

# 100 yr of primary succession highlights stochasticity and competition driving community establishment and stability

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**Abstract.** The study of community succession is one of the oldest pursuits in ecology. Challenges remain in terms of evaluating the predictability of succession and the reliability of the chronosequence methods typically used to study community development. The research of William S. Cooper in Glacier Bay National Park is an early and well-known example of successional ecology that provides a long-term observational data set to test hypotheses derived from space-for-time substitutions. It also provides a unique opportunity to explore the importance of historical contingencies and as an example of a revitalized historical study system. We test the textbook successional trajectory in Glacier Bay and evaluate long-term plant community development via primary succession through extensive fieldwork, remote sensing, dendrochronological methods, and newly discovered data that fills in data gaps (1940s to late 1980s) in continuous measurement over 100+ years. To date, Cooper's quadrats do not support the classic facilitation model of succession in which a sequence of species interacts to form predictable successional trajectories. Rather, stochastic early community assembly and subsequent inhibition have dominated; most species arrived shortly after deglaciation and have remained stable for 50+ years. Chronosequence studies assuming prior composition are thus questionable, as no predictable species sequence or timeline was observed. This underscores the significance of assumptions about early conditions in chronosequences and the need to defend such assumptions. Furthermore, this work brings a classic study system in ecology up to date via a plot size expansion, new baseline biogeochemical data, and spatial mapping for future researchers for its second century of observation.

**Key words:** chronosequence theory; community assembly; competition; ecology; ecosystem development; facilitation; Glacier Bay; long-term observation; primary succession; succession; time-series.

## INTRODUCTION

The growth and temporal evolution of ecosystems has long attracted the interest of botanists, naturalists, and other scientists. Early naturalists (Buffon 1742) noted that plant communities alter the environment and facilitate the establishment of successive communities, such as through the alteration of the light environment via the gradual growth of competing species. Henry David Thoreau coined the term “succession” to explain the transition of tree species in the developing forests of New England (Thoreau 1860). Understanding this process of temporal change, termed plant succession, became one of the original goals in the field of ecology, attracting many early pioneers in this emerging science (Cowles 1899, Clements 1916, Gleason 1917). These researchers often took a dynamic view of the

interactions between temporally distinct processes, from landform evolution to its influence on vegetation succession, and then, in turn, succession's influence on landform development and change, “a variable approaching a variable” in the words of Cowles (1901). Others looked for stability, theorizing that complex communities represent vegetation types that reach a climax state as governed by local climate, topography, and interactive factors (Clements 1916). Many ideas have become popular only to lose prominence, and occasionally be resurrected again (Egerton 2015), but the goal of predicting plant communities through time has remained a central pursuit in ecology (e.g., Mora et al. 2015, Norden 2015).

Although the original conceptions of succession, and even the meaning of the word itself, suggest a fundamentally temporal process, the emphasis of the field is really on abiotic and biotic factors and interactions that drive change, or lack thereof, in communities over time. Anticipating compositional change is more pressing than ever as climate and land use change (Sirami et al. 2017) have already led to shifts in species dominance (Kelly and

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Goulden 2008), expansion or contraction of biomes (Beck et al. 2011), and colonization of new areas (Lenoir and Svenning 2015). An understanding of the individual, species, and community interactions that give rise to ecosystem change is thus more necessary than ever.

Much theoretical ground has been explored via studies that generally land between two extreme endpoints: niche-based, deterministic models built on plant competitive traits and neutral models based primarily on stochastic community assemblage processes (Chase and Myers 2011). Niche-based perspectives focus on the tight relationship between species and the environment, attempting to explain net community change dynamics via plant traits that confer competitive advantages for low resource levels (Tilman 1988), under different competitive environments (Grime 1988), and via interactions that alter potential environmental filters (e.g., lack of available nitrogen) through time (Chapin et al. 1994, Kraft et al. 2015, Boukili and Chazdon 2017). In this framework, and assuming all species are available to colonize a given location, predictable succession is likely as communities become dominated by the species with the most competitive traits for that given location.

Neutral community assembly, on the other hand, focuses on random processes such as chance seed dispersal and early site history (Chase 2003), emphasizing the role of temporal order-of-arrival and stochastic processes (Chesson and Warner 1981, Chave 2004, McGill 2007). In this conception, alternative stable equilibria are determined by local site establishment history, potential site productivity, and richness and relative abundances of the local species pool.

Reality is often a mix, with stochastic community assembly processes dominating early succession and niche-based dynamics becoming more significant as the community grows (Chang 2018, Måren et al. 2018). This unification of stochastic processes with the more niche-based concept of resource exploitation strategies was proposed with stochastic niche theory (e.g., Tilman 2004) and formalized via the asymmetric exploitation of resources model (DeMalach et al. 2016), which suggests that competitive dominance in plant communities can be explained by the degree to which larger individuals disproportionately utilize available resources. If competition is asymmetric, increasing rates of monopolization of a resource allow individuals to exclude species that may otherwise be more competitive in a symmetrical competition scenario. Under this framework, stochastic events such as early vs. late arrival thus confer an advantage in early successional environments that can “weight” competition even among symmetrically competitive species, for example, by giving a certain species an early height advantage (and thus access to light) by virtue of establishment timing, even if all species are generally the same height in isolation (DeMalach et al. 2016). This framework suggests that low species diversity environments may result in multiple stable equilibria if species arrival times are different, providing an

updated mechanism for “lottery competition” (Chesson and Warner 1981) in which the first species to arrive out-compete others for a limited number of spots. This can result in a patchy, randomly distributed mosaic of alternate cover types on the landscape, maintained by competitive dominance of the larger, mature individuals.

