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NOTE

New Multicentury Evidence for Dispersal Limitation during Primary Succession

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ABSTRACT: Primary succession is limited by both ecosystem development and plant dispersal, but the extent to which dispersal constrains succession over the long-term is unknown. We compared primary succession along two co-occurring arctic chronosequences with contrasting spatial scales: sorted circles that span a few meters and may have few dispersal constraints and glacial forelands that span several kilometers and may have greater dispersal constraints. Dispersal constraints slowed primary succession by centuries: plots were dominated by cryptogams after 20 years on circles but after 270 years on forelands; plots supported deciduous plants after 100 years on circles but after >400 years on forelands. Our study provides century-scale evidence suggesting that dispersal limitations constrain the rate of primary succession in glacial forelands.

Keywords: arctic, biomass, ecosystem development, foreland, glacier, growth form, soil C, sorted circle.

Introduction

Primary succession encompasses the earliest and most fundamental stages of community assembly, yet the relative contributions of the main drivers that control its rate remain largely unknown (Anderson 2007; del Moral and Chang 2015). The driver most often studied is ecosystem development, represented by the accumulation of nutrients and carbon (C) in soils and plants (Schmidt et al. 2008; Peltzer et al. 2009; Walker and Wardle 2014; Heckmann et al. 2015). At high latitudes, ecosystem development also comprises increased soil temperature, decreased wind speeds, and increased duration of snow cover (Cutler et al. 2008). A driver less often studied is plant dispersal (Johnson and Miyanishi 2008; del Moral and Magnússon 2014), in spite

of its central roles in secondary succession (Cook et al. 2005; Anderson 2007) and community organization in general (Schupp et al. 2010; Low-Décarie et al. 2015). The potential importance of dispersal during primary succession is suggested by early successional species being characterized by high dispersal ability (Caccianiga et al. 2006; Robbins and Matthews 2009), the presence of seeds in the youngest soils (Marcante et al. 2009), and the abundances of dominant successional species being highly correlated with distance from a seed source (Fastie 1995). Clearly, both ecosystem development and dispersal operate as filters regulating the rate of succession because dispersal must occur before biologically driven ecosystem development can occur (Anderson 2007), but the contribution of dispersal to regulating plant populations and thus ecosystem development has received relatively little attention (Walker and Wardle 2014).

If primary succession is driven only by ecosystem development, then experimentally enhancing dispersal by adding seeds to early successional seres (stages) should have little effect on plant community composition. In contrast, several seed addition experiments show that dispersal does indeed limit plant establishment (Wood and del Moral 1987; Jumpponen et al. 1999; Lichter 2000; Jones and del Moral 2009; Marteinsdottir et al. 2010). On the other hand, seed addition experiments are of durations that are brief (a few months) relative to the duration of primary succession (decades to centuries; Schupp et al. 2010), such that the long-term impact of dispersal on primary succession remains uncertain.

Here we introduce a novel method that quantifies the contributions of both ecosystem development and dispersal in constraining the rate of primary succession over a time-scale of centuries. We use a comparative approach involving two types of arctic successional sequences similar in abiotic and biotic factors but differing greatly in scale and thus dispersal constraints.

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The first of these sequences occurs in forelands exposed by melting glaciers. Here succession is characterized by shifts in dominant growth form, from cyanobacteria and bryophytes on recently exposed overburden, to deciduous vascular plants in intermediate seres, to evergreen plants in later seres (Chapin et al. 1994; Hodkinson et al. 2003; Jones and Henry 2003; Nakatsubo et al. 2005; Robbins and Matthews 2009). High latitudes are expected to be especially prone to anthropogenic climate warming, accelerating glacial melt and the exposure of forelands (Heckmann et al. 2015). The second sequence occurs in sorted circles (1–5 m diameter; fig. A1; figs. A1, A2 and tables A1, A2 are available online), which comprise a gradient of time since disturbance from newly exposed, cryogenically mixing soils in the center to older, more stable soils at the edge (Klaus et al. 2013). Sorted circles occur within glacial forelands, as well as outside them, and are a widespread geomorphic feature of high latitudes (Kessler and Werner 2003; Haugland and Beatty 2005; Walker et al. 2008). Successional sequences on sorted circles are similar to those on glacial forelands, comprising a gradient from cyanobacterial crusts near the center to evergreen plants at the edge (Haugland and Beatty 2005; Walker et al. 2008; Makoto and Klaminder 2012).

