Introduction. This project aims to relate the existence, extent, and composition of cryptoendolithic microbial ecosystems that colonize sandstone surfaces in the Antarctic Dry Valleys to the long-term erosion rates of these surfaces. We will accomplish this by pairing a survey of cryptoendolith distribution and community structure with quantitative measurements of surface erosion rates using cosmic-ray-produced radionuclides. Our overall goal is to determine whether cryptoendoliths are an important agent of rock surface erosion that have a significant geomorphic impact on the bare-rock landscapes of the Dry Valleys, or opportunists who can only thrive in a specific erosion-rate environment that is set by external geologic and climate factors.

The Antarctic cryptoendolithic microbial community consists of a variety of microorganisms, predominantly lichens, algae, and cyanobacteria, that inhabit the intergranular pore space several millimeters below the surface of quartz sandstone rocks in cold, dry ice-free regions of Antarctica (Figure 1; Friedmann, 1982; Sun et al., 2006 and references therein). This microbial community is important not only because of its adaptation to the extreme environment of the Antarctic cold desert, but also because it accounts for nearly all primary productivity in Antarctic bedrock landscapes (Friedmann, 1982), and ii) metabolic byproducts secreted by the organisms dissolve intergranular cement and result in exfoliative weathering of the sandstone. Cryptoendoliths are also hypothesized to exist on other planets such as Mars (Sun et al., 2006 and references therein; Onofri et al., 2008).

In this proposal we are interested in the hypothesis that cryptoendoliths are an important agent of rock surface weathering and erosion in the Antarctic cold desert where, due to the absence of liquid water, there are few physical mechanisms that can cause erosion (e.g., Putkonen et al., 2008). Existing efforts to evaluate this hypothesis have focused on estimating the time required for a colonization-exfoliation cycle from radiocarbon, biomass, and productivity data (order ~10,000 years; Sun and Friedmann, 1999; Bonani et al., 1988). However, we are not aware of any attempts to independently quantify erosion rates of colonized surfaces, or to determine the range of erosion rates prevalent on colonized and uncolonized surfaces. The purpose of the present proposal is to investigate the relationship between microbial communities and erosion rates using an independent method, based on the measurement of trace cosmic-ray-produced nuclides, of estimating long-term sandstone surface erosion rates.

The genesis of this proposal is a set of cosmogenic-nuclide measurements of sandstone surface erosion rate that were collected by one of us (Balco) during geological research in the McMurdo Dry Valleys. As described in detail below, we sought to relate these measurements to the presence or absence of cryptoendolithic communities at our sample sites. We hypothesized that microbial colonization would be associated with higher surface erosion rates. However, we were surprised to see the opposite relationship -- we found evidence for cryptoendolith colonization only in low-erosion-rate surfaces -- which implies that this ecosystem may in fact only be able to develop where geologic factors set a low erosion rate. This existing data set is sparse and ad hoc, and is not the result of a well-designed study. However, it highlights two important things. First, the relationship between sandstone erosion rates and microbial colonization is important: quantifying it would shed light on the dynamics and productivity of these communities, to what extent they create and modify their environment, and to what extent they control landscape form and sediment fluxes in the bare-rock landscapes of the Transantarctic Mountains. Second, the relatively recently developed technique of erosion rate measurement using cosmic-ray-produced nuclides provides the tool needed to quantify this relationship. In the remainder of this proposal we outline a plan to accomplish this.

This proposal aims to apply tools and approaches from two very different research fields (cosmogenic-nuclide geochemistry and geomicrobiology), that have not interacted extensively in the past, to a common problem that could not be addressed within each field alone. We argue that this collaboration will provide new and fundamental information about the interaction of microbial ecology and landscape-forming processes. However, the research techniques themselves that we will use are robust and well-established within each field, and we will use them to address clear and straightforward hypotheses.
Thus, we view this project as an ideal platform for undergraduate research. As such, this proposal is a collaboration between a microbiologist at an undergraduate-focused institution (McCormick; Hamilton College) and a geochemist at a research institute (Balco; Berkeley Geochronology Center), in which we intend that the majority of the research will be conducted by undergraduate students.