The interplay between niche-based and stochastic community assembly is best explored via long-term, repeat-measurement, plant community succession studies. William S. Cooper’s research in Glacier Bay National Park, Alaska is a well-known primary succession study, and the availability of long-term, repeat measurement data on these chronosequence sites makes his network a model system for testing these concepts. In 1916, Cooper established a series of geographically clustered quadrats in bare, recently deglaciated areas in Glacier Bay (Fig. 1) on similar substrates (gently sloping glacial till) to minimize abiotic differences (Cooper 1923). Corners were marked with steel rebar or ~25 cm steel nails for precise resurveying. Cooper revisited the quadrats every 5–10 yr until the 1930s, and at each visit estimated percent cover by species while also precisely recording and mapping the location of individual plants within each quadrat. Cooper ceased visiting Glacier Bay in the 1930s, but sampling was then undertaken by his student Donald Lawrence, who maintained the record until 1988 at which point the quadrats were abandoned. Because of low species diversity, a well-described series of chronosequence studies (e.g., Chapin et al. 1994), and suite of facilitative and inhibitory interactions, the common expectation for successional change on this network is the classic sequence of mosses to *Dryas*, then to *Alnus viridis* (green alder), *Picea sitchensis* (Sitka spruce), and finally *Tsuga heterophylla* (western hemlock), each having successively higher tolerance of low resource availability.

We utilized Cooper’s network to explore these assumptions and determine if trait-based, stochastic, and/or asymmetrical processes best describe community assemblage and successional trajectories. We additionally used this network to test the utility of historic plant community sampling methodologies over the many stages of plant community development. We were specifically curious whether or not Cooper’s original 1-m<sup>2</sup> quadrats, which were large enough for early successional communities (Buma et al. 2017), were representative of the broader community surrounding the quadrats 100 yr later. This methodological constraint of historic data is especially relevant to long-term studies where dramatic change is anticipated, successional change in this case, but climate change, disturbance, or other processes as well, as these changes will require reconsideration of not only the appropriateness of sampling methods but also of spatial and temporal scales of sampling. Therefore, we evaluate and expand the sampling extent of this 101-yr network, testing conclusions from the 1-m<sup>2</sup> quadrats and establishing new, broader-scale, baseline data for a second century of monitoring.

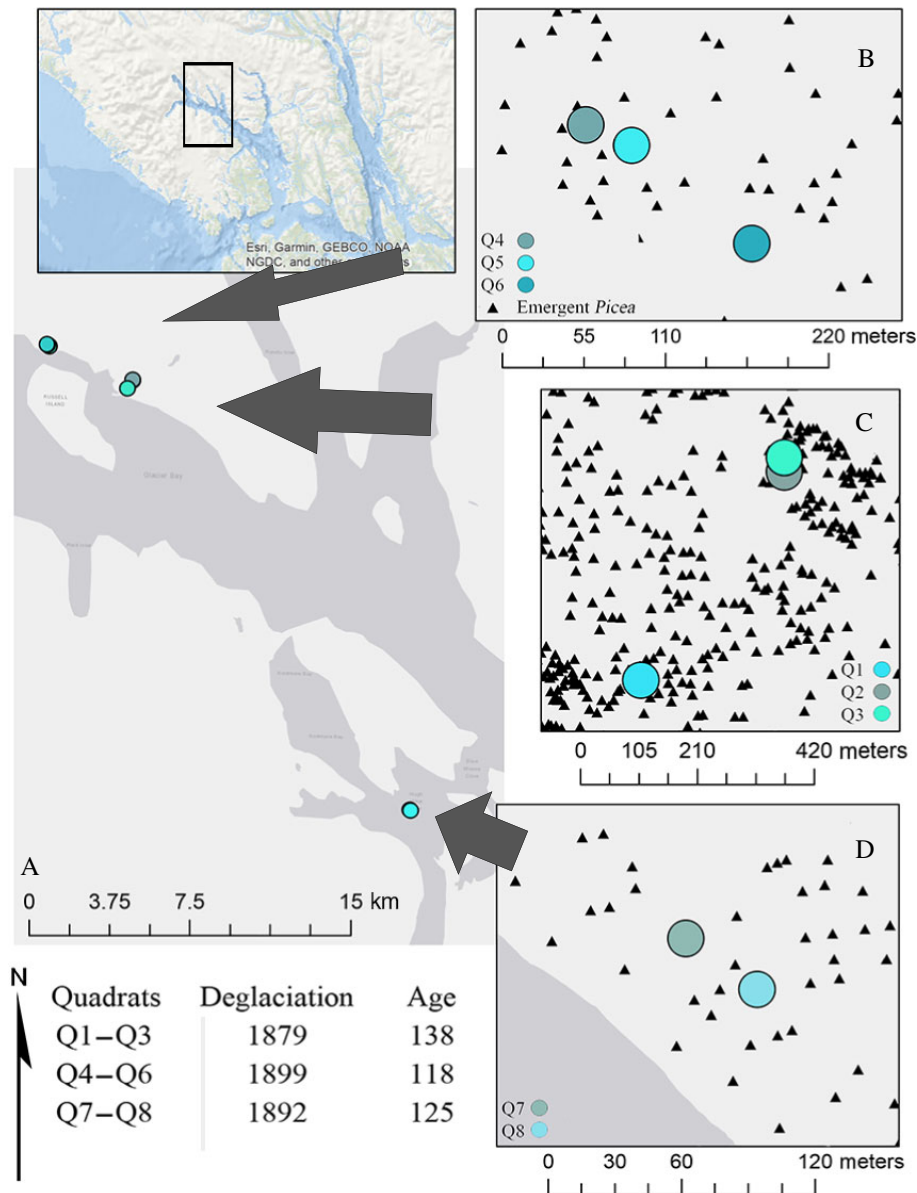


FIG. 1. (A) Broad-scale map and (B–D) fine-scale views of quadrats. The broad scale shows the location of each quadrat on the landscape, while fine-scale maps show the distribution of emergent *Picea* around each quadrat (denoted as triangles). Note differences in scale.

## METHODS

Our investigation was intended to (1) explore the overall successional trends of the network of quadrats to determine if succession is predictable and the landscape is converging to a similar composition, both at the species and community diversity level, (2) determine if convergence is likely in the future based on seedling densities, and (3) assess which factors inhibit convergence: establishment history/subsequent competition, light, nutrient availability, and/or climate.