We used the differences in spatial scale between glacial forelands and sorted circles to test for the role of plant dispersal as a factor limiting the rate of primary succession. In glacial forelands, the chronosequence spans some kilometers (Hodkinson et al. 2003; Nakatsubo et al. 2005; Robbins and Matthews 2009), but in sorted circles, the successional chronosequence spans several meters (Kessler and Werner 2003; Haugland and Beatty 2005; Walker et al. 2008). Thus, propagules need to disperse several kilometers on forelands but only a few meters on circles. Therefore, if ecosystem development alone limits succession, then similar vegetation should appear in both sequences at similar ages. In contrast, if plant dispersal limits succession, any given vegetation ser should appear on sorted circles much sooner than on glacial forelands. In terms of hypotheses, no significant difference between foreland and circle successional seres would indicate that ecosystem development alone limits rates of succession. Significantly greater ages on forelands than on circles would indicate a role for dispersal limitation.

Similarly, if plant dispersal limits succession, then plant-driven ecosystem properties such as biomass and soil C should occur much earlier on circles than on forelands. Soil C is a measure of ecosystem development that incorporates above- and belowground productivity as well as decomposition, and it is globally important because soil contains about 70% of terrestrial organic C and belowground production and decomposition regulate CO₂ fluxes to the atmosphere that are approximately 10 times greater than those from anthropogenic sources (Chapin et al. 2002). Delays in

biomass and soil C accumulation on large-scale forelands relative to small-scale circles would suggest that these ecosystem properties are also regulated by dispersal, as opposed to purely endogenous rates of element accumulation.

Last, the rate of ecosystem development in the absence of dispersal limitation may be inferred from succession on sorted circles. If dispersal does not constrain succession on small sorted circles, then any difference in age among seres is likely attributable to ecosystem development. Therefore, the extent to which dispersal limits primary succession will be reflected by differences between circles and forelands in the ages of successional seres. In summary, the ages of seres in small-scale circles where propagules can freely disperse reflect constraints imposed by rates of ecosystem development, whereas the ages of seres in large-scale forelands where propagules are more susceptible to dispersal constraint reflect both dispersal and ecosystem development, allowing the influence of dispersal to be isolated.

Comparisons of multiple primary successions have provided insights into the roles of nutrients (Walker and del Moral 2003), weathering (Wardle et al. 2012), competition, and abiotic restraints (Anderson 2007). However, our study of two successional sequences at different spatial scales but with similar species pools of plants and abiotic conditions is a unique opportunity to examine the long-term roles of ecosystem development and plant dispersal during primary succession in the field over centuries. Our primary hypothesis was that successional seres have greater ages on large-scale forelands than on small-scale circles.

Methods

Design

We examined two successional sequences, glacial forelands (hereafter “forelands”) and sorted circles (hereafter “circles”), in August 2011 and 2012 near Abisko in northern Sweden (68°N, 19°E). We studied both sequences in each of three valleys (Ballinriehppi, Guhkesriehppi, and Moarhmmábákti, hereafter Ballin, Guhkes, and Moarhmmá) to encompass the considerable geographic variation characteristic of foreland vegetation (Robbins and Matthews 2009). Valleys were 6–16 km apart. All valleys have bedrock dominated by hard schists.

In each valley and in each of the two successional sequences, we sampled four seres that represented the range of primary succession: overburden without vegetation, cryptogamic soil (including mosses and lichens), herbaceous and deciduous woody vegetation (mostly *Salix herbacea* [dwarf willow]), and evergreen woody vegetation (mostly *Cassiope tetragona* [Arctic bell-heather] and *Cassiope hypnoides* [moss bell-heather]). Each of the four seres was sampled along each foreland sequence (1–3 km long, 1,170–1,370 m asl) in three

plots (20 cm × 20 cm) separated by >10 m. All plots for each sere were at similar elevations to avoid topographical variation in community composition (Garibotti et al. 2011). Each sere was also sampled in three sorted circles (2–3 m diameter, separated by >10 m) within each foreland, in one plot (20 cm × 20 cm) per sere in each circle. In circles, unvegetated overburden occurred in the center, and the other three seres were arrayed along transects from the center to the edge of the circles. Plots were arbitrarily located near the middle of each sere in each sequence. In summary, we sampled three replicate plots in four seres of two sequences (forelands and circles) in three valleys.

