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## **Twenty years of research on fungus-microbe-plant interactions on Lyman Glacier forefront – lessons learned and questions yet unanswered**

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1

2 **Twenty years of research on fungus-microbe-plant interactions on Lyman Glacier**  
3 **forefront – lessons learned and questions yet unanswered**

4

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16

17 *Keywords:* community assembly, community convergence, community divergence,  
18 community trajectory, establishment, glacier forefront, mycorrhizae, propagule

19

20

21 **ABSTRACT**

22

23 Retreating glaciers and the periglacial areas they vacate for organismal colonization  
24 produce a harsh environment of extreme radiation, nutrient limitations, and temperature  
25 oscillations. They provide a model system for studying mechanisms that drive  
26 establishment and early assembly of communities. Here, we synthesize more than twenty  
27 years of research at the Lyman Glacier forefront in the North Cascades Mountains,  
28 comparing the results and conclusions for plant and microbial communities. Compared to  
29 plant communities, the trajectories and processes of microbial community development  
30 are difficult to deduce. However, the combination of high throughput sequencing, more  
31 revealing experimental designs, and analyses of phylogenetic community provide insights  
32 into mechanisms that shape early microbial communities. While the inoculum is likely  
33 randomly drawn from regional pools and accumulates over time, our data provide no  
34 support for increases in richness over time since deglaciation as is commonly observed for  
35 plant communities. Re-analyses of existing datasets suggest that microbial, particularly  
36 fungal, communities are insensitive to time since substrate exposure from underneath the  
37 retreating glacier but responsive to plant establishment both in biomass and community  
38 composition. Further research on functional aspects, organismal activity, or ecosystem  
39 services in early successional environments will provide deeper appreciation for the  
40 dynamics of these communities.

41

42

## 43 **Introduction**

44

45 Many alpine glaciers reached their glacial maximum during the Little Ice Age in the mid-  
46 19<sup>th</sup> century (Egli *et al.* 2001) and have been retreating over the past century and a half at  
47 increasing rates (Dyurgerov & Meier 2000, Hodge *et al.* 1998, Pelto 2006). Glacial retreat  
48 exposes a mineral substrate void of organic legacies and often deficient in mineral nitrogen  
49 (Matthews 1992, Strauss *et al.* 2009, Tscherko *et al.* 2003), factors that globally limit  
50 ecosystem productivity (Vitousek *et al.* 1997). These nutrient limitations are often  
51 combined with extreme fluctuations of daily temperatures, limited barriers against wind  
52 damage, poor water retention, and high irradiation, all of which may limit plant  
53 establishment and survival (Jones & del Moral 2009, Jumpponen *et al.* 1999b, Lichter 2000,  
54 Stocklin & Baumler 1996). Additionally, glaciers and their forefronts most often occur at  
55 high latitudes and altitudes characterized by short growing seasons and substantial snow  
56 cover during the winters. Together, these abiotic stressors make the primary successional  
57 forefronts challenging environments but also provide unique opportunities to study early  
58 assembly of communities (Cázares *et al.* 2005).

59

60 Many mechanisms controlling primary succession in plant communities have been recently  
61 clarified (Pickett *et al.* 2009, Walker & del Moral 2003) and older theories (Clements 1916,  
62 Connell & Slatyer 1977) reevaluated. Some of these insights have shifted views on  
63 community assembly processes in terrestrial ecosystems. For example, early successional  
64 community development seems not to depend on deterministic colonization by pioneering  
65 species but rather combines stochastic dispersal and establishment controls (del Moral  
66 2009, Fastie 1995) that later are amended by deterministic processes such as biotic  
67 competitive and facilitative controls (del Moral 2009).

68

69 Long-term studies in glacier forefronts are rare because of their remote locations and short  
70 accessible seasons dictated by high altitudes and latitudes. Instead, glacier forefronts have

71 often been subjected to a chronosequence approach (space-for-time substitution), in which  
72 distance from the glacier terminus is considered as a proxy for time since exposure  
73 (Cázares *et al.* 2005, Pickett 1989, Walker *et al.* 2010). While suffering from potential  
74 correlations between position in the chronosequence and substrate chemistry, fluctuations  
75 in weather or climatic conditions, distance to propagule sources, or other environmental  
76 parameters (Fastie 1995, Walker *et al.* 2010), the forefronts benefit from providing a single  
77 location wherein substrates of different ages can be observed in a relatively homogenous  
78 environment (Cázares *et al.* 2005, Jumpponen *et al.* 1998, Matthews 1992, Raffl *et al.* 2006).

79

80 In this contribution, we reflect on and synthesize more than twenty years of research at a  
81 glacier forefront in Washington State's North Cascades Mountains, which contain more  
82 than 700 glaciers (Post *et al.* 1971). Similarly to glaciers globally (Dyurgerov & Meier 2000,  
83 Hodge *et al.* 1998), glaciers in the North Cascades have been receding in recent decades  
84 (Pelto 2006, 2011). To optimize our choice for a forefront environment, we explored  
85 several glaciers to find one that would best serve as the long-term study site. Our criteria  
86 included (1) reasonable accessibility, (2) a forefront with relatively little elevational  
87 change, (3) a subalpine habitat to allow establishment of ectomycorrhizal (EcM), ericoid  
88 mycorrhizal (ErM) and arbuscular mycorrhizal (AM) hosts and fungi as well as typically  
89 nonmycorrhizal plants, (4) a north-south orientation to minimize diurnal shade effects  
90 along the length of the forefront, and (5) accessibility for potential animal vectors of  
91 mycorrhizal spores. These criteria also served well for microbial and molecular studies.  
92 One forefront approached near ideal in all criteria: Lyman Glacier, in the Glacier Peak  
93 Wilderness Area, Wenatchee National Forest (Freeman 1941). The glacier and its recession  
94 had been photographed off and on since the late 19<sup>th</sup> Century (Freeman 1941) and later by  
95 periodic aerial photography by the U.S. Forest Service, including new color aerial  
96 photographs taken specifically for our use. These resources allowed a reasonable  
97 description of the glacier's recession and chronosequence approaches to explore  
98 successional phenomena (Jumpponen *et al.* 1998).

99

100 Many of our studies test hypotheses on establishment and succession of communities. We  
101 have focused on the role of mycorrhizal fungi in primary plant succession and the  
102 subsequent secondary succession. Early studies by Reeves *et al.* (1979) showed that in a  
103 desert ecosystem with a severely disturbed, secondary successional habitat, the early plant  
104 invaders were nonmycorrhizal species, whereas plants that dominated the adjacent  
105 nondisturbed system mostly formed associations with AM fungi. Reeves *et al.* (1979) also  
106 reviewed literature on primary succession of volcanic islands that showed early plant  
107 communities to be nonmycorrhizal. They hypothesized that the early nonmycorrhizal  
108 invaders were poor competitors and therefore rapidly replaced when mycorrhizal hosts  
109 could establish after AM inoculum had entered the disturbed site. These AM hosts were  
110 argued to be better competitors and produced additional AM inoculum in the soil to enable  
111 other mycorrhizal plants to establish. Allen *et al.* (2005) reached similar conclusions on  
112 primary successional tephra resulting from the Mount St. Helens eruption. One of our early  
113 driving questions was whether or not a glacier forefront would present similar primary  
114 and secondary succession.

115

116 While glacier systems differ in numerous characteristics and the conclusions may be  
117 context dependent, many general trends and patterns have proved consistent (Orwin *et al.*  
118 2006, Tscherko *et al.* 2003). Here, we use Lyman Glacier forefront and our research  
119 spanning more than twenty years as a model. We first briefly review patterns of plant  
120 community establishment and trajectories, then compare plant and microbial communities.  
121 Much of our earlier work focused on mycorrhizal fungus communities; more recent studies  
122 broadly emphasize bacterial and fungal communities. Finally, from these cross-domain  
123 comparisons, we identify critical areas that have received little attention and propose  
124 approaches to address them in fungal and/or microbial systems.

125

126 **Community assembly and ecological filtering**

127

128 As a general framework, we rely on assembly rules used in community ecology (Cole 1983,  
129 Hunt 1991). This community assembly model integrates traits and life histories and their  
130 contribution to organismal environmental tolerances (Jumpponen & Egerton-Warburton  
131 2005). Factors determining successful establishment are considered as abiotic and biotic  
132 filters that select community components from local, regional, and ecologically suited  
133 species pools (Booth & Swanton 2002, Weiher & Keddy 1995, Weiher & Keddy 2001). Local  
134 and regional propagule pools determine candidate species with potential for being  
135 included in the community, but the ecological filters (Weiher & Keddy 1995, Weiher &  
136 Keddy 2001) remove candidates that fail to establish or persist under the present local  
137 environmental (Grubb 1977, Southwood 1988). Combined, the assembly rules outline  
138 constraints on selection of communities from larger potential constituent species pools  
139 (Weiher & Keddy 2001). These assembly rules can also elucidate processes that produce  
140 communities present in a habitat or environment (Booth & Swanton 2002, Drake *et al.*  
141 1993). In conclusion, assembly rules and ecological filtering are particularly useful in  
142 successional ecology, because they account for both stochastic (*e.g.*, distribution of suitable  
143 establishment sites and random distribution of propagules in seed and spore banks) and  
144 deterministic factors (*e.g.*, facilitative and competitive processes once communities  
145 establish) in a unified framework.