## Quadrat scale ( $1 \text{ m}^2$ )

At the quadrat-scale (Q1–8, Q9 lost early on in study), extensive community analyses were compiled from repeat measurements to test if successional trajectories are predictable based on the time since deglaciation or if early establishment patterns continue to dominate quadrat composition. For woody species and erect herbaceous plants, individuals were tracked through time; mosses and mat-forming species (e.g., *Dryas*) were mapped by area covered rather than tracked by

individual, and cover was converted to individual count estimates via published methods (Buma et al. 2017). For the community analyses, we combined data from the entire record of Cooper's and Lawrence's visits (1916, 1921, 1929, 1935; see Cooper 1923, 1931, 1939), unpublished data from subsequent years (1944, 1949, 1950, 1952, 1955, 1967, 1972, 1982, and 1988; collected by Lawrence), and recent data from 2016 and 2017 (collected by the authors). Time since deglaciation varies across the network of quadrats; Q1–3 were exposed in 1879, Q4–6 in 1899, and Q7–8 in 1892 (Fig. 1). Copies of the unpublished data sheets, photographs, and notes associated with the 1916 to 1988 sampling period were obtained from the University of Minnesota Elmer R. Andersen archival library.

Diversity metrics were calculated with data from across the entire record of sampling (1916–2017) to test if community diversity (independent of specific species) followed a predictable trajectory over time. Where noted, grouping according to dominant species type was necessary due to unknown identity in the historical record (i.e., genus identified but lacking species) or to provide consistency across time steps. *Salix* species (willow) were pooled for this reason (*S. alaxensis*, *S. arctica*, *S. barclayi*, *S. commutata*, *S. glauca*, and *S. sitchensis*). Species richness, the probability of interspecific encounter (PIE; Hurlbert 1971), and effective number of species (ENS; Jost 2006, Chase and Knight 2013) were calculated for each quadrat at each point in time (up to 14 per quadrat;  $n = 89$  from 1916 to 2017). PIE is the probability that two individuals drawn from a population will be the same species; low PIE indicates higher dominance by a single species. ENS is a simple transformation of PIE to assess species' abundances, with a high ENS corresponding to a more even community.

#### Plot scale (707 m<sup>2</sup>)

To expand the historical 1-m<sup>2</sup> quadrats to a broader area more appropriate for maturing forests and to capture regeneration and growth patterns relevant to our questions, we installed 15 m radius circular plots around each quadrat. Within those circular plots, all non-*Salix* stems > 1.37 m tall were measured for diameter and stem-mapped to within 10 cm (1.37 m corresponds to historical diameter measurements, done at 4.5 feet); *Salix* was excluded because of the extreme density of the generally shrubby species. Percent cover was estimated for all canopy species, with *Salix* grouped as a genus due to finely interlocking crowns making species-level cover estimates difficult at that scale. Individual stems of all species, including *Salix*, >10 cm but < 1.37 m tall (hereafter seedlings) were individually mapped, measured for basal diameter, and assessed to determine vegetative (layering or resprouting) vs. seed regeneration history. Layering determination was based on (1) the branch assuming a vertical growth form and (2) thickening and adventitious rooting of the branch after it left the

original tree. The purpose of the mapping was to determine if any significant clustering was observable, indicating hidden substrate preferences by species.

To explore light limitation on seedling establishment, photosynthetically active radiation (PAR, 400–700 nm) was measured via two Apogee line quantum sensors (Apogee Instruments, Logan Utah, USA) at six locations of varying lag distances from each quadrat (two 1-m and two 10-m east/west, two 15-m north/south) and covering the extent of the plot. Four simultaneous above/below canopy measurements (photon flux density;  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) were taken facing the cardinal directions between 10:00 and 14:00 at each location, for a total of 28 paired samples. Total absorbed PAR was calculated as the fraction of below-canopy to above-canopy PAR.

To test the idea that early nutrient limitation determined current trajectories, we compared carbon (C) and nitrogen (N) percentages from Buma et al. (2017) to historical measures of *Dryas* coverage at the quadrat scale: the maximum number of *Dryas* individuals observed in a single year and average number of *Dryas* observed over all observations. We then also compared current *Alnus* percent coverage at the plot scale to N percentage to explore if current species composition is a better predictor of nitrogen.

Finally, we verified establishment sequence and tested the tree growth-climate relationship, under the hypothesis that the dominant canopy's growth rates were tied to climate rather than competition. This was done via dendrochronology and dendroclimatology. All emergent *Picea* (meaning above the *Alnus/Salix* canopy) and a subset of *Alnus* were cored. If no *Picea* were on the 15-m plot, nearby *Picea* were opportunistically sampled. Cores were taken with a standard 5 mm diameter increment borer as close to the root collar as feasible. Where multiple cores were taken from the same tree, the duplicates were used to create a height correction (1 yr/6.6 cm height) to account for missing rings below coring height. Minimum height of coring sampling location was 10 cm (mean 32 cm) due to the large length of borer required, and it is possible that slow growth in the very early years was missed, so age estimates should be considered minimum ages. Ring widths were measured to 0.001 mm via CoRecorder 8.1. If no growth release was observed, the *Picea* were assumed to have established before or prior to *Alnus* (no effect of competition; Fastie 1995). To further verify establishment sequence, observations of *Alnus* seedling establishment and *Alnus* age from cores was also compared to estimated ages. *Picea* cores were also processed for latewood blue intensity (Wilson et al. 2017). The ring width and latewood blue intensity were compared to regional climate (CRU TS4.01; Harris et al. 2014) and the Pacific Decadal Oscillation (PDO) index (Mantua et al. 1997) to determine if climate was the main determinant of growth. Growth rates were also compared to the late-successional *Picea* forest growing in the southern portion of the bay on older substrates. Where possible, field notes



from Cooper (1916–1930s), Lawrence (1940s–1988), and Worley (1982, 1988) were used to corroborate estimated ages and growth rates. Full details are in Appendix S1.

