately 50% of Yellow Cedar habitat with currently sufficient snowpack will be susceptible to additional decline by late 21st century (Buma et al. 2016). Since Yellow Cedar colonizes marginal soils and can be a keystone species for the presence of temperate rainforest, this decline will lead to a major

ecosystem shift. Marine west coast forests maintain by far the greatest capacity for carbon storage on the American continent (Zhu et al. 2012), and thus the impacts of this decline could be global.

The total capacity for carbon uptake by plants is dependent on both the population dynamics and physiology of individual species. Certain species have much greater potential for carbon storage (Neilson et al. 2005). Trees, especially, create major stocks of carbon and tree death on a large scale will result in a major flux of stored carbon into the atmosphere. Not only that, but tree mortality produces large fuel supply for wildfires and an opened canopy will increase the albedo of the landscape and cool the land surface (Campbell 1993). All of the effects of tree mortality will create ensuing feedback cycles important on both a local and global scale.

My results show that the organic matter in Yellow Cedar soils is less bioavailable than the organic matter in soils without the presence of Yellow Cedar. Bioavailability is an indication of what proportion of carbon in the soil is available for microbial activity. The bioavailability of organic matter in soils decreases both with the age of the Yellow Cedar stand ($p = 0.024$) and as the basal ratio of the species increases ($p = 0.003$) (*Figure 16*). The slower flux of CO_2 into the atmosphere when Yellow Cedar is present indicates a much greater carbon storage capacity for these soils. The difference of $160.1 \text{ kg CO}_2/\text{m}^2$ ($p = 0.019$) (*Figure 15*) between the soils has global relevance when scaled to Yellow Cedar's considerable range spanning 20° of latitude, especially considering the extent of current and future decline (Buma et al. 2016). This positive flux of carbon into the atmosphere when the temperate rainforest loses the presence of Yellow Cedar will contribute to global warming. A shift in ecosystems - which is possible in most areas of

decline - will likely create an even greater imbalance in the net carbon equilibrium. As Yellow Cedar declines, the net increase in carbon in the atmosphere as indicated by these results will create a positive feedback cycle, inducing more warming, which will lead to greater mortality of Yellow Cedar as snowpack diminishes further.

Adaptive strategies to mitigate harm to biosphere

The unprecedented magnitude of climate change will place great ecological pressures on our biosphere. It is probable that many species will follow Yellow Cedar's acceleration towards extinction, with southern ranges experiencing mortality and northern migration failing to match the shift in suitable habitat. We have the capacity to form adaptive strategies to help conserve and sustain species vulnerable to climate change (McLachlan et al. 2006). Already certain strategies have been implemented, such as the human-aided expansion of the endangered tree species *Torreya* over 500 km northward from its current range (Schwartz et al. 2006). While a strategy of aggressive assisted migration would be the best option to minimize species loss, a lack of understanding of the impacts of migration could place existing communities at a high risk of disruption (McLachlan et al. 2006). It is difficult to predict whether species will be invasive due to an uncertainty in ecological understanding of controls on species distribution (Kolar and Lodge 2001).

To properly assist in a migration of a species without unintended consequences, there should be developed a quantitative model of the predictive outcome and a cohesive management plan, which requires a comprehensive understanding of the species' role in ecosystem dynamics (McLachlan et al. 2006). Furthermore, research should be conducted

to reveal potential interactions of an introduced population that might limit the success of colonization (Case et al. 2005). These prerequisites for proper assisted migration will limit the extent to which we can save species due to finite resources. As a result, we should prioritize species of the highest ecological and economic importance that are at the greatest risk of extinction (McLachlan et al. 2006). To maximize the success of colonization, natural resource managers should match species to environments that they are optimally adapted to and help facilitate seedling survival and the successional processes (Hamman and Wang 2006).

Yellow Cedar - of great importance and great risk of extinction - should be prioritized for assisted migration. Already research from the University of Alaska - Southeast (Krapek 2016) and the US Forest Service (Hennon 1992) has been conducted to better understand the implications of assisted migration. A study of a plantation of Yellow Cedar north of its historic range indicates that forest managers can plant Yellow Cedar on productive sites and expect success of colonization. Survival is particularly high on clear-cut sites with the lowest levels of competition from other species. Good soil drainage improves the growth, but survival is also robust on sites with poor drainage. Areas of dense deer populations should be avoided when selecting sites due to the high impact of grazing on seedling success (Hennon 1992).

My results further indicate that human-aided migration would be beneficial for the net carbon equilibrium because Yellow Cedar aids in the carbon storage capacity of soils and thus sustaining the species will decrease the flux of carbon into the atmosphere. Furthermore, Yellow Cedar's observed impacts on ecosystem biogeochemistry are seen to improve ecosystem function and engineer greater species diversity, another cause to

assist in its survival. Analysis of its mode of migration indicates that the risk of Yellow Cedar becoming an invasive species is incredibly low (Krapek 2016). While it would be beneficial to gain an even greater understanding of Yellow Cedar's impacts on the ecosystem biogeochemistry and net carbon equilibrium to further minimize the risks of assisted migration, there is a pressing need to aid in the longevity of this highly important tree species. Its decline is continuing to accelerate in magnitude and threatens even the northern extent of its historic range. An adaptive strategy of migration should be implemented without pause to sustain this economically, culturally, and ecologically important niche species.

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