146

## 147 **Plant community dynamics**

148

### 149 *Plant establishment*

150

151 Microsites (safe sites sensu Harper *et al.* 1961) where plants establish in primary  
152 succession are not random (Jumpponen *et al.* 1999b) but characterized as assemblages  
153 with low levels of organization (Robbins & Matthews 2009) where the importance of biotic  
154 and abiotic controls shifts over time (del Moral 2009). As a result of environmental  
155 heterogeneity, some microsites trap larger propagule numbers or may be more favourable

156 for germination and seedling establishment (Harper *et al.* 1965, Jumpponen *et al.* 1999b,  
157 Oswald & Neuenschwander 1993, Titus & del Moral 1998).

158

159 Studies in glacier forefronts have identified surface depressions, nearby rocks, and coarse  
160 surface particles as the characteristics positively associated with plant occurrence  
161 (Erschbamer *et al.* 2001, Jones & del Moral 2005a, Jumpponen *et al.* 1999b, Schlag &  
162 Erschbamer 2000, Stocklin & Baumler 1996). The underlying mechanisms include shade,  
163 increased soil moisture, and changes in surface temperatures (Jones & del Moral 2005a,  
164 Jumpponen *et al.* 1999b, Schlag & Erschbamer 2000), suggesting the importance of physical  
165 environmental amelioration. Plant establishment is also controlled by seed (propagule)  
166 availability and size (Clark *et al.* 2007, Primack & Miao 1992, Turnbull *et al.* 2000)  
167 determined by the surrounding communities, relative fecundities of component species,  
168 and the distance of safe sites from the propagule sources (Jones & del Moral 2009, Schlag &  
169 Erschbamer 2000). Safe sites may facilitate seed trapping, thereby increasing their resident  
170 seed banks (Jones & del Moral 2009, Jumpponen *et al.* 1999b).

171

172 Safe site requirements for seed germination and seedling establishment appear similar  
173 among plant species during early primary succession (del Moral & Wood 1993, Jones & del  
174 Moral 2005a, Jumpponen *et al.* 1999b, Walker *et al.* 2006). Shifts in safe site preferences  
175 likely indicate relaxation of abiotic environmental stressors, leading to dominant  
176 competitive interactions and greater requirements for differentiation in resource use in  
177 later succession. Established plants simultaneously compete for resources with newly  
178 establishing seedlings. Consequently, the balance between competition and facilitation may  
179 be difficult to determine (Chapin *et al.* 1994, Jumpponen *et al.* 1998). Nitrogen fixing plants,  
180 such as infrequent *Alnus* spp. and *Lupinus* spp. at Lyman Glacier forefront, have been  
181 argued to be particularly important because they reduce the nitrogen limitation in addition  
182 to improving water retention in the developing soils and providing shade to reduce  
183 irradiation (Walker *et al.* 2003).



184

185 *Patterns of plant community development*

186

187 To describe plant community diversity, and heterogeneity at Lyman Glacier, we recorded  
188 plant species (vascular plant checklist is available as Supplemental Table S1) in clusters of  
189 four 0.25m<sup>2</sup> sub-plots located at 20m intervals along four equidistant transects for a total  
190 of 228 1m<sup>2</sup> sampling units. From these data we calculated plant species richness (S),  
191 Shannon-Wiener diversity (H'), and evenness ( $-H'/\ln S$ ) and compared community  
192 compositions using Nonmetric Multidimensional Scaling (NMS - McCune & Grace 2002). To  
193 construct a metric for community heterogeneity, we estimated similarity of community  
194 compositions among plots, using percent similarity (PS) as described in del Moral (2002),  
195 and regressed that against distance from the glacier terminus to test whether or not our  
196 communities tended to converge or diverge over time (del Moral & Jones 2002, del Moral  
197 2009), *i.e.*, whether the community PS would decrease or increase over time since  
198 deglaciation.

199

200 In contrast to Coleman Glacier on Mount Baker, also in Washington state (Jones & del Moral  
201 2005b), the most recently deglaciated plots at Lyman Glacier were devoid of vegetation,  
202 and nonvegetated plots occurred even near the terminal moraine (Fig. 1). The first  
203 individuals of the nonmycorrhizal *Luzula piperi* and *Saxifraga ferruginea*, and the  
204 ectomycorrhizal *Abies lasiocarpa* had established after approximately 15 years since  
205 deglaciation, suggesting a limited control of establishment by the mycorrhizal habit  
206 (compare with Read 1991) and limited dependence on presence of mycorrhizal fungus  
207 propagules (see also Collier & Bidartondo 2009, Reeves *et al.* 1979). Overall, the species  
208 richness in our sampling limited to a 1m<sup>2</sup> scale was low, but comparable to that observed at  
209 Coleman Glacier (Jones & del Moral 2005b). At Lyman Glacier, richness reached a  
210 maximum of  $6.25 \pm 0.82$  (mean  $\pm$  1 st dev) near the terminal moraine. The most species  
211 recorded in any one plot was ten.

212

213 As common in early primary succession (Matthews 1992, Reiners *et al.* 1971), plant species  
214 richness and diversity increased with time since deglaciation as evidenced by our linear  
215 regression analyses (Fig. 2a, 2b). Evenness was low ( $0.23 \pm 0.08$ ) and constant with time  
216 since deglaciation. These patterns stem from sparse plant occurrence near the glacier  
217 terminus and increasing but still heterogeneous cover near the terminal moraine. Although  
218 the increasing plant richness and biomass are common observations in chronosequence  
219 studies (Matthews 1992, Reiners *et al.* 1971), our observations contrast with those  
220 reported in similar scale for Coleman Glacier (Jones & del Moral 2005b): no dense canopies  
221 have established at Lyman Glacier forefront in the first hundred years since glacier retreat.

222

223 To classify plant community types (CTs), the 228 experimental units were assigned into  
224 seven clusters by complete linkage clustering (JMP version 7.01, SAS Institute, Cary North  
225 Carolina) similarly to del Moral (2002), so that clusters retained ~75% of the information  
226 on the plot level (Supplemental Figure S1). The seven CTs were characterized by two  
227 species that were most strongly associated with that cluster (see insert in Fig. 1).  
228 Evaluation of the CT frequencies along the Lyman Glacier forefront permits an assessment  
229 of community trajectories and their dynamics. Nonvegetated patches and early establishing  
230 nonmycorrhizal plants (CTs 1 and 4, with *Juncus drummondii* + *Saxifraga ferrugina*) occur  
231 commonly but in variable frequencies throughout the forefront. The common communities  
232 near the terminal moraine are CTs 2 and 7, comprised primarily of plant species frequent  
233 in the montane parkland habitat outside the forefront, including the AM-forming *Luetkea*  
234 *pectinata* and the ErM plants *Cassiope mertensiana* + *Phyllodoce empetriformis*. None of the  
235 EcM Pinaceae (*Abies lasiocarpa*, *Larix lyalii*, + *Tsuga mertensiana*), common in forested  
236 patches among the alpine meadows adjacent to the forefront, are frequent enough to weigh  
237 in the community assignments.

238

239 These analyses suggest that, not only the successional trajectories, but also the  
240 environmental heterogeneity in this system dictate the CT occurrence. To exemplify, CTs 3,  
241 5 and 6 comprised of *Luzula piperi* + *Salix phylicifolia*, *Veronica wormskjoldii* + *Pedicularis*  
242 *groenlandica*, and *Pedicularis groenlandica* + *Carex scopularis*, respectively, occur mainly in  
243 depressions and near creeks that likely maintain high soil moisture. This emphasizes the  
244 difficulties of applying the space-for-time chronosequence approach (Walker *et al.* 2010),  
245 but simultaneously indicates the sensitivity of CT analyses to primary determinants of  
246 plant community development.

247

#### 248 *Deterministic vs. stochastic processes in the plant community succession*

249

250 Plant community convergence towards a terminal (climax) state community was integral in  
251 early concepts of succession (Clements 1916). If the deterministic processes were to  
252 increase with succession, then plant community composition should follow a predictable  
253 trajectory (del Moral 2009) and become more homogenous over successional time (Leps &  
254 Rejmanek 1991). However, convergence towards a stable community (Pickett 1989) may  
255 depend on factors such as heterogeneity of the local species or their propagule pools,  
256 strength of the biological legacies, importance of priority effects, and sensitivity to  
257 conditions during initial stages of succession (Walker *et al.* 2010). We discuss below  
258 trajectories based on ordination analyses and changes in community similarities among  
259 plots along the chronosequence.

260

261 In our plant community ordination analyses, NMS scores for the first axis increased  
262 linearly, suggesting a predictable trajectory along this axis (Fig. 3) as suggested in early  
263 concepts of succession (Clements 1916). Changes in the other two axes were not linear but  
264 were best characterized by regression models that included quadratic terms (data not  
265 shown). When standard deviations of NMS axis scores were analyzed by linear regression,  
266 they increased linearly for axis 1 (Fig. 4) and axis 2 (not shown). While communities may

267 be changing to include a greater component from surrounding late successional  
268 communities, the increasing standard deviations suggest a strong contribution of stochastic  
269 processes or priority effects during nearly a century since deglaciation (del Moral 2009).  
270 More importantly, the increasing standard deviations suggest that these periglacial plant  
271 communities are characterized by community divergence rather than convergence during  
272 early succession.