### Landscape scale (3.14 ha)

At broader scales, we assessed the distribution of *Picea* and *Tsuga* across the landscape using SPOT 2.5-m resolution satellite imagery to examine the relationship between the establishment of late-successional species and substrate, with clustering likely indicating species-specific substrate preferences that could confound our results. Based on field data, which found little to no sub-canopy *Picea* and no *Tsuga* (see *Results*), the distribution of emergent *Picea* and *Tsuga* was considered generally representative of the pattern of the species on the landscape. All emergent individuals in a 3.14 ha (100 m radius) circle around each plot were geolocated in ESRI ArcMap (ESRI, Redlands, California, USA). The radii around Q7 and Q8 were reduced to 50 m (0.785 ha), as they are located near a bluff on the edge on the shoreline.

### Analyses

Quadrat-level trends in species richness, PIE, and ENS as a function of time since deglaciation were analyzed via linear regression for both individual quadrats and quadrats pooled by current dominant vegetation (where noted). The presence of spatial patterns within both the 707-m<sup>2</sup> plot (for *Alnus* and *Picea*) and the larger 3.14-ha plot (for *Picea* and *Tsuga*) was assessed by comparing observed patterns to 1999 Monte Carlo simulations of a uniform Poisson process via a chi-squared test (CSR [Complete Spatial Randomness] test; Baddeley et al. 2015). All statistical analyses were conducted in R 3.5.1 (R Core Team 2018). Dendrochronological and dendroclimatological analyses were conducted in

RCSigFree (Cook et al. 2014). Ancillary information, including presence of mammals and birds, were collected from the archives for interpretation purposes (Appendix S2).

## RESULTS

### Quadrat scale successional trajectories

On all quadrats, there are clear differences in current composition due to early establishment patterns rather than to the chronological age of the quadrat or any specific sequence of species change (Fig. 2; Appendix S3; Fig. S1). Three quadrats (Q1, Q7, and Q8) are *Alnus* dominated, one is *Picea* dominated (Q2, growing slightly off plot but extending completely over), and four are *Salix* dominated (Q3, Q4, Q5, and Q6 [Q6 has a high overstory component of *Alnus*; Buma et al. 2017]). Historically, *Dryas drummondii*, an early colonizer and N-fixer, was present for a short time on all but Q1 (though on Q5, limited to one small group in 1949). *Alnus* appears to strongly inhibit *Dryas* presence, with *Dryas* disappearance generally occurring immediately after *Alnus* arrival (Table 1).

Multiple *Salix* species were abundant early (1916) on all quadrats except Q2, which had 100% *Dryas* coverage for the early decades and is currently dominated by *Picea*. Across all quadrats, the number of *Salix* individuals rapidly declined and were replaced by a few larger *Salix* stems over time. No *Alnus* seedlings established on the quadrats currently dominated by *Salix* or *Picea*, nor did any *Alnus* seedlings establish after the 1949–1972 period.

### Quadrat-scale diversity trends

Trends in vascular richness are also related to establishment history rather than time since deglaciation. All

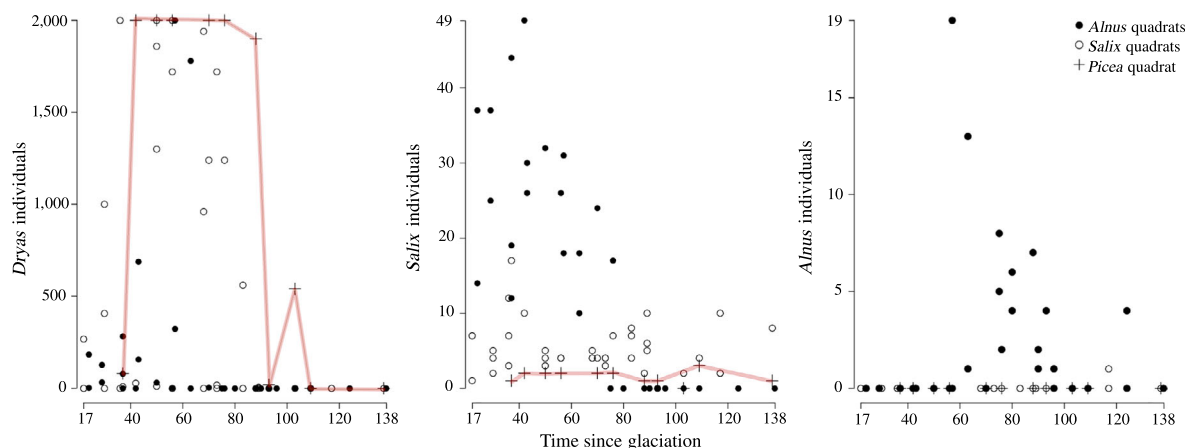


FIG. 2. *Dryas*, *Salix*, and *Alnus* individuals on the Cooper quadrats over the entire observational period. Quadrats are distinguished by their current (2017) cover and data points represent individuals rooted and alive at that given point in time. Quadrats dominated by *Alnus*, for example, may not have an *Alnus* rooted directly in the plot but did have *Alnus* as the entire overstory. The red line indicates the *Picea* dominated quadrat (Q2), which had consistently high *Dryas*, consistently low *Salix*, and no *Alnus* in its history.

TABLE 1. Dates of *Picea*, *Alnus*, and *Dryas* establishment from historical data or dendrochronological estimates.

Plot	First <i>Picea</i> establishment†	First <i>Alnus</i> establishment	First <i>Dryas</i> establishment noted/Disappearance noted‡
1	1953	1955†	1939/1949
2	1960	NA	1916/1982
3	1961	NA	1916/1955
4	1974	1971§	1916/1972
5	NA	1987§	1949/1949
6	1960	1982§	1916/1988
7	1982	1949†	1916/1949
8	1949	1952†	1916/1955

Note: *Dryas* disappearance from the quadrat record occurs at a similar time as *Alnus* arrival.  
† From oldest individual at the plot scale.  
‡ Only quadrat scale data available.  
§ Indicates estimated minimum date from *Alnus* tree cores and thus may be underestimates of true age if stem was a second-generation resprout.

quadrats with early successful *Alnus* establishment (Q1, Q7, Q8) had high initial vascular plant richness followed by significant downward trends over the last 101 yr ( $n = 3$  plots,  $P < 0.05$  for each,  $r^2 = 0.45\text{--}0.59$ ) and remain dominated by second or third generation *Alnus* individuals (see dendrochronological results below). The remainder of the quadrats, which are *Salix* or *Picea* dominated, show no significant trends in vascular richness over time ( $P > 0.05$  for each; Fig. 3).