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**Cryptoendolithic microbial ecosystems in the Dry Valleys.** The physical conditions in the high-elevation landscapes of the Antarctic Dry Valleys where cryptoendolithic microbial communities are common are characterized by seasonal prolonged darkness or light, extreme cold (mean annual air temperatures below -20° C and lows approaching -60° C) and a near absence of liquid water (Friedmann et al., 1987; Witherow et al., 2006). Relative to the vast majority of extant life, this constitutes an extreme environment. One of the few widespread habitable spaces lies within porous, translucent sandstones, where insolation and shelter from the wind permit temperatures above ambient, and the rock matrix helps retain what little moisture is present. This is the habitat of the cryptoendolithic microbial communities. As no vascular plants exist in this setting, primary production is mediated by microbial phototrophs and the food webs are simple, comprised entirely of microbes. The simplicity of these ecosystems has made them attractive models for studying the relationship between community composition and ecosystem function (Walker et al., 2007a; Cary et al., 2010).

Most cryptoendolithic communities in the Dry Valleys can be broadly categorized into two groups based on the morphological identity of the photoautotrophic primary producer in each: Lichen dominated communities (LDCs) or cyanobacteria dominated communities (CDCs), although some authors also recognize the presence of algae dominated communities (Sun et al., 2006; Nienow et al., 1993). Of these, the cryptoendolithic lichens are most common (Friedmann, 1982). Lichens are not single organisms but rather obligate symbiotic associations comprised of fungal (mycobiont) and photoautotrophic (phycobiont) partners. By combining the autotrophic (CO$_2$ fixing) and often nitrogen fixing capabilities of the phycobiont with the structural protection and diverse enzymatic/biogeochemical capabilities of the mycobiont, lichens thrive in low nutrient environments like the surfaces of rocks and tree trunks where we commonly encounter them. Cryptoendolithic lichens in the Dry Valleys similarly exhibit an interdependent association between mycobiont and phycobiont but in a less familiar habitat in that both partners invade the intergranular spaces within sandstone and grow some distance below the surface. Likewise, cryptoendolithic cyanobacterial communities grow optimally below the rock surface where the environment is buffered from extreme variations in temperature and UV exposure and also benefit from enhanced retention of moisture (Friedmann, 1982).
Early characterizations of the lichen and cyanobacterial endolithic communities relied upon microscopic descriptions of cell morphology and cultured phenotypes (Sun et al., 2006). Subsequent molecular characterizations of these same communities (based on the abundances of rRNA genotypes) revealed a lower diversity of primary producers than previously indicated (de la Torre et al., 2003; Friedmann et al., 1988; Walker et al. 2007b). Using a suite of clone libraries constructed using combinations of universal and domain specific primers, de la Torre et al. found both communities to be diverse but simple in that they were dominated by just a few taxa (presumed to be the primary producers). Where prior morphology based studies had identified two major taxa of cyanobacteria within the CDCs, Gloeocapsa spp. and Hormathonema spp., phylogenetic analysis revealed only one dominant genotype belonging to the Leptolyngbya-Phormidium-Plectonema group, indicating morphological plasticity within the same genus or closely related genera. On the basis of rRNA gene copies, the CDCs also contained a Blastomonas-like alphaproteobacteria and a Thermus-Deinococcus related bacteria in near equal abundance to the cyanobacteria, suggesting a possible syntrophic association. Interestingly, the Balstomonas spp. are known to be aerobic anoxygenic phototrophs, microbes that harvest energy from light but metabolize complex carbon (i.e., they are heterotrophs). Despite the inability to fix CO₂, these Balstomonas-like bacteria may contribute to primary productivity by directing a larger fraction of carbon to cell growth than could otherwise occur in heterotrophs due to the reduced catabolic demands enabled by phototrophy. In the LDCs, clone libraries again revealed a simple community dominated by a common ascomycete fungal lichen mycobiont (Texosporium sancti-jacobi) and an algal lichen phycobiont (Trebossia jamesii). Beyond the dominant phylotypes observed in CDCs and LDCs, a diverse collection of heterotrophic bacteria was observed in each.