273

274 To further illuminate the determinism in the plant communities, we calculated percent  
275 similarity (PS) for each group of plots representing equal time since deglaciation (see del  
276 Moral & Jones 2002). In contrast to increasing determinism in the primary successional  
277 system at Mount St. Helens in Washington state (del Moral 2009), our PS estimates  
278 decreased with time since deglaciation (Fig. 5). This observation corroborates the analyses  
279 of the NMS standard deviations and points to stochastic processes. These findings are  
280 primarily attributable to the occurrence of a large number of different CTs and the  
281 persistence of the early successional communities near the terminal moraine. In sum, we  
282 conclude that plant communities at Lyman Glacier site are diverging rather than  
283 converging at these stages of succession.

284

## 285 **Fungal community dynamics**

286

### 287 *Sources and distribution of fungal propagules*

288

289 Establishment of fungal propagule banks from atmospheric sources in newly exposed  
290 substrates is little debated, but distribution of these banks has received little attention. It is  
291 uncertain whether microtopological characteristics similar to those for plant safe sites  
292 accumulate microbes as a result of reduced air velocities or water flow. The Baas-Becking  
293 hypothesis (Martiny *et al.* 2006) states that because of their small size and enormous

294 numbers the microbial propagules are everywhere and environment selects from the  
295 established propagule banks. In contrast to such environmentally based niche models,  
296 recent work suggests that microbial communities, like those of macroscopic eukaryotes,  
297 may suffer from dispersal limitations. They may thus be assembled by stochastic  
298 immigration, establishment, and local extinction events (Peay *et al.* 2010).

299

300 The Lyman Glacier forefront is surrounded by bountiful sources of seeds and spores plus  
301 living fragments of plants and fungi. Its east and west sides are bounded by cliffs and  
302 benches leading to ridges with meadows and subalpine trees. The lowermost moraine has  
303 adjacent meadows and groups of conifers and willows. Only at the head of the glacier there  
304 are cliffs and crags with little vegetation. The plant and fungal propagules may be dispersed  
305 onto the forefront by abiotic factors such as wind, rain, flowing water and landslides, as  
306 well as by biotic means: birds, mammals and arthropods. The continuous input of material  
307 and propagules onto the glacier and periglacial areas is evidenced by frequent deposits of  
308 woody debris covered by lichens.

309

310 A propagule rain falls on the glacier and its forefront during wind and rain storms,  
311 particularly when epigeous, *i.e.* above-ground fruiting mushrooms, release spores.  
312 Consequently, propagules of EcM fungi are likely to be available to hosts in early  
313 succession. This was implicit in the EcM conifer seedlings appearing early in the primary  
314 succession. Collier & Bidartondo (2009) reported on heathlands where EcM spores are  
315 rare, pines and birches establish and persist at least a year after germination without EcM  
316 formation, in effect waiting for the EcM inoculum to arrive. This is not likely the case in the  
317 Lyman forefront: all Pinaceae sampled, even 1<sup>st</sup> year seedlings, were colonized by EcM  
318 fungi (Cázares *et al.* 2005). The two systems differ fundamentally: Collier's & Bidartondo's  
319 (2009) heathland systems have high soil organic matter that provides water retention and  
320 nutrients. In contrast, the periglacial outwash at Lyman has little organic matter to sustain  
321 seedlings while they wait for EcM colonization to establish. These phenomena are inferred

322 from few seedling samples, because depletion of seedlings by large-scale sampling would  
323 have drastically interfered with early successional stages.

324

325 Early EcM colonization seems plausible, because soil recently exposed from under the ice  
326 contained DNA of *Laccaria*, a genus commonly fruiting among the EcM trees in the  
327 forefront (Jumpponen 2003). Older soil, *i.e.* at the terminal moraine, contained a greater  
328 diversity of fungi than the recently exposed soils. Propagule numbers also increase over  
329 time as shown by a study with EcM-forming *Pinus contorta* as bait (Trowbridge &  
330 Jumpponen 2004). These results corroborate the presence of fungal propagules in recently  
331 deglaciated substrates, although their numbers were low. Accordingly, it is likely that – in  
332 addition to falling on the exposed glacial till – spores also land on the glacier, to be washed  
333 into crevasses and ultimately into the water and soil emerging from under the ice. This  
334 propagule dispersal likely establishes a resident propagule bank soon after deglaciation.  
335 Microtopology that determines air and water flow likely distribute the propagule pools  
336 unevenly across the landscape, thereby establishing safe sites that differ in their spore  
337 numbers and compositions.

338

339 Although relatively infrequent over the glacier forefront, establishment of EcM willows and  
340 conifers and accumulation of leaf litter under their crowns supports fruiting of EcM fungi.  
341 Repeated searches over more than a decade on the forefront revealed that in all,  
342 sporocarps of only 13 species of EcM fungi were found on the forefront; only a few of the  
343 nearly 70 species in the adjacent subalpine parklands appeared on the forefront  
344 (Jumpponen *et al.* 1999a). Several species recorded on the forefront, in return, were not  
345 found in surrounding areas (Jumpponen *et al.* 2002). The most abundant genera were  
346 *Cortinarius*, *Inocybe* and *Laccaria*. These genera were also common in primary successional,  
347 upper montane and subalpine habitats under *Salix* on volcanic substrates on Mt. Fuji, Japan  
348 (Nara *et al.* 2003a). Two species, *Cortinarius decipiens* and *Inocybe lacera*, were observed  
349 locally abundant at both Lyman Glacier and Mt. Fuji. A major propagule source of *I. lacera*  
350 and *Cortinarius* and *Laccaria* spp. at Lyman was the old outwash meadow/willow habitat

351 probably several thousand years old immediately below the terminal moraine (J. Trappe,  
352 unpublished data).

353

354 Nara *et al.* (2003b) determined that in early succession the fungi forming EcM were  
355 generally the same as fruited aboveground and the diversity of fungal species gradually  
356 increased with plant community development. Based on fruiting body data, this was also  
357 true to a degree at Lyman Glacier (Jumpponen *et al.* 2002): no EcM fruiting bodies were  
358 observed up to 300 m from the terminus, two species fruited from 300-400m, and eight  
359 from 800-900m. Nara *et al.* (2003b) found from molecular analysis that several EcM fungi  
360 were resupinate; the same is largely true of the Lyman forefront (Trowbridge &  
361 Jumpponen 2004). No fruiting bodies of resupinate fungi have been recorded at Lyman  
362 (Jumpponen *et al.* 2002), but spores of hypogeous fungi reliant on animal mycophagy for  
363 dispersal were detected on the forefront in scats of yellow-pine chipmunks, hoary  
364 marmots, pikas, and mule deer (Cázares & Trappe 1994). None of the fungi represented by  
365 those spores were found fruiting on the forefront. Indeed, only one fruiting of a hypogeous  
366 fungus was recorded over the several years of sampling: a tiny new species, *Hymenogaster*  
367 *glacialis*, fruited among willow mycorrhizae (Cázares & Trappe 1990). Because of its small  
368 size (< 3-6mm broad), it could have been more common but overlooked. Nonetheless,  
369 dispersal of hypogeous fungal spores is stochastic, depending on animal vectors that  
370 establish spore deposits locally enriched for particular species. Animals can also disperse  
371 spores of epigeous EcM fungi. Deer are effective in inoculation of pines with both  
372 hypogeous and epigeous fungi in primary successional habitats in coastal sand dunes  
373 (Ashkannejhad & Horton 2006).

374

375 AM fungi increase steadily after disturbance in many early successional ecosystems,  
376 indicating successional dynamics of these communities (Allen & Allen 1980, Gemma &  
377 Koske 1990, Greipsson & El-Mayas 2000, Koske & Gemma 1997). However, compared to  
378 old-field or dune systems, patterns of AM establishment in a montane glacial system may  
379 be stochastic, dictated by dispersal by movement of soil that contains inoculum (Warner *et*

380 *al.* 1987). We inferred stochastic AM spore deposition from mycorrhizal colonization,  
381 because spores of Glomeromycota were rarely encountered (Cázares *et al.* 2005). At the  
382 Lyman Glacier forefront, dispersal is likely mainly on the feet or in the feces of visiting  
383 animals (see also Allen *et al.* 1984, Warner *et al.* 1987), with small avalanches or land slides  
384 from cliffs and benches that border the forefront, or perhaps in water flow from  
385 established plant communities on lateral moraines. These dispersal mechanisms are likely,  
386 because AM plants were often more common at the edges than in the center of the  
387 forefront. The most recently exposed substrates (15-25 yrs) had no or few AM plants, but  
388 otherwise no clear patterns were evident, further evidencing the stochastic nature of AM  
389 spore dispersal. Helm *et al.* (1996) reported that AM colonization and spores were  
390 infrequent and showed no particular patterns on the forefront of an Alaskan low-elevation  
391 glacier, further evidencing spore dispersal limitation in these habitats.