There was an overall decline in diversity (both PIE and ENS) across the entire observation period (Appendix S3: Fig. S2). This trend was marginal (ENS  $P = 0.05$ ,  $r^2 = 0.03$ ; PIE  $P = 0.01$ ,  $r^2 = 0.07$ ). The plots currently dominated by *Alnus* drove the downward temporal trend for PIE (pooled together;  $P = 0.05$ ,  $r^2 = 0.09$ ); the *Salix* and *Picea* plots had no significant

trends. There was no significant correlation with ENS at the species cover-type level for any individual cover type.

Plot scale

The cover of the 707-m<sup>2</sup> plots around the quadrats reflects the finer-scale quadrat cover. *Alnus*-dominated quadrats had significantly higher *Alnus* in the surrounding plots compared to the others, averaging 4,433 stems/ha around *Alnus*-dominated quadrats compared to 1,028 elsewhere ( $P < 0.05$ ), though no significant presence of seedlings (non-vegetative reproduction) was noted. Scattered *Populus* occurred infrequently and were a minor component on plots where present. Mature *Picea* occurred on four of the eight plots, though in very low densities (Table 2). Cones were prolific on the mature individuals and have been for several decades (1970s to present), however seedlings were only found on two plots, one of which included the *Picea* quadrat (Q2). In all cases, the remaining cover was dominated by very dense *Salix* (not mapped), and no sign of significant *Picea* ingress into *Alnus* plots or *Alnus* into *Salix* plots was noted. The lack of *Picea* regeneration or *Alnus* seed regeneration precludes an in-depth analysis of spatial regeneration patterns beyond association.

Across all plots, *Alnus* stems were not randomly spatially distributed (two-sided pooled CSR test,  $P = 0.04$ ). Follow up CSR tests on individual plots, however, indicate this result is driven by strong clustering on plots around Q1–3, partially driven by spatial aversion to *Picea* (Appendix S3: Fig. S3). *Alnus* were randomly distributed on the other plots (around Q4–8). *Picea* were randomly distributed on Q2 (CSR,  $P > 0.05$ ), the only plot with enough individuals for a valid test (Table 2). On that plot, seedlings and vegetative sprouting were clustered nonrandomly around the mature trees ( $P < 0.05$  for each).

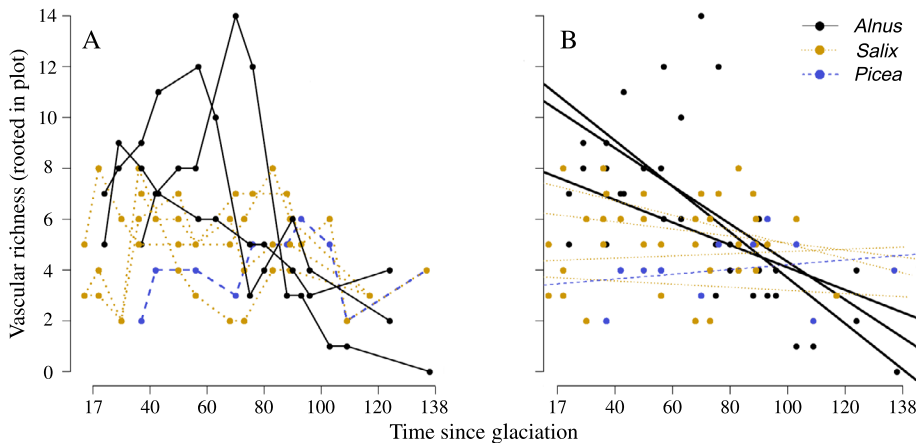


FIG. 3. Vascular species richness as a function of time since deglaciation at the quadrat scale. (A) Individual quadrats through time, color indicates current (2017) species dominance. (B) Trends in species richness through time, clustered by successional trajectory. *Alnus*-dominated quadrats show continued and significant declines; the other cover types show no trends through time.

TABLE 2. Density and cover of dominant woody species in the expanded 707-m<sup>2</sup> plots around the central Cooper 1-m<sup>2</sup> quadrat.

Q	Quadrat cover	Plot mature stem density (stems/ha)			Plot estimated cover (%)					<i>Picea</i> density (individuals/ha)		
		<i>Alnus</i>	<i>Picea</i>	<i>Populus</i>	<i>Alnus</i>	<i>Picea</i>	<i>Populus</i>	<i>Salix</i>	Other	Seedlings	Cumulative stems	Landscape
1	<i>Alnus</i>	5255	14	42	80	5	0	15	0	28 (0)	42	10.2
2	<i>Picea</i>	708	85	14	25	20	0	47	8	113 (255)	453	10.5
3	<i>Salix</i>	1997	0	0	32	0	2	62	4	0	0	10.8
4	<i>Salix</i>	1317	0	14	25	0	1	74	0	0	0	5.4
5	<i>Salix</i>	538	0	14	10	0	0	85	5	0	0	8.9
6	<i>Salix</i> /high <i>Alnus</i>	581	42	28	62	1	2	35	0	0	42	8.6
7	<i>Alnus</i>	4150	0	0	70	15	1	10	4	0	0	15.3
8	<i>Alnus</i>	3895	42	14	95	0	0	5	0	0	42	20.4

Notes: Mature stems are > 1.37 m tall. *Picea* seedling density in parentheses refers to vegetative reproduction, only relevant on Q2.

#### Plot scale, PAR

The distribution of transmitted PAR varied across the plots, from a minimum of 0% to a maximum of 41% (highly skewed toward low values; median 7%), indicating near total monopolization of light by the existing canopy. The *Salix*-dominated plots had a median transmittance of 8%, while the *Picea* plot had 1%. The *Alnus* plots had a median transmittance of 2%.