Dispersal and Sequence Age

We tested for the role of dispersal by testing the hypothesis that the age of each successional sere was less in the circles than in the forelands. The age of each plot was determined using the diameter of map lichens (*Rhizocarpon geographicum*; Karlén and Black 2002):

$$\text{lichen age (years)} = 0.9617 \times D^{1.33},$$

where D represents lichen diameter (in millimeters). This function was developed in the study area, using forelands sampled twice over 30 years and 270-year-old mine spoils, and validated using ^{14}C dating, tree rings, and historical weather data. Lichen dating has been used on several glacier forelands and sorted circles (Matthews 2005; Haugland 2006) and is accurate up to about 400 years (Karlén and Black 2002).

For each foreland plot, the sizes of the three largest lichens within 5 m were recorded, and the mean was used to determine age. In circles, we determined plot age using regression analysis. In each circle, we divided the distance between the center and the edge into five distance classes (0%–10%, 10%–20%, 20%–40%, 40%–60%, and 60%–100%). For each class, the diameter of the largest lichen and its distance from the center of the circle were measured. These data were used to calculate a regression relationship for each circle that described lichen diameter as a function of distance from the circle center ($r^2 = 0.70\text{--}0.85$, $P = .002\text{--}.014$). This relationship allowed us to predict lichen diameter and age for each plot based on the distance of each plot from the center of its respective circle (Makoto and Klaminder 2012).

Vegetation and Soil C

In each plot, before any destructive sampling, we recorded the cover of bare ground, cryptogams (cryptogamic soil, mosses, and lichens), and each vascular plant species (Daubenmire 1959). Next, aboveground vegetation was harvested,

dried for 1 week at 80°C, and weighed. Cryptogamic soil was collected within a subplot (10 cm × 10 cm, 2 cm deep) using a knife and washed and sorted by hand to retain belowground lichen and moss biomass, which was dried and weighed. After cryptogamic soil collection, roots were sampled with a core (2 cm diameter, 5 cm deep), washed, dried, and weighed. Belowground biomass was the sum of cryptogams in the soil and roots.

In each plot, we collected one soil core (5 cm diameter, 5 cm deep). The core for soil analysis did not include litter or cryptogamic soil crust. We focused on surface soil because the extremely rocky nature of the soil (fig. A1) prevented deeper sampling and because this is the location of the majority of soil C (Jobbágy and Jackson 2000) and thus is most likely to reflect the influence of vegetation (Nave et al. 2013). A 5-g subsample was weighed, dried, and weighed again to determine soil water content. The remainder of each core was sieved (2-mm mesh) and homogenized. Soil organic carbon concentration was measured using a CN analyzer (JM1000CN; JScience Lab, Kyoto, Japan) after adding a few drops of 1 M HCl solution to exclude carbonate.

Statistical Analysis

Response variables were $\log_{10}$ transformed and analyzed using ANOVAs, with sequence (foreland or circle), sere, and the sequence × sere interaction nested within valley, using JMP, version 10 (SAS Institute). ANCOVAs were used to test whether soil C varied with vascular plant cover and between sequences, with cover, sequence, and the cover × sequence interaction nested within valley.

Results

Sequence Age

Age varied significantly between sequences, with forelands generally having much greater ages than circles (fig. 1; table A1). Age also varied among seres and with the interaction between sequence and sere, because the extent to which forelands were older than circles varied among seres. Age was severalfold greater in forelands than in circles for seres dominated by cryptogamic soil (pairwise contrast $t = 5.06$, $P < .001$) and deciduous vascular plants ($t = 5.08$, $P < .001$). Age was also greater in forelands than in circles for seres dominated by evergreen vascular plants, but not significantly so ($t = 1.48$, $P = .14$). The age of the earliest sere (unvegetated overburden) was significantly greater in circles (15 years) than in forelands (4 years; $t = 4.98$, $P < .001$). Age did not vary significantly among valleys. Data underlying all figures and tables are deposited in the Dryad