Interestingly, of the 25 and 26 phylotypes identified in the LDC and CDCs, respectively, none were common to both, suggesting that each microbial assemblage comprised a true ecological community characterized by consistent composition co-occurring in a defined habitat (Walker et al., 2007a; Friedmann et al., 1984). Subsequent comparison of the lichen phylotypes with cryptoendolithic lichens in distant locations (e.g. Colorado Rockies) showed the communities were nearly identical in regard to the dominant algal rRNA sequences (Walker et al., 2007a). This finding supports the hypothesis that endolithic communities comprise a global metacommunity in which freshly exposed rocks are seeded (likely via air dispersal) by closely related organisms that are adapted to the endolithic niche (Walker et al., 2007a).

**Role of cryptoendolithic communities in rock weathering.** A variety of evidence shows that endolithic microbial communities act to weather their host rock (Büdel et al., 2004; Ascaso et al., 1998; Blackhurst et al., 2005; Friedmann et al., 1987). Basically, they secrete a variety of metabolic products that dissolve and/or reprecipitate mineral constituents, thus weakening the rock and enhancing weatherability by biotic or abiotic factors.

Mineral dissolution by biogenic organic acids is frequently cited as the primary such mechanism (Friedmann et al., 1987; Chen et al., 2000; Weed et al., 1991; Johnston et al., 1993). Ligands such as oxalate or citrate, produced by lichens or bacteria, coordinate with surface cations, altering the charge distribution and weakening the metal oxygen bond, thus permitting hydrolysis and dissolution of the metal-ligand complex. Oxalate is implicated as the principal biogenic agent involved in sandstone weathering, solubilizing iron and mobilizing it towards the surface and deeper into an iron accumulation zone commonly observed in LDCs (Weed et al., 1991; Johnston et al., 1993). In contrast, in CDCs increased pH resulting from cyanobacteria photosynthesis in the confined cryptoendolithic environment (termed *bioalkalization*) enhances Si solubility, resulting in quartz dissolution (Büdel et al., 2004).

These processes act to weaken the rock matrix several millimeters below the surface in the colonized zone, which makes the overlying thin layer of rock more susceptible to spalling. Exfoliation of this layer may occur due to expansion and contraction of the cryptoendolith biomass in response to changes in ambient moisture (Friedmann et al., 1987; Chen et al., 2000; Sun et al., 1999), or due to abiotic factors such as wind abrasion and salt-induced flaking (Chen et al., 2000). Note, however, that biogenic exopolysaccharides and filaments are implicated in stabilizing sandstone against wind abrasion in the U.S. desert southwest (Kurtz et al., 2001). One additional, most likely abiotic, mechanism that stabilizes...
sandstone surfaces in the Dry Valleys is silicification of the rock surface, which forms a quartz rind similar to the rock varnish observed in other semiarid or desert areas of the world (Friedmann et al., 1987).

Because of the clear link between colonization and rock matrix dissolution by metabolic byproducts, most prior studies of Dry Valley cryptoendolithic communities either explicitly or implicitly assume that colonization results in accelerated erosion of rock surfaces. However, we are not aware of any attempts to quantitatively measure long-term erosion rates of these surfaces by independent methods or to compare long-term erosion rates between colonized and uncolonized rocks. Given the complex processes at play, as well as the fact that microbial communities are only one of many environmental factors acting to weather rock surfaces, it is not apparent that colonization always results in accelerated weathering. In fact, given that exfoliation results in a decrease in community biomass (and the dominant taxa), there appears to be an inherent incentive for cryptoendolithic communities to preserve their habitat. Thus it is conceivable that, in some locations, colonization may act to stabilize the sandstone environment relative to the abiotic weathering that would otherwise occur. Given the evidence that LDCs and CDCs form true ecological communities, such ecosystem engineering would be an example of biogeomorphologic feedback (Corenblit, 2011), in which each endolithic ecosystem reflects an optimum combination of community composition interacting with the ambient rock matrix to determine the long-term substrate erosion rate.