#### Plot scale, biogeochemistry

Soil biogeochemistry was strongly related to vegetation rather than time since deglaciation. The *Picea* plot was included in the *Salix*-dominated plots for these analyses, because the dominant cover type at the 15-m scale was *Salix*. Plots dominated by *Alnus* had a higher mean %N than those dominated by *Salix* (2.05 vs. 1.64; Welch's two-sample *t* test, *P* = 0.04, *t* = 2.7). *Alnus* coverage was strongly correlated with quadrat scale percent C ( $r^2$  = 0.84, *P* < 0.05) and marginally correlated with C:N ratio ( $r^2$  = 0.38, *P* = 0.08; Appendix S3: Fig. S4). As anticipated, *Alnus* density was also positively related to percent N, though not significantly ( $r^2$  = 0.21, *P* = 0.17, Appendix S3: Fig. S4). Neither metric of historic *Dryas* coverage (maximum vs. average number of individuals) was related to percent C, percent N, or C:N ratio.

#### Plot scale, age structure

A total of 126 readable cores were taken from 68 trees, with *Picea* and *Alnus* establishing at similar times rather than sequentially (Table 1). The average date of establishment of living *Alnus* stems was 1978 (oldest estimated date: 1955, youngest: 1999; *n* = 29), which together with the lack of seedlings suggests potential vegetative self-replacement of the original *Alnus* canopy (which established starting in 1949; Fig. 2). In addition, *Alnus* establishment was described much earlier near Q1 (though not on the quadrat itself; Cooper 1931),

estimated to have established in 1915 (36 yr after deglaciation). Fourteen *Populus* were also cored, with an average year of establishment at 1972 (earliest: 1954; latest 1992).

Thirty-three *Picea* were cored. The average estimated age of non-vegetative *Picea* stems was 47 (establishment year estimated at 1972), with the earliest in 1942 and the latest in 2011: a 2.9-cm sapling on Q2. On that quadrat, vegetative regeneration from layering (*n* = 9) was clustered close to an early stem (established circa 1956) and considerably younger, with an average year of "establishment" of 1986 (earliest 1967, latest 2000).

Growth has been rapid and sustained for all *Picea* cored (Appendix S1: Fig. S2), and emergent trees are large (mean diameter at breast height [DBH] = 67 cm) and reproductively mature, as evidenced from cone crops. Since 1960, estimated radial growth rates averaged ~7 mm/yr, fluctuating slightly (from ~6 to 8 mm/yr) on approximately 20-yr cycles. The *Picea* on Q2, the one quadrat dominated by the species, was last measured in 1988 at 59.7 cm DBH. It is now 96.3 cm, a radial growth rate of 6.3 mm that well matches estimated radial growth from the cores. Few clear instances of growth release can be seen (Appendix S1: Fig. S2). *Picea* growth tracks regional climate very closely in all months of the year. Average land temperature was highly correlated with both widths and latewood blue intensity (Appendix S1: Figs. S3 and S4). Fluctuations on a decadal basis appear driven by PDO, with widths significantly correlated with the PDO index (99% level) between January and June, and blue intensity significantly correlated all months of the year.

#### Landscape scale

Across the landscape, there were enough *Picea* and *Tsuga* to assess spatial patterns (Appendix S3: Fig. S5). All locations had generally similar densities of mature individuals, with a slight decline in abundance in areas further from the mouth of Glacier Bay (Table 2). There was no significant pattern associated with *Picea* spatial

arrangement at the landscape scale (two-sided pooled CSR test,  $P = 0.14$ ).

## DISCUSSION

As a test of theoretical predictions of plant community succession, we used the 1916–2017 Cooper network in Glacier Bay National Park to evaluate trends in plant community composition over that 101-yr period. We see support for the concept of lottery competition and size asymmetry of resource exploitation, with initial stochastic differences in establishment timing leading to a multiple, long-term stable communities. The single limiting resource appears to be light, as evidenced by the lack of spatial patterning, the insignificance of early N fixers on subsequent trajectories, and the lack of any requisite species sequence. Competition for this resource is intense, with near complete monopolization of light by dominant species. A lack of seed reproduction by any species further underscores the dominance of mature individuals, and the prevalence of vegetative regeneration points to an important pathway of stability across generations. Although the long-term record is limited to eight quadrats and results should be interpreted with that in mind, they are representative of the larger 15 m radius plots installed around them. The story they tell is one of continual divergence rather than convergence in trajectories.

### *The trajectories are more related to early establishment than to time since deglaciation or species' traits*

Initial establishment appears to have been primarily a stochastic process. We do not see convergence of communities over time, nor any sign that species composition is shifting toward more low-resource-tolerance species, supporting the concept of early assembly patterns ossifying as mature individuals began to disproportionately monopolize resources. This was not immediately apparent: while variations in the species and density of those species were clear from the beginning, for the first decades, the quadrats behaved similarly. This suggested a somewhat orderly process related to age and unrelated to substrate or location (Cooper 1923). A slight increase in richness across all quadrats in the early stages of development (until 40–60 yr of age) was likely associated with both the continual influx of seed and the prevalence of open establishment sites on most quadrats.

After that point, however, the trends diverged. *Alnus* establishment was first noted in 1949 on a 57-yr-old plot (Fig. 2). Canopy closure associated with *Alnus* dominance resulted in significant declines in plant diversity, for example, the loss of light-demanding *Dryas* within a decade (e.g., Appendix S1: Fig. S1). Neither declines in richness nor a rapid loss of *Dryas* were noted on the quadrats dominated by *Salix*, despite its presence since the first surveys in 1916. Richness did not decline on the *Picea* quadrat (Q2), likely due to initial and long-term

complete dominance of *Dryas*, which kept richness values low early on, and current presence of limited, single-individual/rare species (Buma et al. 2017).