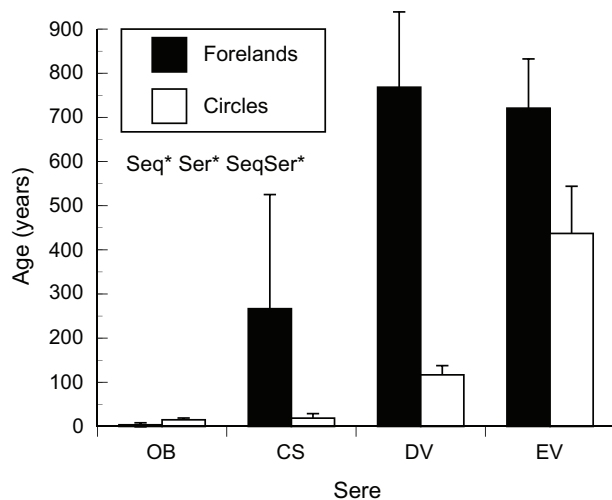


Figure 1: Age (mean $\pm$ 1 SE) of four successional seres (unvegetated overburden [OB], cryptogamic soil [CS], deciduous vascular plants [DV], and evergreen vascular plants [EV]) in two successional sequences (glacial forelands and sorted circles). Seq = sequence effect; Ser = sere effect; SeqSer = sequence by sere interaction. An asterisk indicates $P < .05$. ANOVA results are in table A1, available online.

Digital Repository: <http://dx.doi.org/10.5061/dryad.85j01> (Makoto and Wilson 2016).

Vegetation

The covers of bare ground and growth forms were very similar between forelands and circles (fig. 2; table A1). The cover of bare ground varied significantly among seres, decreasing steadily with increasing age (fig. 2A). The cover of cryptogams varied significantly among seres and was significantly greater in circles than in forelands (significant sequence effect; fig. 2B). The total cover of deciduous vascular plants varied significantly among seres but not between circles and forelands (fig. 2C). The total cover of evergreen vascular plants varied significantly among seres but not between circles and forelands (fig. 2D). There was a significant interaction between sere and sequence for evergreen vascular plants, because they occurred in all vegetated seres in circles but only in one sere on forelands. The most common vascular plant species included the evergreen shrubs *Cassiope tetragona* and *Cassiope hypnoides*, the deciduous shrub *Salix herbacea*, and the graminoids *Carex* sp. (sedge) and *Festuca ovina* (sheep fescue; fig. A2).

Biomass and Soil Carbon

Aboveground biomass varied significantly among seres but not between sequences or with the interaction between

sere and sequence (fig. 3A; table A2). Belowground biomass varied significantly among seres as well as between sequences and with the interaction between sere and sequence, because belowground biomass in circles was greater than in forelands, especially for the oldest, evergreen sere (fig. 3B). Neither above- nor belowground biomass varied significantly among valleys.

Soil carbon (C) content varied significantly among seres but not between circles and forelands (fig. 3C; table A2). Soil C also varied significantly among valleys (table A2;