Figure 2. Figures from Sun and Friedman (1999) illustrating the pattern of crust formation during the exfoliation cycle (left panel) and proposed models of cryptoendolithic growth between exfoliation events (right panel). The top scheme depicts the “rapid growth” model while the bottom depicts the “continuous growth” model.

Existing research on rates of colonization and surface erosion: Surface exfoliation due to rock matrix weakening diminishes the endolithic community as well, so both surface erosion and changes in biomass in colonized sandstones are episodic. Biomass accumulates in the subsurface colonized zone. Over time, biochemical weathering mechanisms weaken the iron-leached region that underlies the populated horizon within the LDCs. Exfoliation of a flake, typically 1-10 cm in lateral dimension, leaves behind the bleached surface of the iron-depleted zone (Figure 1; Figure 2). This surface is recolonized, and a new surface crust forms and slowly darkens, progressing through shades of orange and brown. The contrasting hues of adjacent zones at different stages of the exfoliation cycle result in the patchy surface pattern commonly reported in Beacon sandstones (Figure 1; Sun and Friedmann, 1999).

Sun and Friedmann (1999) proposed two models of microbial growth coupled to exfoliation: a) rapid growth followed by extended steady-state maintenance of biomass at the carrying capacity; and b) constant growth throughout the weathering cycle (an extended log growth phase) with exfoliation occurring when carrying capacity is reached (i.e., exhaustion of the endolithic space) (Figure 2; also see Rivkina et al., 2000). They found that total organic nitrogen (as a proxy for total biomass) increased with
color development in multiple samples, which supports the hypothesis that color is a proxy for age since exfoliation. They found this relationship held true even though the total biomass content varied regionally, attributable to local constraints on growth (e.g. regional variation in porosity of the rock matrix, light exposure, moisture, etc). As biomass increased monotonically throughout the exfoliation cycle, they concluded that the constant growth model prevailed. However, as the authors note, the relationship between crust color and exposure age is not well constrained and may be non-linear.

Erosion-rate measurements by cosmic-ray-produced radionuclides: basic principles. In this section, we discuss a relatively recently developed geochemical method of quantifying long-term rock surface erosion rates. The premise of this proposal is that this method -- analysis of cosmic-ray-produced radionuclides in rock surfaces -- provides a quantitative method of estimating rock surface erosion rates that requires no knowledge of, and is completely independent of, the presence or absence of cryptoendoliths.

Cosmic rays are high-energy particles, primarily neutrons and protons with a few fragments of heavier nuclei, originating from astronomical sources (texts on cosmic-ray physics include Rossi, 1964 and Gaisser, 1991). The Earth’s magnetic field deflects low-energy particles, but high-energy particles that intersect the Earth’s path interact with atomic nuclei in the upper atmosphere via high-energy reactions that cause fragmentation of target nuclei (“spallation reactions”). This initiates a cascade of secondary reactions in the atmosphere, such that the majority of cosmic-ray-derived particles reaching ground level are secondary neutrons. These retain enough energy to induce further spallation reactions in surface materials, and these reactions have geochemical importance because they give rise to trace nuclides that are not produced in any other way (a comprehensive text on geochemical applications of cosmic-ray-produced nuclides is Dunai, 2010). For example, nuclides produced in the common mineral quartz (SiO₂) include ¹⁰Be from neutron spallation of a ¹⁶O nucleus, and ²⁶Al and ²¹Ne from spallation of ²⁸Si.