392

393 Our analyses above show that CTs with *Cassiope* and *Phyllodoce* increase late on the Lyman  
394 Glacier chronosequence. While arrival of the ErM fungi could not be observed directly, ErM  
395 colonization of the susceptible hosts gradually increased over time since soil exposure  
396 (Cázares *et al.* 2005), suggesting gradual buildup of an inoculum pool, likely from air-  
397 and/or ungulate-borne propagules. Similarly to ErM, dark septate endophyte (DSE)  
398 colonization gradually increased over the chronosequence regardless of the mycorrhizal  
399 habit of the host (Cázares *et al.* 2005). These observations parallel those of Peay *et al.*  
400 (2010): dispersal seems a key control of fungal community composition in early  
401 successional stages.

402

403 *Patterns of fungal community development*

404

405 To attempt fungal community analyses comparable to those performed for plants, we  
406 reanalyzed an EcM dataset (Trowbridge & Jumpponen 2004) and two others on soil  
407 communities (Jumpponen 2003, Jumpponen 2007). These data may not compare directly



408 with those for plants because of differences in data volumes and recording. However, they  
409 illustrate contrasts and similarities between fungal and plant communities and identify  
410 further research needs.

411

412 In contrast to plant communities, where we directly estimated development as a function  
413 of time since deglaciation, we decoupled the effects of plant establishment and time since  
414 deglaciation on fungal communities. Trowbridge & Jumpponen (2004) described EcM  
415 communities of *Salix* spp. and observed that richness, diversity and evenness estimates  
416 were rather insensitive to distance from the glacier terminus as well as to the willow  
417 canopy microenvironment. Whereas the community metrics were unresponsive, individual  
418 components (EcM morphotypes identified through ITS-RFLP and sequencing) showed  
419 preferences for canopy or intercanopy environments while some increased in frequencies  
420 with time since deglaciation. Trowbridge & Jumpponen (2004) argued these results  
421 suggested niche preferences related to organic legacies associated with soil development.

422

423 To compare successional trajectories between fungal and plant communities, we used  
424 complete linkage clustering with the EcM morphotype data. We analyzed these data with  
425 and without including the nonmycorrhizal root tips into the community type (CT)  
426 constituents. With nonmycorrhizal tips included, two clusters were identified retained  
427 71.2% of the plot-level variability (not shown) and were defined by two of the three  
428 morphotypes assigned to Sordariales in the original analyses (Trowbridge and Jumpponen  
429 2004). Exclusion of the nonmycorrhizal roots revealed five clusters that retained 74.3% of  
430 total variability on the plot level (Supplemental Fig. S3). These community analyses were  
431 uninformative with respect to time since deglaciation or canopy environment because  
432 three of the five clusters occurred only once, twice, and three times in the 30 samples. The  
433 most common cluster, occurring 19 times, was rather defined by its heterogeneity than by  
434 unifying community components: the common morphotypes (two Sordariales and two  
435 Cortinariaceae; Supplemental Fig. S3) were common constituents of this CT.

436

437 These analyses highlight fundamental issues that complicate fungal community analyses. A  
438 ten-fold increase in sampling, similar to that for plant communities, would be difficult to  
439 achieve by microscopic EcM morphotyping and molecular identification. Moreover, while  
440 the EcM communities may not be as diverse as those in soil (Buée *et al.* 2009), their  
441 complete characterization even in an early successional system with limited diversity  
442 would be difficult. However, development of high throughput parallel sequencing tools  
443 (Cardenas & Tiedje 2008) combined with DNA-tagging (Meyer *et al.* 2008) might solve the  
444 issues necessary to differentiate among the root-inhabiting fungal communities.

445

446 *Deterministic vs. stochastic processes in fungal community succession*

447

448 We analyzed combined datasets (from Jumpponen 2003, Jumpponen 2007) to see if we  
449 could draw inferences on responses of the fungal communities and/or their components.  
450 Like Emerson and Gillespie (2008), our analyses assume immigration and environmental  
451 filtering, not speciation, as the fundamental processes of community assembly in early  
452 succession. The scale of a glacier forefront is unlikely to lead to cladogenic speciation,  
453 mainly because the large allochthonous source populations maintain geneflow into the  
454 periglacial environment.

455

456 To test whether the EcM communities associated with *Salix* were undergoing community-  
457 level convergence or divergence, we analyzed the NMS axis score standard deviations and  
458 estimated PS as described in del Moral & Jones (2002) and as above for plant communities.  
459 When the standard deviations of the NMS axis scores were analyzed by linear regression  
460 with vs without the terms that would account for the canopy environment plus interaction  
461 terms, the axis score standard deviations showed no significant effects of either time since  
462 deglaciation or canopy ( $P > 0.15$  for all effect tests using ANOVA or t-tests for null

463 hypotheses that parameter estimates equal zero). Similarly, none of the simple linear or  
464 multiple regression models analyzed to test effects of *Salix* canopies and time since  
465 deglaciation on PS differed significantly for convergence or divergence ( $P > 0.30$  for all  
466 effect tests using ANOVA or t-tests for null hypotheses that parameter estimates equal  
467 zero). In other words, we found no support for patterns similar to those observed for plant  
468 communities.

469

470 We also targeted general fungal communities associated with soils underneath *Salix*  
471 canopies vs. intercanopy areas using an approach similar to that described above. In these  
472 analyses, we tested whether differential phylogenetic clustering between the two canopy  
473 environments could be detected or whether phylogenetic patterns could be visualized in  
474 relation to time since deglaciation. Using the data matrices comparing within-sample  
475 phylogenetic distances among the experimental units, we sought stochastic vs.  
476 deterministic trajectories of fungal communities. To do this, we re-analyzed Small Sub-Unit  
477 (SSU) sequences of the ribosomal RNA gene from two clone library studies (Jumpponen  
478 2003, Jumpponen 2007) characterizing soils collected from canopy or intercanopy  
479 locations along a Lyman chronosequence. The soil samples originated from 0-900m from  
480 glacier terminus and included fifteen from underneath *Salix* canopies (Jumpponen 2007)  
481 and seventeen intercanopy samples across the chronosequence (Jumpponen 2003). We  
482 reanalyzed representative sequences from the two studies and MUSCLE-aligned them using  
483 Geneious Pro 5.3.4 (Biomatters Ltd., Chirstchurch, New Zealand). The alignments were  
484 analyzed by neighbor joining (NJ) method and the tree distance matrix obtained was  
485 analyzed with Fast Unifrac (Hamady *et al.* 2010) with a Principal Coordinates Analysis  
486 (PCoA). The PCoA scores obtained for the first three axes (representing 20.6%, 11.0%, and  
487 7.1% of the variability) and the NJ distance matrix were used to analyze community  
488 similarity described above by use of both the standard deviations of PCoA scores and  
489 within-sample mean NJ distances to test hypotheses on community convergence or  
490 divergence.

491

492 Analyses of PCoA axis scores indicated that Axis 1 and Axis 3 scores did not vary  
493 significantly with time since deglaciation or canopy condition. In contrast, Axis 2 seemed to  
494 drive the observed patterns in a full model (goodness of fit;  $F_{3,28}=6.4361$ ,  $P=0.0019$ ) with  
495 time since deglaciation and canopy condition main effects and their interaction. In this  
496 model, Axis 2 PCoA scores increased with time since deglaciation (Fig. 6;  $F_{3,28} = 4.829$ ,  $P =$   
497  $0.0364$ ) indicating a trajectory in fungal community composition based on SSU sequence  
498 data. We interpret these data to indicate that the communities are shifting somewhat  
499 predictably and incorporating different community members to lead to such trajectory. In  
500 contrast, we found no evidence for canopy effects on community composition. Analyses of  
501 standard deviations of PCoA axis scores similar to those we used for plant communities  
502 indicated that Axis 3 score standard deviations decrease with distance from glacier  
503 terminus (Fig. 7; full model goodness of fit  $F_{3,28} = 9.1490$ ,  $P = 0.0002$ ) suggesting  
504 phylogenetic convergence with time since deglaciation. However, standard deviations for  
505 Axis 1 and 2 scores showed no response to time since deglaciation, suggesting minor  
506 convergent patterns.

507

508 These analyses of the PCoA scores and their standard deviations provide a starting point  
509 for asking which organisms may be enriched in the late primary successional soils. Our  
510 earlier studies indicate that EcM fruiting bodies (Jumpponen *et al.* 2002), root-associated  
511 propagules (Trowbridge & Jumpponen 2004), and the root colonization of various hosts  
512 (Cázares *et al.* 2005) increase over successional time. However, only *Tomentella*  
513 (Thelephoraceae; GenBank Accession DQ092920) increased in frequency with time since  
514 deglaciation and none decreased. Others also increasing with time since deglaciation  
515 included taxa with various non-symbiotic life history strategies: *Mycoacia* (Merulinaceae;  
516 DQ873636) and *Pulvinula* (Pyronemataceae; U62012). Thus, the increasing trajectory of  
517 Axis 2 PCoA scores and convergence indicated by declining Axis 3 PCoA score standard  
518 deviations corroborate results of our earlier studies and evidence a relationship of plant  
519 establishment with subsequent fungal community enrichment.