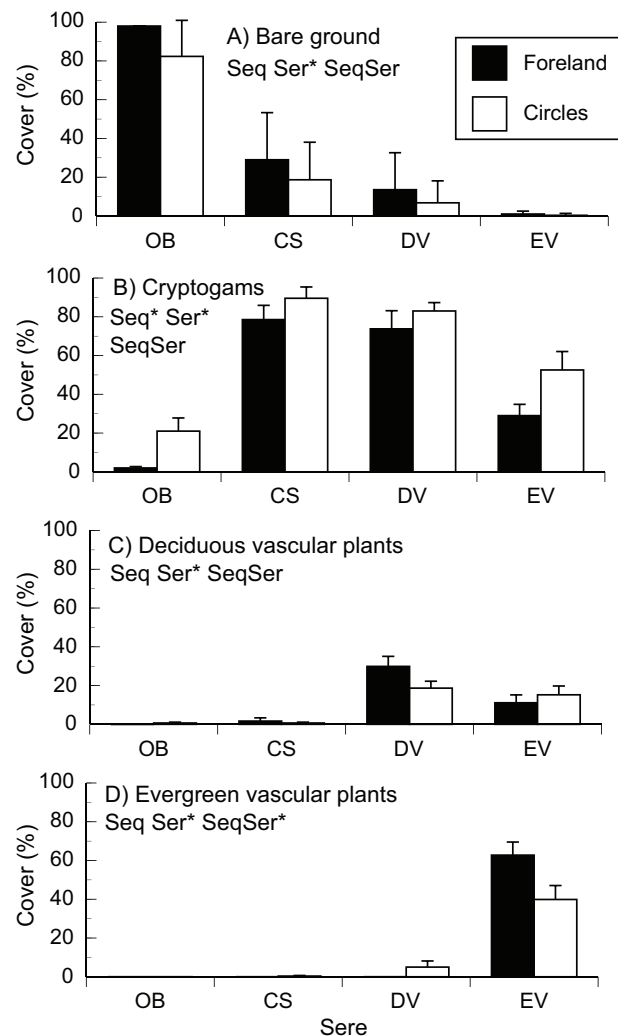


Figure 2: Cover (mean $\pm$ 1 SE) of bare ground (A), cryptogams (B), deciduous vascular plants (C), and evergreen vascular plants (D) in four successional seres (unvegetated overburden [OB], cryptogamic soil [CS], deciduous vascular plants [DV], and evergreen vascular plants [EV]) in two successional sequences (glacial forelands and sorted circles). Seq = sequence effect; Ser = sere effect; SeqSer = sequence by sere interaction. An asterisk indicates $P < .05$. ANOVA results are in table A1, available online.

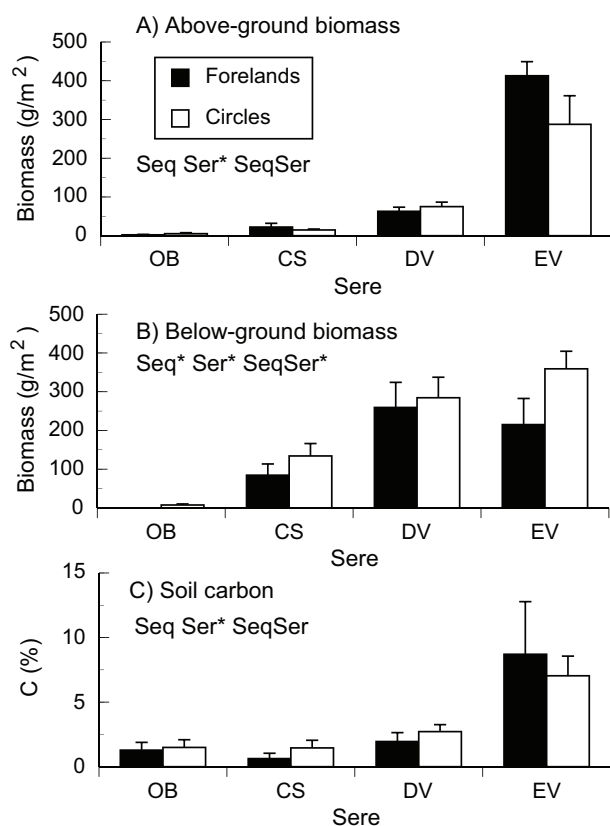


Figure 3: Mean (± 1 SE) aboveground (A) and belowground (B) biomass and soil carbon (C) in four successional seres (unvegetated overburden [OB], cryptogamic soil [CS], deciduous vascular plants [DV], and evergreen vascular plants [EV]) in two successional sequences (glacial forelands and sorted circles). Seq = sequence effect; Ser = sere effect; SeqSer = sequence by sere interaction. An asterisk indicates $P < .05$. ANOVA results are in table A2, available online.

Ballin: $3.14\% \pm 0.33\%$ (mean $\pm$ SE); Guhkes: $1.25\% \pm 0.42\%$; Moarhmmá: $5.09\% \pm 1.78\%$).

Discussion

Successional seres that supported vegetation occurred in circles centuries before they occurred in forelands (seres CS, DV, EV in fig. 1). Further, patterns of plant growth forms, soil C, and biomass among seres were generally similar between circles and forelands. Taken together, the convergent distributions of growth forms and ecosystem properties between circles and forelands in spite of their great differences in scale and age suggest that the rate of foreland primary succession over centuries is influenced by plant dispersal. Dispersal, in turn, may contribute to regulating rates of plant- and microbe-driven ecosystem development such as the accumulation of nutrients and organic matter in

soil (Tscherko et al. 2005; Johnson and Miyanishi 2008; Walker and Wardle 2014).