Two properties make many of these nuclides geologically useful. First, these are either i) radioactive with geologically short half-lives, or ii) easily lost by thermal diffusion at relatively shallow depths. As nearly all the (primary or secondary) cosmic-ray flux stops in the upper few meters of the Earth’s crust (see below), rocks that are formed or reside for a time in the subsurface (these conditions apply to nearly all rocks) have negligible inventories of cosmic-ray-produced nuclides. Second, production rates of these nuclides are approximately constant over time and can be accurately estimated from first-principles calculations and empirical measurements (changes in the Earth’s magnetic field induce some production-rate variation; see Dunai, 2010, and Balco et al., 2008a for reviews). Therefore, any geological process that brings fresh rock to the surface for the first time begins the accumulation of cosmic-ray-produced nuclides. At a later time, one can measure the concentration of these nuclides and use the independently known production rate to determine the age since the surface-forming event occurred. This technique, commonly known as “exposure dating,” is widely used for determining the age of a variety of geologic events, for example glacier advances and retreats, earthquake fault ruptures, and changes in sea level (Cerling and Craig, 1994; Dunai, 2010; Balco, 2011). Exposure dating has been applied extensively to surface deposits in the Dry Valleys (e.g., Schaefer et al., 1999; Bruno et al., 1997; Brook et al., 1995).

More relevant to this proposal is the fact that surface erosion moves subsurface rock towards the surface by stripping off rock that lies on top of it. Nuclide production occurs in a zone that remains stationary with respect to the surface, so erosion can be thought of as pushing subsurface material through the production zone. If the erosion rate is fast, a particle of material spends a short time in the production zone and accumulates a low nuclide concentration; if the erosion rate is slow, it spends a long time in the production zone and arrives at the surface with a high nuclide concentration. Thus, the concentration of cosmic-ray-produced nuclides in an eroding rock surface is inversely proportional to the erosion rate.

This relationship can be quantified as follows. The nuclide production rate $P$ (atoms/g mineral/yr) decreases with depth according to an exponential function:

$$P(z) = P_0 e^{\frac{-z \rho}{\Lambda}}$$  \hspace{1cm} (1)
where \( P_0 \) is the production rate at the surface (atoms/g mineral/year), \( z \) is depth below the surface (cm), \( \rho \) is rock density (g/cm\(^3\)), and \( \Lambda \) is an effective attenuation length (140 g/cm\(^2\) for Antarctic latitudes). For purposes of this proposal, Equation (1) is an adequate approximation of the actual production rate-depth function; additional minor complications are reviewed in Stone et al. (1998) and Balco et al. (2008a). In a surface-fixed reference frame, material is advected toward the surface at an erosion rate \( \epsilon \) (cm/yr). In the simple case of a stable nuclide, when a parcel of material reaches the surface its nuclide concentration \( N \) (atoms/g mineral) is given by:

\[
N = P_0 \int_0^\infty \exp \left( -\frac{\epsilon t \rho}{\Lambda} \right) dt = \frac{P_0 \Lambda}{\epsilon \rho} \quad (2)
\]

As the surface production rate \( P_0 \) can be independently estimated, one can measure the surface concentration of a cosmic-ray-produced nuclide in a rock surface and use Equation (2) to compute the erosion rate (Figure 2).

The technology needed to measure the concentrations of trace cosmic-ray-produced radionuclides at Earth surface levels was developed in the 1980’s and 1990’s, and since then cosmogenic-nuclide erosion rate measurements have been applied to a wide variety of Earth science problems, including investigating the effect of anthropogenic disturbance on erosion and sediment fluxes; quantifying the relationship between surface climate and erosion rates; and understanding feedbacks between tectonic uplift and surface erosion that act to form mountain ranges (see reviews in von Blanckenburg et al., 2006 and Bierman et al., 2004). At present, the technique has been well studied and validated (e.g., Granger et al., 1996), and measurement of the relevant nuclides is routine and straightforward.