520

521 In addition to PCoA, we analyzed the SSU RNA gene NJ distance matrix to directly compare  
522 sample-level distances in *Salix* canopy and intercanopy soils along the forefront  
523 chronosequence. These analyses tested if these communities show a random assembly  
524 from the regional propagule pools and would therefore possess equal ability to establish  
525 across the periglacial substrates. Alternatively, if environmental filters shape the  
526 establishing communities, the communities should show phylogenetic structuring –  
527 perhaps related to the establishment of few organisms that share similar preferences for  
528 habitat or hosts but are not competitively exclusive. In contrast to the analyses of Axis 2  
529 PCoA scores, fungal community NJ distances did not vary with time since deglaciation ( $F_{1, 28}$   
530 = 0.0068,  $P = 0.93$ ) so the fungal communities are not strongly affected by time of substrate  
531 exposure from underneath the glacier (Fig. 8). However, judging from these analyses,  
532 fungal communities of canopy soils had significantly lower NJ distances than those from  
533 non-vegetated areas (Fig. 8;  $F_{2,28} = 11.1$ ,  $P = 0.0022$ ). The nonsignificant interaction term  
534 indicates canopy effects regardless of position in the periglacial chronosequence. We  
535 conclude that fungal communities converge in the canopy soils relative to nonvegetated  
536 soils and plant establishment homogenizes soil fungal communities. Although the results of  
537 our PCoA and NJ analyses are incongruent, a simple explanation that, while the intercanopy  
538 communities may be a random draw of propagules, the canopy soils in the sparsely-  
539 vegetated early plant communities are enriched for fungi that rely on host photosynthates  
540 or litter. To better tie this to the community assembly model that we introduced previously  
541 (Jumpponen & Egerton-Warburton 2005), this convergence can be argued to result from  
542 selection of fungi from the local propagule pool based on their compatibility with the *Salix*  
543 and its canopy soil environment. This is best exemplified by foliage-associated *Coniochaeta*  
544 (GenBank Accession GQ154624), the only taxon positively associated with canopies: it did  
545 not respond to time since deglaciation in our analyses.

546

547 The convergence inferred from the NJ distances corroborates our earlier PLFA studies  
548 (Ohtonen *et al.* 1999), in which microbial communities differed between canopy and  
549 intercanopy soils. These results emphasize the importance of plant establishment in  
550 shaping early microbial communities (Ohtonen *et al.* 1999). While compositional changes

551 with time since deglaciation were not obvious, the samples collected underneath  
552 established plants were more tightly clustered in the NMS ordination than those collected  
553 from nonvegetated areas (see Fig. 2 in Ohtonen *et al.* 1999). Although those data do not  
554 permit a more thorough convergence analysis, we propose that, in combination with our NJ  
555 distance analyses, plants tend to homogenize microbial communities and select subsets of  
556 compatible microorganisms from stochastic propagule pools.

557

558 These conclusions parallel results from a replicated soil transfer on the Lyman forefront  
559 (Jumpponen *et al.* 1998). In those studies, small mesh bags were filled with willow canopy  
560 soil and an equal number with intercanopy soils. Seeds of *Pinus contorta*, which occurs on  
561 the forefront, were planted in each bag. Separate holes to accommodate one bag of each  
562 soil type were dug under canopies and in intercanopy sites. Seedling emergence and  
563 survival were recorded 8 weeks after sowing and were low in all treatments (2 soil types x  
564 2 locations) but on average twice as high in the canopy soil transferred to intercanopy  
565 spaces than in other treatments. Canopies thus appeared to suppress emergence/survival  
566 and intercanopy soils were similarly adverse in that respect. The superior performance of  
567 seedlings in canopy soil in intercanopy sites indicates that the combined enhancement of  
568 nutrients and microbes provided greater benefit when the suppressive effects of the  
569 canopies themselves were removed.

570

## 571 **Successional trajectories of plant and microbial communities compared**

572

573 Our synthesis of the work conducted on Lyman Glacier forefront over more than two  
574 decades identified research gaps in our current understanding of the fundamental  
575 processes of early microbial community assembly. Early propagule accumulation and the  
576 processes that control it prior to the community assembly are poorly understood for both  
577 microbial and plant communities. A framework of safe microsites for plant seed  
578 accumulation and seedling establishment exists, but the presence of such sites for

579 microbial communities remains uncertain. Mechanisms that control selection of active  
580 microbial community members from established propagule banks are equally unclear. The  
581 difficulty of selecting an appropriate scale for 'microbial landscape' and its ecology  
582 complicates these issues.

583

584 Our parallel analyses of plant and microbial communities highlight some clear and distinct  
585 dissimilarities between the two, because plant establishment modifies soil chemistry and  
586 the physical environment. To account for plant controls of microbial communities, our  
587 analyses aimed to decouple effects of substrate exposure and plant establishment. Early  
588 plant community development at Lyman Glacier forefront can be characterized by  
589 increasing species richness and community divergence over time since deglaciation, but  
590 analyses of the microbial communities provide no strong evidence for similar changes. In  
591 contrast, establishing plants appear to homogenize soil-inhabiting microbial communities  
592 in our periglacial system, and these effects may strengthen over time. Our analyses of  
593 microbial communities using PLFA and SSU sequence data that broadly characterize  
594 microbial communities show a tighter clustering of the samples obtained from soils  
595 underneath plant canopies compared to soils from open, nonvegetated areas. In sum, the  
596 fungal and microbial communities of canopy soils converge relative to intercanopy soils.

597

598 We hope that these analyses and discussions will arouse lust for further analyses of  
599 microbial community trajectories as well as for patterns and mechanisms of bacterial and  
600 fungal community divergence and convergence. Microbial communities tend to be orders of  
601 magnitude more complex than those of plants and animals, but the extreme environments  
602 in primary successional ecosystems limit microbial richness. Furthermore, recent studies  
603 provide insights into microbial ecosystem functions and processes, particularly into those  
604 preceding establishment of plants (Schmidt *et al.* 2008) and comprised of unexpected  
605 and/or novel community constituents (Freeman *et al.* 2009, Nemergut *et al.* 2007). Our  
606 analyses here and those published elsewhere evidence that successional processes of  
607 microbial communities are unlikely to be successfully modeled after those of plants, albeit

608 the plant controls of microbial communities must be accounted for after plant  
609 establishment. We conclude that microbial communities and their dynamics express novel  
610 community level processes with important consequences for plant community  
611 development: the field is wide open for research, especially with newly available molecular  
612 and statistical techniques.

613

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615

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631

## 632 **References**

633



634 Allen EB, Allen MF, 1980. Natural re-establishment of vesicular-arbuscular mycorrhizae  
635 following stripmine reclamation in Wyoming. *Journal of Applied Ecology* **17**: 139-147.  
636

637 Allen MF, Crisafulli CM, Morris SJ, Egerton-Warburton LM, MacMahon JA, Trappe JM, 2005.  
638 Mycorrhizae and Mount St. Helens: story of a symbiosis. In: Dale VH, Swanson FJ, Crisafulli  
639 CM (Eds.), *Ecological Responses to the 1980 Eruption of Mount St. Helens*. Springer Verlag,  
640 New York, pp. 221-231.  
641

642 Allen MF, Macmahon JA, Andersen DC, 1984. Reestablishment of Endogonaceae on Mount  
643 St. Helens - survival of residuals. *Mycologia* **76**: 1031-1038.  
644

645 Ashkannejhad S, Horton TR, 2006. Ectomycorrhizal ecology under primary succession on  
646 coastal sand dunes: interactions involving *Pinus contorta*, suilloid fungi and deer. *New*  
647 *Phytologist* **169**: 345-354.  
648

649 Booth BD, Swanton CJ, 2002. Assembly theory applied to weed communities. *Weed Science*  
650 **50**: 2-13.  
651

652 Borneman J, Hartin RJ, 2000. PCR primers that amplify fungal rRNA genes from  
653 environmental samples. *Applied and Environmental Microbiology* **66**: 4356-4360.  
654

655 Bowers RM, Lauber CL, Wiedinmyer C, Hamady M, Hallar AG, Fall R, Knight R, Fierer N,  
656 2009. Characterization of airborne microbial communities at a high-elevation site and their  
657 potential to act as atmospheric ice nuclei. *Applied and Environmental Microbiology* **75**:  
658 5121-5130.  
659

660 Buée M, Reich M, Murat C, Morin E, Nilsson RH, Uroz S, Martin F, 2009. 454 Pyrosequencing  
661 analyses of forest soils reveal an unexpectedly high fungal diversity. *New Phytologist* **184**:  
662 449-456.  
663

664 Calkin PE, Ellis JM, 1980. A lichenometric dating curve and its applications to Holocene  
665 glacier studies in the central Brooks Range, Alaska. *Arctic and Alpine Research* 245-264.  
666

667 Cardenas E, Tiedje JM, 2008. New tools for discovering and characterizing microbial  
668 diversity. *Current Opinion in Biotechnology* **19**: 544-549.

669

670 Cázares E, Trappe JM, 1990. Alpine and sub-alpine fungi of the Cascade Mountains. 1.  
671 *Hymenogaster glacialis* sp. nov. *Mycotaxon* **38**: 245-249.