The results provide an estimate for the rate of succession (Prach et al. 1993) controlled by ecosystem development in the absence of dispersal constraints. If dispersal alone controlled succession, and if all propagules reach all parts of the small-scale circles (diameter ~ 2.5 m) easily, then all seres in the circles would have similar ages. Instead, circle seres were dominated by cryptogamic soil after ~ 20 years, by deciduous vascular plants after a century, and by evergreen vascular plants after four centuries. Thus, ecosystem development alone clearly contributes to regulating the rate of primary succession.

The extent to which dispersal constrains succession can be inferred from differences between circles and forelands in the ages of the successional seres. Plots dominated by cryptogamic soil were ~ 20 years old on circles but were 270 years old on forelands (fig. 1), suggesting that dispersal constraints slowed succession, increasing the time required to reach this stage from decades to centuries. Plots dominated by deciduous plants were ~ 100 years old on circles but were >400 years old on forelands, suggesting that dispersal constraints increased the time required for succession to this sere by a factor of four or more.

Foreland age associated with vascular plants can be estimated only as >400 years because the lichen age-size relationship is less reliable beyond 400 years (Karlén and Black 2002), but the trend of greater ages of forelands was consistent for all vegetated seres. Other forms of dating, such as ^{14}C (Bardgett et al. 2007) and infrared-stimulated luminescence (Kadereit et al. 2010), could be employed to increase the range of our dates. There are no direct comparisons of lichen ages on forelands and circles, but measures from forelands and mine spoils show similar relationships between lichen age and size (Karlén and Black 2002), and circle ages have been validated with ^{14}C dating (Makoto and Klaminder 2012). In spite of uncertainty about ages greater than 400 years, the ages of our successional seres correspond well to those on lava flows of known ages at similar latitudes in Iceland (Cutler et al. 2008).

The influence of dispersal on primary succession has previously been investigated using seed addition experiments (Wood and del Moral 1987; Stöcklin and Bäumler 1996; Lichter 2000; Marteinsdottir et al. 2010), which are valuable but address a short duration relative to succession (Jones and del Moral 2009; Schupp et al. 2010). Our results confirm the influence of dispersal on primary succession but do so over a time span of centuries. The role of dispersal receives almost no attention in recent reviews (Walker and Wardle 2014; Heckmann et al. 2015), but a meta-analysis pointed out that dispersal is likely to be most important in the early stages of primary succession in isolated habitats (Anderson 2007). Our large-scale forelands may serve as an

example of this: succession was delayed on large-scale forelands, and the size of this effect was greatest on seres dominated by cryptogamic soil and deciduous vegetation (fig. 1), the seres farthest from the continuous vegetation beyond the foreland. Distance to propagule sources also influences the rate of succession at Glacier Bay, Alaska (Fastie 1995).

Apart from sere age, most response variables did not vary significantly between forelands and circles. On one hand, the nonsignificant differences between forelands and circles reflect their common abiotic environments and species pools. On the other hand, the nonsignificant differences emerged in spite of the great differences between forelands and circles in spatial scale and age. The two exceptions to nonsignificant differences were the cover of cryptogams (fig. 2B) and belowground biomass (fig. 3B), both of which were significantly greater in circles than in forelands in all seres. Greater cover of cryptogams in circles may reflect greater cryoturbation in circles than in forelands (Klaus et al. 2013), resulting in greater turnover of vascular plant mass and opening up space for cryptogams. Greater belowground biomass in circles may reflect the small particle size of circle soils, produced by the upwelling of fine sediments in the centers of circles (Walker et al. 2008). Our results for belowground biomass were in the same range as those from another primary succession sequence (Uselman et al. 2007).

Soil C content increased with succession, typical for both forelands (Hodkinson et al. 2003; Nakatsubo et al. 2005; Tanner et al. 2013) and circles (Walker et al. 2008). The presence of soil C in young overburden might be attributable to preglacial organic matter that dominates soil C in soils <50 years old in an Austrian foreland (Bardgett et al. 2007). We found no significant difference between forelands and circles in soil C and no interaction between sequence and seres (fig. 3C), suggesting that C varied among seres in a similar manner in both forelands and circles. Nonetheless, soil C was lower in circles than in forelands in the younger seres but greater in the oldest, evergreen sere (fig. 3C). Greater soil C in the foreland evergreen sere may be related to its much greater age relative to the same sere in circles (fig. 1), allowing more time for C to accumulate (Percival et al. 2000). Greater soil C in the foreland evergreen sere may also be related to the low quality of litter from the dominant evergreen woody species, which is high in lignin and suberin and tends to form recalcitrant organic matter (Hobbie and Gough 2004; Freschet et al. 2013). Analysis of quality and age of the soil C could clarify mechanisms underlying succession-driven sequestration.