**Erosion rates and geomorphic processes in the Dry Valleys:** Early geologic researchers in the Dry Valleys immediately observed a number of features, including well-developed ventifacts (wind-polished rocks) and surface boulders weathered to the point of disintegration, that implied an extremely long period of undisturbed surface exposure. Extensive subsequent geologic research in the western Dry Valleys, primarily by Dave Marchant and colleagues, revealed volcanic ashes preserved on Dry Valleys surfaces in their original, undisturbed, depositional configuration. Geochemical dating of this ash revealed unexpectedly old ages between \(~4\text{-}14\) million years (Marchant et al., 1993a, 1993b, 1996; Marchant, 1996). The ash chronology showed that many Dry Valleys surfaces had remained essentially unmodified -- specifically, subject to at most tens of cm of erosion --- for millions of years. These erosion rates are extremely low relative to nearly anywhere else on Earth.

Most subsequent applications of cosmogenic-nuclide geochemistry in the Dry Valleys focused on glacially transported clasts, not the bedrock substrate, and were intended to date glacier advances. However, a cosmogenic-nuclide exposure age also limits the erosion rate of the surface: if it were higher than a certain value, the surface could not have survived long enough to attain the observed age. Thus, the common occurrence of exposure ages greater than \(~1\) Ma in the Dry Valleys (Schafer et al., 1999; Bruno et al., 1997; Brook et al., 1995) implies that rock surface erosion rates in this environment are commonly less than \(~0.5\) m/Myr. Summerfield et al. (1999) made cosmogenic \(^{21}\)Ne measurements on a variety of sandstone bedrock surfaces in the upper Dry Valleys and quantified erosion rates of these surfaces at 0.1-1 m/Myr. In recent field projects in the Dry Valleys (see Results of Prior Research below), one of us (Balco) used cosmogenic \(^{10}\)Be, \(^{26}\)Al, and \(^{21}\)Ne analyses to measure long-term sandstone bedrock erosion rates (so far published only in abstracts: see Balco et al., 2008b). at a variety of sites between 1200-2100 m elevation in the western Dry Valleys. Erosion rates at these sites are 0.08-2 m/Myr, in agreement with (although spanning a slightly larger range than) previous observations. To summarize, although sandstone surface erosion rates in the Dry Valleys are extremely low relative to erosion rates elsewhere on Earth, they display approximately an order of magnitude variation, and are in some cases high enough (meters per Myr) to significantly modify landforms over the several million years these landscapes have been exposed.

**Genesis of this proposal:** After collecting the data set, described above, of erosion-rate measurements from Dry Valleys sandstone surfaces, we later sought to determine which surfaces, if any, were colonized by cryptoendolithic communities. Unfortunately, cosmogenic-nuclide analysis requires destroying the
sample, and this idea did not occur to us until some time after the analyses were complete. Small chips of the original samples were archived, but these chips did not include original upper surfaces. Thus, our only means of establishing the presence or absence of cryptoendolithic communities was photographs of the samples. In many cases (Figure 4, left two panels), these photographs showed clear evidence of colonization, including the characteristic subsurface zonation and exfoliation patterns shown in Figure 1. In other cases, photographs showed clearly that these features were absent (Figure 4, right panel).

Figure 4. Examples of sandstone samples collected in erosion rate studies for which photos were adequate to identify or exclude evidence of surface colonization by cryptoendoliths.

Figure 5. Upper panel, distribution of sandstone bedrock erosion rates in the western Dry Valleys inferred from cosmogenic-nuclide measurements on rock surfaces. These include both $^{10}$Be and $^{26}$Al measurements from sites where geologic evidence indicates steady erosion without significant ice cover; the erosion rate calculation follows Balco et al. (2008a). Lower panels, distribution of erosion rates for surfaces apparently inhabited and not inhabited by cryptoendolithic communities.
Of 33 samples used for erosion-rate estimates, photographs displayed either clear evidence of colonization, or a clear absence of such evidence, in 22 cases (Figure 4, left panels). In 11 cases, the photographs were inadequate to determine whether evidence of colonization was present or not: in most cases, this meant that photographs were taken from too great a distance or the rock had not been broken appropriately to show a cross-sectional view of the potential zone of colonization.