672

673 Cázares E, Trappe JM, 1994. Spore dispersal of ectomycorrhizal fungi on a glacier forefront  
674 by mammal mycophagy. *Mycologia* **86**: 507-510.

675

676 Cázares E, Trappe JM, Jumpponen A, 2005. Mycorrhiza-plant colonization patterns on a  
677 subalpine glacier forefront as a model system of primary succession. *Mycorrhiza* **15**: 405-  
678 416.

679

680 Chapin FS, Walker LR, Fastie CL, Sharman LC, 1994. Mechanisms of primary succession  
681 following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* **64**: 149-175.

682

683 Clark CJ, Poulsen JR, Levey DJ, Osenberg CW, 2007. Are plant populations seed limited? A  
684 critique and meta-analysis of seed addition experiments. *American Naturalist* **170**: 128-  
685 142.

686

687 Clements FE, 1916. *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie  
688 Institution of Washington, Washington, D.C.

689

690 Cole BJ, 1983. Assembly of mangrove ant communities - patterns of geographical  
691 distribution. *Journal of Animal Ecology* **52**: 339-347.

692

693 Collier FA, Bidartondo MI, 2009. Waiting for fungi: the ectomycorrhizal invasion of lowland  
694 heathlands. *Journal of Ecology* **97**: 950-963.

695

696 Connell JH, Slatyer RO, 1977. Mechanisms of succession in natural communities and their  
697 role in community stability and organization. *American Naturalist* **111**: 1119-1144.

698

699 del Moral R, 2009. Increasing deterministic control of primary succession on Mount St.  
700 Helens, Washington. *Journal of Vegetation Science* **20**: 1145-1154.

701

702 del Moral R, Jones C, 2002. Vegetation development on pumice at Mount St. Helens, USA.  
703 *Plant Ecology* **162**: 9-22.

704

705 del Moral R, Wood DM, 1993. Early primary succession on a barren volcanic plain at Mount  
706 St. Helens, Washington. *American Journal of Botany* **80**: 981-991.

707

708 Drake JA, Flum TE, Witteman GJ, Voskuil T, Hoylman AM, Creson C, Kenny DA, Huxel GR,  
709 Larue CS, Duncan JR, 1993. The construction and assembly of an ecological landscape.  
710 *Journal of Animal Ecology* **62**: 117-130.

711

712 Dyurgerov MB, Meier MF, 2000. Twentieth century climate change: Evidence from small  
713 glaciers. *Proceedings of the National Academy of Sciences of the United States of America* **97**:  
714 1406-1411.

715

716 Egli M, Mirabella A, Fitze P, 2001. Clay mineral formation in soils of two different  
717 chronosequences in the Swiss Alps. *Geoderma* **104**: 145-175.

718

719 Emerson BC, Gillespie RG, 2008. Phylogenetic analysis of community assembly and  
720 structure over space and time. *Trends in Ecology & Evolution* **23**: 619-630.

721

722 Erschbamer B, Kneringer E, Schlag RN, 2001. Seed rain, soil seed bank, seedling  
723 recruitment, and survival of seedlings on a glacier foreland in the Central Alps. *Flora* **196**:  
724 304-312.

725

726 Fastie CL, 1995. Causes and ecosystem consequences of multiple pathways of primary  
727 succession at Glacier Bay, Alaska. *Ecology* **76**: 1899-1916.

728

729 Fattorini M, Halle S, 2004. The dynamic environmental filter model: how do filtering effects  
730 change in assembling communities after disturbance? In: Temperton VM, Hobbs RJ, Nuttle

731 T, Halle S (Eds.), *Assembly Rules and Restoration Ecology*. Island Press, Covelo, Washington,  
732 pp. 96-114.

733

734 Finlay BJ, 2002. Global dispersal of free-living microbial eukaryote species. *Science* **296**:  
735 1061-1063.

736

737 Frankland JC, 1998. Fungal succession - unravelling the unpredictable. *Mycological*  
738 *Research* **102**: 1-15.

739

740 Freeman O, 1941. The recession of Lyman Glacier, Washington. *The Journal of Geology* **49**:  
741 764-771.

742

743 Freeman KR, Martin AP, Karki D, Lynch RC, Mitter MS, Meyer AF, Longcore JE, Simmons DR,  
744 Schmidt SK, 2009. Evidence that chytrids dominate fungal communities in high-elevation  
745 soils. *Proceedings of the National Academy of Sciences of the United States of America* **106**:  
746 18315-18320.

747

748 Frenot Y, Gloaguen JC, Cannavacciuolo M, Bellido A, 1998. Primary succession on glacier  
749 forelands in the subantarctic Kerguelen Islands. *Journal of Vegetation Science* **9**: 75-84.

750

751 Gemma JN, Koske RE, 1990. Mycorrhizae in recent volcanic substrates in Hawaii. *American*  
752 *Journal of Botany* **77**: 1193-1200.

753

754 Greipsson S, El-Mayas H, 2000. Arbuscular mycorrhizae of *Leymus arenarius* on coastal  
755 sands and reclamation sites in Iceland and response to inoculation. *Restoration Ecology* **8**:  
756 144-150.

757

758 Grubb PJ, 1977. Maintenance of species richness in plant communities - importance of  
759 regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* **52**: 107-145.

760

761 Hamady M, Lozupone C, Knight R, 2010. Fast UniFrac: facilitating high-throughput  
762 phylogenetic analyses of microbial communities including analysis of pyrosequencing and  
763 PhyloChip data. *ISME Journal* **4**: 17-27.

764

765 Harper JL, McNaughton IH, Sagar GR, Clatworthy JN, 1961. Evolution and ecology of closely  
766 related species living in the same area. *Evolution* **15**: 209-&.

767

768 Harper JL, Williams JT, Sagar GR, 1965. The behavior of seeds in soil. 1. The heterogeneity  
769 of soil surfaces and its role in determining the establishment of plants from seed. *Journal of*  
770 *Ecology* **53**: 273-&.

771

772 Helm DJ, Allen EB, 1995. Vegetation chronosequence near Exit Glacier, Kenai Fjords  
773 National Park, Alaska, U.S.A. *Arctic and Alpine Research* **27**: 246-257.

774

775 Helm DJ, Allen EB, Trappe JM, 1996. Mycorrhizal chronosequence near Exit Glacier, Alaska.  
776 *Canadian Journal of Botany* **74**: 1496-1506.

777

778 Hodge SM, Trabant DC, Krimmel RM, Heinrichs TA, March RS, Josberger EG, 1998. Climate  
779 variations and changes in mass of three glaciers in western North America. *Journal of*  
780 *Climate* **11**: 2161-2179.

781

782 Hodkinson ID, Webb NR, Coulson SJ, 2002. Primary community assembly on land - the  
783 missing stages: why are the heterotrophic organisms always there first? *Journal of Ecology*  
784 **90**: 569-577.

785

786 Hunt GL, 1991. Occurrence of polar seabirds at sea in relation to prey concentrations and  
787 oceanographic factors. *Polar Research* **10**: 553-559.

788

789 Johnson NC, Zak DR, Tilman D, Pflieger FL, 1991. Dynamics of vesicular arbuscular  
790 mycorrhizae during old field succession. *Oecologia* **86**: 349-358.

791

792 Jones CC, del Moral R, 2005a. Effects of microsite conditions on seedling establishment on  
793 the foreland of Coleman Glacier, Washington. *Journal of Vegetation Science* **16**: 293-300.

794

795 Jones CC, del Moral R, 2005b. Patterns of primary succession on the foreland of Coleman  
796 Glacier, Washington, USA. *Plant Ecology* **180**: 105-116.

797

798 Jones CC, del Moral R, 2009. Dispersal and establishment both limit colonization during  
799 primary succession on a glacier foreland. *Plant Ecology* **204**: 217-230.

800

801 Jumpponen A, 2003. Soil fungal community assembly in a primary successional glacier  
802 forefront ecosystem as inferred from rDNA sequence analyses. *New Phytologist* **158**: 569-  
803 578.

804

805 Jumpponen A, 2007. Soil fungal communities underneath willow canopies on a primary  
806 successional glacier forefront: rDNA sequence results can be affected by primer selection  
807 and chimeric data. *Microbial Ecology* **53**: 233-246.

808

809 Jumpponen A, Egerton-Warburton LM, 2005. Mycorrhizal fungi in successional  
810 environments – a community assembly model incorporating host plant, environmental and  
811 biotic filters. In: Dighton J, White JF, Oudemans P (Eds.), *The Fungal Community*. CRC Press,  
812 New York, pp. 139-180.

813

814 Jumpponen A, Jones K, 2009. Massively parallel 454 sequencing indicates hyperdiverse  
815 fungal communities in temperate *Quercus macrocarpa* phyllosphere. *The New Phytologist*  
816 **184**: 438-448.

817

818 Jumpponen A, Jones KL, Mattox D, Yaeger C, 2010. Massively parallel 454-sequencing of  
819 fungal communities in *Quercus* spp. ectomycorrhizas indicates seasonal dynamics in urban  
820 and rural sites. *Molecular Ecology* **19**: 41-53.