To some extent, studies of primary succession have emphasized ecosystem development over dispersal, whereas studies of secondary succession have emphasized dispersal over ecosystem development. Differences in emphasis may depend on the differences in temporal scale, with primary

succession being amenable to considering ecosystem development over centuries or millennia (Peltzer et al. 2009), whereas secondary succession is often studied as an ongoing process in which dispersal is readily observable and amenable to experimentation (Cook et al. 2005; Anderson 2007). Clearly, however, both ecosystem development and dispersal act as filters that regulate both primary and secondary succession, and a more comprehensive understanding of succession will require the inclusion of both (Anderson 2007; Walker and Wardle 2014).

Our method does not factor out other differences between circles and forelands that may contribute to differences between them. Forelands encompass a greater range of altitude and thus a greater range of temperature and precipitation. Circles are characterized by gradients of greater cryoturbation in the center and lesser at the edges (Makoto and Klaminder 2012), whereas the location of cryoturbation on forelands depends on landscape-scale patterns of soil water flux (Matthews et al. 1998). While the contributions of these and other factors to differences between circles is uncertain, there is perfect certainty that they differ in scale and thus susceptibility to dispersal limitation.

The comparison of small- and large-scale successional sequences allowed us to parse the contributions of ecosystem development and dispersal in controlling the rate of primary succession. In general, succession attributable to ecosystem development (on meter-scale circles, free of dispersal constraints) was a century for vascular plant dominance and several centuries for evergreen plant dominance. Adding dispersal constraints (over kilometer-scale forelands) delayed the age of cryptogam and deciduous vascular plant seres severalfold, suggesting that arctic primary succession and associated soil C dynamics at the timescale of centuries are partly limited by plant dispersal.

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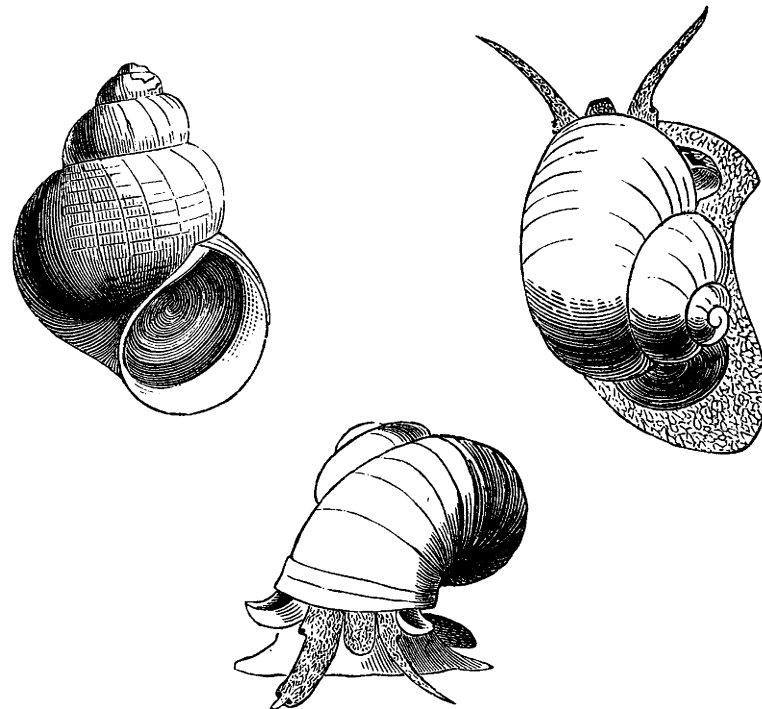
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"It will be noticed that there are two distinct folds, one on each side of the aperture of the shell, and these form regular conduits for the water to enter and bathe the gills for respiration; the water entering by the right opening, and finding egress by the left one. . . . *Vivipara intertexta* Say . . . has a very globose shell, yellowish green or brownish horn color, having numerous nearly obsolete revolving lines." From "Our Common Fresh-Water Shells" by E. S. Morse (*The American Naturalist*, 1869, 3:530–535).