After the pulse of *Alnus* establishment, little sign of directional change has been observed. It appears that, upon canopy closure, be it by *Salix*, *Alnus*, or *Picea*, the species dominating the canopy prevails. This is likely due to the extreme monopolization of light by the larger individuals, which precludes smaller individuals from establishing, including those of the same species. There is little sexual regeneration of canopy species either within or between cover types. The ability of the dominant species to reproduce asexually likely limits the potential for change further by maintaining a cohort of individuals to immediately exploit any gaps. This current stability appears to be the historical norm. Field notes from 1988 noted both the presence of ample seed and the obvious lack of seedlings: “We saw no conifer seedlings going to and from the plot [Q4], even though we went through old alders and beneath a very large spruce with a wide canopy and many cones” (I. Worley, *Personal communication*). Core ages and historical stem maps/photographs suggest (1) self-replacement by *Alnus* and *Salix* canopy individuals and (2) a lack of new establishment by *Picea*, excluding vegetative reproduction immediately around individuals that established early following deglaciation. That *Picea* generally showed no growth releases early in their lifespan suggest they established before or contemporaneously with *Alnus* (Fastie 1995, Appendix S1: Fig. S2). Overall, the differences between canopy species are not a reflection of time since deglaciation but rather appear to be a function of early establishment granting an advantage in resource exploitation (DeMalach et al. 2016) that precludes other species, even those that could be considered “later successional.” That difference is maintained via vegetative reproduction, resulting in stable landscape heterogeneity.

### *Alternative hypotheses*

*Spatial differences.*—The observed differences and stability in canopy composition could be determined by distance-driven selection for light-seeded, long-dispersing species. For example, Knapp et al. (2016) note that colonization rates explain species change in old-field systems (over 25 yr). In topographically complex regions, this is a three-dimensional question, as seed sources may be distributed vertically (e.g., higher elevations) as well as horizontally. Buma et al. (2017) noted some trends in richness related to quadrat distance from the mouth to the West Arm of Glacier Bay and Fastie (1995) noted the significance of dispersal in the rate and amount of *Picea* colonization using maps of potential seed sources in the eastern portion of the Bay. The slight gradient in *Picea* density at the landscape scale in this study confirms that observation (Table 2). However, this trend is not present at the quadrat or plot scale, and the *Picea*-dominated quadrat (Q2) is farther from the entrance,



and thus seed sources, than other quadrats. Moreover, the documented presence of a variety of canopy-forming species very early near all quadrats, including *Pinus contorta*, *Tsuga heterophylla*, and *Picea sitchensis* (Cooper 1931, 1939, and dendrochronological data here) suggest that even presumed infrequent, long-distance dispersal events were sufficient to establish a presence on the landscape early on (Table 2). Field notes from the 1960s to present note the consistent presence of cones as well, suggesting that despite the absence of seedlings for decades all quadrats have had seed available from mature *Picea* individuals, though we note that a formal multi-year seed trap study has not been done. Thus, while stochastic processes driven by spatial arrangement likely influenced the initial template, they are unable to explain the stability since the 1940s, suggesting a resource-related explanation for the lack of change (Chase and Myers 2011).

*Climatic differences.*—A second potentially significant factor driving differential establishment and/or stability is climate differences among sites. Harsh climates, suggesting a stronger ecological filter, can influence the role of stochastic vs. niche-based successional processes (Chase 2003), and differences in climate can maintain a given community over decades of succession (e.g., Canadian boreal forests; Girard et al. 2017). The West Arm of Glacier Bay is generally cooler and drier than other locations in the Bay (Streveler and Paige 1971).

An unexplored hypothesis in this system is whether or not temporal differences in climate mediate the strength of competition and facilitation processes themselves. The stress-gradient hypothesis (Callaway 2002, Michalet et al. 2014) states that relatively stressful environments favor more facultative interactions, whereas more favorable landscape conditions promote more intense competition. The older portions of other Glacier Bay chronosequences (e.g., Chapin et al. 1994) were based on areas that deglaciated prior to these sites and thus developed under slightly cooler conditions; in these cases, perhaps competition was less intense early in site development due to more harsh abiotic conditions. However, we suggest this is an unlikely explanation given that patterns of “early” successional dominance have been seen in other, cooler post-glacial systems as well (e.g., Cooper 1942). Furthermore, *Picea* growth has been rapid and sustained in all individuals (Appendix S1), with no indication of climatic stress. In fact, the growth of *Picea* on these plots greatly outpaces *Picea* from the mouth of Glacier Bay (Appendix S1: Fig. S5), suggesting that climate is not skewing species establishment.

*Microsite differences.*—A third counter hypothesis would be that current species distributions are constrained by the distribution of favorable vs. unfavorable microsites that influence establishment and stability (Boukili and Chazdon 2017, Girard et al. 2017). We address this possibility in two ways: spatial patterning of

individuals and soil nutrient concentrations. A non-random distribution of individuals would not be antithetical to the hypothesis that early establishment patterns are still imprinted on the landscape, but it would suggest that some edaphic or topographic filter was shaping that pattern (Manabe et al. 2000). However, the *Picea* individuals are not clustered on the landscape at the scales measured, suggesting there are not favorable sites (at those scales).

Soil nutrient concentrations are related to both quadrat level composition (Buma et al. 2017) and broader plot-scale cover of *Alnus* (presented here). Because there is no prior soil chemistry information, we cannot compare early establishment with early soil chemistry. However, the strong correlation between soil chemistry and *Alnus* density in the present, but not to either metric of historical *Dryas* coverage, suggests that the observed structure between plots is a consequence of overstory vegetation over the last ~60 yr rather than a driver. To date, there appears to be no N-facilitation in the establishment of other species (although long-term productivity may be impacted in areas with lower N).

### Overall impressions

Succession theory has several frameworks that incorporate the various drivers of community change, such as resource availability, trade-off strategies, and/or chance (e.g., Chase and Myers 2011, Zhang et al. 2015, DeMalach et al. 2016, Måren et al. 2018). But testing successional theories is difficult due to an often necessary reliance on inferential methods. Cooper’s long-term, primary succession network in Glacier Bay provides a unique opportunity to test successional theory in a simple system, via a dense historical record (Appendix S3: Table S1), a limited species pool, and a relatively homogenous landscape. This eliminates much of the fine-scale factors that drive change (e.g., Chang 2018) and enables testing of more general ecosystem processes.