821

822 Jumpponen A, Mattson K, Trappe JM, Ohtonen R, 1998. Effects of established willows on  
823 primary succession on Lyman Glacier forefront, North Cascade Range, Washington, USA:  
824 Evidence for simultaneous canopy inhibition and soil facilitation. *Arctic and Alpine Research*  
825 **30**: 31-39.

826

827 Jumpponen A, Trappe JM, Cazares E, 1999a. Ectomycorrhizal fungi in Lyman Lake Basin: a  
828 comparison between primary and secondary successional sites. *Mycologia* **91**: 575-582.

829

830 Jumpponen A, Trappe JM, Cazares E, 2002. Occurrence of ectomycorrhizal fungi on the  
831 forefront of retreating Lyman Glacier (Washington, USA) in relation to time since  
832 deglaciation. *Mycorrhiza* **12**: 43-49.

833

834 Jumpponen A, Väre H, Mattson KG, Ohtonen R, Trappe JM, 1999b. Characterization of 'safe  
835 sites' for pioneers in primary succession on recently deglaciated terrain. *Journal of Ecology*  
836 **87**: 98-105.

837

838 Koske RE, Gemma JN, 1997. Mycorrhizae and succession in plantings of beachgrass in sand  
839 dunes. *American Journal of Botany* **84**: 118-130.

840

841 Leps J, Rejmanek M, 1991. Convergence or divergence - what should we expect from  
842 vegetation succession. *Oikos* **62**: 261-264.

843

844 Lichter J, 2000. Colonization constraints during primary succession on coastal Lake  
845 Michigan sand dunes. *Journal of Ecology* **88**: 825-839.

846

847 Martiny J, Bohannon B, Brown J, Colwell R, Fuhrman J, Green J, 2006. Microbial  
848 biogeography: putting microorganisms on the map. *Nature Reviews Microbiology* **4**: 102-  
849 112.

850

851 Matthews JA, 1992. *The Ecology of Recently-Deglaciated Terrain: A Geoecological Approach*  
852 *to Glacier Forelands and Primary Succession*. Cambridge University Press, Cambridge.

853

854 McCune B, Grace JB, 2002. *PC-ORD Multivariate Analysis of Ecological Data*. MjM Software  
855 Design, Glendale Beach, Oregon.

856

857 McIntosh RP, Odum EP, 1969. Ecological succession. *Science* **166**: 403-404.

858

859 Meyer M, Stenzel U, Hofreiter M, 2008. Parallel tagged sequencing on the 454 platform.  
860 *Nature Protocols* **3**: 267-278.

861

862 Nara K, Nakaya H, Hogetsu T, 2003a. Ectomycorrhizal sporocarp succession and production  
863 during early primary succession on Mount Fuji. *New Phytologist* **158**: 193-206.

864

865 Nara K, Nakaya H, Wu BY, Zhou ZH, Hogetsu T, 2003b. Underground primary succession of  
866 ectomycorrhizal fungi in a volcanic desert on Mount Fuji. *New Phytologist* **159**: 743-756.

867

868 Nemergut DR, Anderson SP, Cleveland CC, Martin AP, Miller AE, Seimon A, Schmidt SK,  
869 2007. Microbial community succession in an unvegetated, recently deglaciated soil.  
870 *Microbial Ecology* **53**: 110-122.

871

872 Niering WA, 1963. Saguaro - a population in relation to environment. *Science* **142**: 15-23.

873

874 Odum EP, 1969. Strategy of ecosystem development. *Science* **164**: 262-270.

875

876 Ohtonen R, Fritze H, Pennanen T, Jumpponen A, Trappe J, 1999. Ecosystem properties and  
877 microbial community changes in primary succession on a glacier forefront. *Oecologia* **119**:  
878 239-246.

879

880 Orwin KH, Wardle DA, Greenfield LG, 2006. Context-dependent changes in the resistance  
881 and resilience of soil microbes to an experimental disturbance for three primary plant  
882 chronosequences. *Oikos* **112**: 196-208.

883

884 Oswald BP, Neuenschwander LF, 1993. Microsite variability and safe site description for  
885 western larch germination and establishment. *Bulletin of the Torrey Botanical Club* **120**:  
886 148-156.

887

888 Peay KG, Garbelotto M, Bruns TD, 2010. Evidence of dispersal limitation in soil  
889 microorganisms: Isolation reduces species richness on mycorrhizal tree islands. *Ecology*  
890 **91**: 3631-3640.

891



892 Pelto MS, 2006. The current disequilibrium of North Cascade glaciers. *Hydrological*  
893 *Processes* **20**: 769-779.

894

895 Pelto MS, 2011. Methods for assessing and forecasting the survival of North Cascade,  
896 Washington glaciers. *Quaternary International* **235**: 70-76.

897

898 Pickett STA, 1989. Space for time substitutions as an alternative to long-term studies. In:  
899 Likens GE (Ed.), *Long-Term Studies in Ecology*. Springer, New York, pp. 110-135.

900

901 Pickett STA, Cadenasso ML, Meiners SJ, 2009. Ever since Clements: from succession to  
902 vegetation dynamics and understanding to intervention. *Applied Vegetation Science* **12**: 9-  
903 21.

904

905 Post A, Richardson DW, Rossellot FF, 1971. *Inventory of Glaciers in the North Cascades,*  
906 *Washington*. U.S. Department of the Interior Geological Survey Professional Paper 705-A,  
907 Washington D.C.

908

909 Primack RB, Miao SL, 1992. Dispersal can limit local plant distribution. *Conservation*  
910 *Biology* **6**: 513-519.

911

912 Raffl C, Mallaun M, Mayer R, Erschbamer B, 2006. Vegetation succession pattern and  
913 diversity changes in a glacier valley, Central Alps, Austria. *Arctic Antarctic and Alpine*  
914 *Research* **38**: 421-428.

915

916 Read DJ, 1991. Mycorrhizas in ecosystems. *Experientia* **47**: 376-391.

917

918 Redford AJ, Fierer N, 2009. Bacterial succession on the leaf surface: a novel system for  
919 studying successional dynamics. *Microbial Ecology* **58**: 189-198.

920

921 Reeves FB, Wagner D, Moorman T, Kiel J, 1979. Role of endomycorrhizae in revegetation  
922 practices in the semi-arid west. 1. Comparison of incidence of mycorrhizae in severely  
923 disturbed vs natural environments. *American Journal of Botany* **66**: 6-13.

- 924
- 925 Reiners WA, Worley IA, Lawrence DB, 1971. Plant diversity in a chronosequence at Glacier  
926 Bay, Alaska. *Ecology* **52**: 55-69.
- 927
- 928 Robbins JA, Matthews JA, 2009. Pioneer vegetation on glacier forelands in southern  
929 Norway: emerging communities? *Journal of Vegetation Science* **20**: 889-902.
- 930
- 931 Schlag RN, Erschbamer B, 2000. Germination and establishment of seedlings on a glacier  
932 foreland in the central Alps, Austria. *Arctic Antarctic and Alpine Research* **32**: 270-277.
- 933
- 934 Schmidt SK, Reed SC, Nemergut DR, Grandy AS, Cleveland CC, Weintraub MN, Hill AW,  
935 Costello EK, Meyer AF, Neff JC, Martin AM, 2008. The earliest stages of ecosystem  
936 succession in high-elevation (5000 metres above sea level), recently deglaciated soils.  
937 *Proceedings of the Royal Society B-Biological Sciences* **275**: 2793-2802.
- 938
- 939 Schütte UME, Abdo Z, Foster J, Ravel J, Bunge J, Solheim B, Forney LJ, 2010. Bacterial  
940 diversity in a glacier foreland of the high Arctic. *Molecular Ecology* **19**: 54-66.
- 941
- 942 Skidmore ML, Foght JM, Sharp MJ, 2000. Microbial life beneath a high Arctic glacier. *Applied  
943 and Environmental Microbiology* **66**: 3214-3220.
- 944
- 945 Southwood TRE, 1988. Tactics, strategies and templets. *Oikos* **52**: 3-18.
- 946
- 947 Stocklin J, Baumler E, 1996. Seed rain, seedling establishment and clonal growth strategies  
948 on a glacier foreland. *Journal of Vegetation Science* **7**: 45-56.
- 949
- 950 Strauss SL, Ruhland CT, Day TA, 2009. Trends in soil characteristics along a recently  
951 deglaciated foreland on Anvers Island, Antarctic Peninsula. *Polar Biology* **32**: 1779-1788.
- 952
- 953 Titus JH, del Moral R, 1998. Seedling establishment in different microsites on Mount St.  
954 Helens, Washington, USA. *Plant Ecology* **134**: 13-26.

955

956 Trowbridge J, Jumpponen A, 2004. Fungal colonization of shrub willow roots at the  
957 forefront of a receding glacier. *Mycorrhiza* **14**: 283-293.

958

959 Tscherko D, Rustemeier J, Richter A, Wanek W, Kandeler E, 2003. Functional diversity of  
960 the soil microflora in primary succession across two glacier forelands in the Central Alps.  
961 *European Journal of Soil Science* **54**: 685-696.

962

963 Turnbull LA, Crawley MJ, Rees M, 2000. Are plant populations seed-limited? A review of  
964 seed sowing experiments. *Oikos* **88**: 225-238.