We conclude that a combination of stochastic establishment of canopy species and subsequent monopolization of a single, primarily limiting resource dominates the Glacier Bay pattern. This is corroborated by (1) the discrete vegetation types, growing rapidly, (2) the dearth of sexual reproduction or apparent species replacement, (3) the pulse of establishment (observed in the historical data and tree ring reconstructions), (4) the random dispersion of individuals on the landscape, (5) the lack of explanatory patterns in soil properties, and (6) the relatively limited role of spatial structure beyond initial establishment probabilities. The tree and shrub establishment period lasted for ~60–70 yr, at which point canopy closure (by either *Salix*, *Alnus*, or *Picea*) became sufficient to fix those patterns on the landscape. Since then, individuals have reproduced asexually, perpetuating that pattern for the last 50–70 yr. The lack of introgression of any species into other plots despite individual turnover is striking. There is no reason to believe the stability

observed here will not continue through the next century unless something else occurs to overcome the apparent high ecological inertia of the system (e.g., disturbance; Buma and Wessman 2011). In a similar system to the west (Prince William Sound), *Alnus* stands perpetuate in excess of 250 yr despite the presence of similarly old *Picea* and *Tsuga* individuals nearby (Cooper 1942). This strongly suggests that inhibition can maintain so-called “early” successional stages on the landscape for centuries.

These results therefore emphasize the role of stochasticity in setting initial communities with competition then promoting stability rather than an orderly succession of species through time as suggested by naïve interpretations of chronosequences (Johnson and Miyanishi 2008). This makes predictions of successional trajectories difficult (e.g., Norden 2015). Experimental work in the 1990s highlighted the mechanisms of inhibition and facilitation in shaping successional stages in the region (Chapin et al. 1994, Fastie 1995). While the role of changing niche availability driven by facilitation (especially the N-fixation by *Alnus* and *Dryas*) is often cited as a classic mechanism for successional change (Johnson and Miyanishi 2008), the role of light limitation on germination and initial growth appears more significant in this case.

Other factors may interact as well, such as seed and seedling predation by insects, mammals (especially moose, *Alces alces*), or birds (Good 1966, Trautman 1966, Larios et al. 2017), though the limited observations suggest that is a minor factor at most (Appendix S2: Tables S1 and S2). Moose specifically did not arrive on the quadrats until quite late in their history (1980s). Other minor factors may include seed or seedling pathogens (Sprague and Lawrence 1960); allelopathic effects (Chapin et al. 1994); lack of associated mycorrhizae (Sprague and Lawrence 1960); lack of mammalian seed or fungal spore dispersers (Maser et al. 1978, Terwilliger and Pastor 1999); or some combination of factors. Overall, the lack of ingress of dominant species within another cover type suggests that the role of facilitative effects is “a moot point” if a species is not present at the time of canopy closure (Chapin et al. 1994). We suspect that locations closer to seed sources had all species establish early, setting up the “classic” Glacier Bay chronosequences (the relay floristics model; Egler 1954), minimizing the overwhelming role of inhibition and, in some cases, confusing the temporal sequence of growth and dominance by life form with a hypothesized temporal sequence of establishment. Several other chronosequence studies in the region (e.g., Crocker and Dickson 1957, Bormann and Sidle 1990) were established in a similar manner, where the older sites were closer to seed sources and dense early establishment (Fastie 1995), alleviating the need for facilitation in terms of seedling establishment. As a result, the inference that facilitation was significant in terms of species transitions can easily be conflated with the role of

facilitation in productivity and ecosystem functioning (Egler 1954, Crocker and Major 1955, Goldthwait et al. 1966, Bormann and Sidle 1990).

Facilitative mechanisms may be important for long-term productivity within a given system (Fastie 1995), though we note growth rates of *Picea* are not noticeably higher on *Alnus* dominated plots (Appendix S1: Fig. S2). Recent work has suggested that phosphorus may be more significant in post-glacial plant productivity than nitrogen (Darcy et al. 2018), and *P* availability is strongly influenced by microbial and fungal communities (Van Der Heijden et al. 2008). It is also likely that differences in initial establishment densities and subsequent sequences (or lack thereof) of *Alnus*, *Picea*, and other species, rather than time, drive some variation in N and C cycling noted in chronosequence studies (a concern noted by Bormann and Sidle [1990]). It could be this historical spatial heterogeneity, rather than environmental, topographic, or climatic variability, that is driving the substantial unexplained variation seen in modern chronosequence work in Glacier Bay and elsewhere (e.g., Mora et al. 2015, Norden 2015, Malone et al. 2018). More detailed investigations of C-cycling and biodiversity at the microbial and fungal are needed, especially those linking the above and belowground communities in relation to early successional history.

An additional methodological value to this study is the attempt to “modernize” long-term studies established in historical periods when typical methods were different, statistical methods unplanned for, or when researchers had different goals. This approach is becoming more common as the need for broader scale syntheses becomes apparent (e.g., Gough et al. 2016, Chang 2018, McNicol et al. 2019). In this case, the original plots (1 m<sup>2</sup>) were appropriate for herbaceous species but less so for a maturing forest. This work “re-scales” the Cooper plots for the next century of monitoring via two mechanisms: checking the inferences made via that rescaling (do conclusions from the Cooper plots reflect the broader reality currently?) and then defining larger permanent plots with relevant baseline data (biogeochemistry, PAR, and regeneration data) for the future. We hope this method is of use to other permanent plot networks as they begin to rescale their networks due to significant vegetation change in the future.

Chronosequences are a viable and valuable tool, but unknowns imposed by historical contingencies, species interactions, and the various other assumptions about successional trajectories (well reviewed in Johnson and Miyanishi [2008]) must be kept in mind. An old joke is particularly relevant: A policeman sees a drunk searching under a streetlight and asks what he’s lost. The drunk says he lost his keys, and so they both look under the streetlight together. After a few minutes, the policeman asks if he is sure he lost them here, and the drunk replies that no, in fact he lost them in the park. “Then why are you searching here?” the policeman, and the drunk replies, “This is where the light is!” Researchers,

especially those that use chronosequences, should recall the proverbial man looking for his keys under the street light and beware of limiting potential explanatory variables to that which can be measured in the present (e.g., slope, water supply, or biotic community) at the expense of historical contingencies which may be hidden but are significant nonetheless to current ecosystem functioning.

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