965

966 Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH,  
967 Tilman GD, 1997. Human alteration of the global nitrogen cycle: Sources and consequences.  
968 *Ecological Applications* **7**: 737-750.

969

970 Walker LR, Clarkson BD, Silvester WB, Clarkson BR, 2003. Colonization dynamics and  
971 facilitative impacts of a nitrogen-fixing shrub in primary succession. *Journal of Vegetation*  
972 *Science* **14**: 277-290.

973

974 Walker LR, del Moral R, 2003. *Primary Succession and Ecosystem Rehabilitation*. Cambridge  
975 University Press, Cambridge.

976

977 Walker LR, Bellingham PJ, Peltzer DA, 2006. Plant characteristics are poor predictors of  
978 microsite colonization during the first two years of primary succession. *Journal of*  
979 *Vegetation Science* **17**: 397-406.

980

981 Walker LR, Wardle DA, Bardgett RD, Clarkson BD, 2010. The use of chronosequences in  
982 studies of ecological succession and soil development. *Journal of Ecology* **98**: 725-736.

983

984 Warner NJ, Allen MF, Macmahon JA, 1987. Dispersal agents of vesicular arbuscular  
985 mycorrhizal fungi in a disturbed arid ecosystem. *Mycologia* **79**: 721-730.

986

987 Weiher E, Keddy PA, 2001. *The Assembly Rules: Perspectives, Advances, Retreats*. Cambridge  
988 University Press, Cambridge Massachusetts.

989

990 Weiher E, Keddy PA, 1995. Assembly rules, null models, and trait dispersion - new  
991 questions front old patterns. *Oikos* **74**: 159-164.

992

993 Whittaker RJ, 1993. Plant population patterns in a glacier foreland succession - pioneer  
994 herbs and later-colonizing shrubs. *Ecography* **16**: 117-136.

995

996 Whittaker RJ, 1991. The vegetation of the Storbreen Gletschervorfeld, Jotunheimen,  
997 Norway. 4. Short-term vegetation change. *Journal of Biogeography* **18**: 41-52.

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999

## 1000 **Figure legends**

1001

1002 **Fig. 1.** Plant community type (CT) frequency dynamics along the time since substrate  
1003 exposure in the forefront of the receding Lyman Glacier. The inset identifies the dominant  
1004 components of the CTs based on two-way complete linkage clustering shown in  
1005 Supplemental Fig. S1. Note that the CT1 – characterized by nonmycorrhizal *Saxifraga* and  
1006 nonvegetated, open areas – is frequent through the chronosequence even close to the  
1007 terminal moraine.

1008

1009 **Fig. 2.** Plant community dynamics as a function of the substrate exposure (time since  
1010 deglaciation) in the forefront of the receding Lyman Glacier: a) plant species richness (S)  
1011 increases, the inset identifies the linear regression model with significant intercept and  
1012 slope terms; b) Shannon-Wiener diversity (H') increases, the inset identifies the linear  
1013 regression model with significant intercept and slope terms. <sup>ns</sup>  $P > 0.05$ ; \*  $P \leq 0.05$ ; \*\*  $0.01 \leq$   
1014  $P < 0.05$ ; \*\*\*  $\leq 0.001$ .

1015

1016 **Fig. 3.** Mean Nonmetric Multidimensional Scaling (NMS) Axis 1 scores of the plant  
1017 community types (CTs) along the Lyman Glacier forefront increase with time since  
1018 deglaciation. The inset identifies the linear regression model with significant intercept and  
1019 slope terms. The linear increase in the NMS scores suggests a successional trajectory in this  
1020 primary successional system and is likely correlated with increasing abundance of the CTs  
1021 with component species from the adjacent montane meadow communities. <sup>ns</sup>  $P > 0.05$ ; \*  $P \leq$   
1022  $0.05$ ; \*\*  $0.01 \leq P < 0.05$ ; \*\*\*  $\leq 0.001$ .

1023

1024 **Fig. 4.** Mean Nonmetric Multidimensional Scaling (NMS) Axis 1 score standard deviations  
1025 of the plant community types (CTs) along the Lyman Glacier forefront increase with time  
1026 since deglaciation. The inset identifies the linear regression model with a significant slope  
1027 term. The increase in the NMS score standard deviations suggests a divergence of the plant  
1028 communities in this primary successional system and is likely a result of stochastic plant  
1029 establishment processes and heterogeneous distribution of the CTs along the successional  
1030 chronosequence. <sup>ns</sup>  $P > 0.05$ ; \*  $P \leq 0.05$ ; \*\*  $0.01 \leq P < 0.05$ ; \*\*\*  $\leq 0.001$ .

1031

1032 **Fig. 5.** Percent similarity (PS) of the plant communities along the Lyman Glacier forefront  
1033 decline with time since deglaciation, the inset identifies the linear regression model with  
1034 significant intercept and slope terms. The decrease in the PS corroborates divergence of the  
1035 plant communities in this primary successional system shown in Fig. 4. <sup>ns</sup>  $P > 0.05$ ; \*  $P \leq$   
1036  $0.05$ ; \*\*  $0.01 \leq P < 0.05$ ; \*\*\*  $\leq 0.001$ .

1037

1038 **Fig. 6.** Principal Coordinates Analysis (PCoA) Axis 2 scores for fungal communities along  
1039 the Lyman Glacier forefront increase with time since deglaciation. The inset identifies the  
1040 linear regression model with significant terms for intercept and slope but not for canopy  
1041 position or interaction. The linear increase in the PCoA scores suggests a successional

1042 trajectory in this primary successional system. <sup>ns</sup>  $P > 0.05$ ; \*  $P \leq 0.05$ ; \*\*  $0.01 \leq P < 0.05$ ; \*\*\*  
1043  $\leq 0.001$ .

1044

1045 **Fig. 7.** Principal Coordinates Analysis (PCoA) Axis 3 score standard deviations for fungal  
1046 communities along the Lyman Glacier forefront decrease with time since deglaciation. The  
1047 inset identifies the linear regression model with significant terms for intercept and slope  
1048 but not for canopy position or interaction. The linear decrease in the standard deviations  
1049 suggests a community convergence over time in this primary successional system. <sup>ns</sup>  $P >$   
1050  $0.05$ ; \*  $P \leq 0.05$ ; \*\*  $0.01 \leq P < 0.05$ ; \*\*\*  $\leq 0.001$ .

1051

1052 **Fig. 8.** Neighbor Joining (NJ) distances (Mean  $\pm$  Standard Deviation) on a sample level for  
1053 fungal communities along the Lyman Glacier forefront are greater in the canopy samples  
1054 than in the intercanopy samples. The inset identifies the linear regression model with  
1055 significant terms for intercept and canopy position but not for slope or the interaction. The  
1056 difference between the canopy and intercanopy samples suggests a canopy soil community  
1057 convergence relative to intercanopy soils in this primary successional system. The two  
1058 groups of samples with different NJ distances are indicated by  $P$ -values (oneway ANOVA)  
1059 above the bars. <sup>ns</sup>  $P > 0.05$ ; \*  $P \leq 0.05$ ; \*\*  $0.01 \leq P < 0.05$ ; \*\*\*  $\leq 0.001$ .

1060

## 1061 **Supplemental Materials**

1062

1063 **Supplemental Figure S1.** Two-way clustering of 228 1m<sup>2</sup> characterize plant community  
1064 types (CTs). Most commonly occurring plant species on the horizontal axis, plots  
1065 themselves on the vertical axis. The plots were clustered into seven CTs so that  
1066 approximately 75% of the plot level variability was retained and the CTs characterized by  
1067 the two most dominant species in each of the seven CTs (see Fig. 1).

1068

1069 **Supplemental Figure S2.** Nonmetric Multidimensional Scaling (NMS) of the plant  
1070 communities types (CTs) on the forefront of Lyman Glacier. CTs are identified by their  
1071 respective numbers and their dominant constituent species can be found in the inset of Fig.  
1072 1. a) NMS of the first two axes. Following the CT identification, the lower-case letter  
1073 indicates differences along Axis 1, the upper case letter differences along Axis 2 based on  
1074 Tukey's Honestly Significant Difference (HSD) test at  $\alpha = 0.05$ . b) NMS of Axes 1 and 3.  
1075 Following the CT identification, the lower-case letter indicates differences along Axis 1, the  
1076 upper case letter differences along Axis 3 based on Tukey's Honestly Significant Difference  
1077 (HSD) test at  $\alpha = 0.05$ . Note that CTs 1 and 4 were distinct from other CTs on the first axis,  
1078 CTs 2 and 7 were separated on the third axis, CT3 was distinct from CTs 6 and 7 on the  
1079 third axis, and CT3 was distinguished from CTs 4 and 6 on the second axis.

1080

1081 **Supplemental Figure S3.** Two-way clustering to characterize fungal community types  
1082 (CTs). Most commonly occurring fungal species on the horizontal axis, samples themselves  
1083 on the vertical axis. The plots were clustered into five CTs so that approximately 75% of the  
1084 sample level variability was retained.

1085

1086 **Supplemental Table S1.** Checklist of vascular plants recorded at Lyman Glacier Forefront  
1087 in the North Cascades Mountains of Washington State, U.S.A.

1088