Clearly this approach has significant flaws, primarily that we could not directly verify the presence or absence of microbial communities. As noted by Friedmann and Weed (1987), the characteristic features of microbial colonization may be fossil rather than active. On the other hand, for technical reasons related to the erosion rate calculations, all the samples were collected from subhorizontal surfaces with a clear view of the sky, at sites where geomorphic evidence showed that significant snow cover was unlikely. These requirements standardize the data set against a number of other factors that are expected to affect the distribution of microbial communities, most importantly aspect and exposure to sunlight.

Figure 5 shows the result of this data compilation. Notably, despite observing a broad range of erosion rates, we only found evidence for cryptoendolith colonization on surfaces with low erosion rates. Erosion rates for surfaces with no evidence of colonization displayed an approximately uniform distribution across the full range of erosion rates observed; however, evidence of colonization was only evident on surfaces with erosion rates below 1.2 m/Myr. Clearly the limitations of our experimental design (or lack thereof) mean that this relationship is suggestive rather than conclusive. However, this striking observation suggested the following hypotheses, which we aim to evaluate in this proposal.

**Hypothesis 1:** Cryptoendoliths cannot colonize/survive if the erosion rate is higher than ca. 1 m/Ma. In some systems, excessive abiotic erosion rates might cause replacement of the surface habitable zone at rates that exceed the maximum growth rates of potential colonizers. In a surface-fixed frame of reference, this can be likened to the behavior of a chemostat, a concept common in biochemical engineering and wastewater treatment that describes a well-mixed bioreactor with continuous flow (input and output). Mass balance considerations reveal that any steady-state microbial population within a chemostat must grow at a rate that matches the reactor dilution rate (flow through the reactor divided by the reactor volume). In excess of the maximum growth rate of any essential member of the community, termed “washout,” results in loss of the entire community (Bailey and Ollis, 1986). A one-dimensional description of this concept for the cryptoendolith system, in which erosion rate substitutes for flow rate and depth of the habitable zone replaces reactor volume, is as follows:

\[ D = \frac{\text{Erosion rate}}{\text{Depth}_{\text{Habitable zone}}} = \mu = \frac{1}{\tau} \quad (3) \]

Where \( D \) = dilution rate, \( \mu \) = instantaneous growth rate, and \( \tau \) = mean residence time (of fluid elements in a chemostat or rock particles in a cryptoendolith system). Interestingly, if we rearrange this expression to solve for the erosion rate in terms of habitable depth (typically 10 mm for the cryptoendoliths) and assume \( \tau \) is equal to a previously proposed average length of the exfoliation life cycle (10,000 years) (Friedmann et al., 1987; Sun et al., 1999; Johnston et al., 1991), we obtain an erosion rate of 1 m/Ma, which closely matches the upper limit of erosion rates at which we observed evidence for colonization.

Cryptoendolith biomasses are unlikely to be truly steady-state (i.e., their growth is not continuous but rather cyclic), so this analogy is not strict. The surface dilution framework is, nevertheless, a useful concept for constraining the upper limits on erosion that could permit growth. Furthermore, if confirmed in our field study, this result argues that an average exfoliation cycle of 10,000 years represents the minimum exfoliation period. Anything faster than that results in washout. Supporting this hypothesis is the observation that rocks with unsilicified surfaces, and thus subject to grain-by-grain weathering and likely higher erosion rates, are not colonized (Friedmann and Weed, 1987).

**Hypothesis 2:** Cryptoendoliths exhibit rapid growth after exfoliation followed by a long period of steady state maintenance near the carrying capacity. An association of high biomass with slow erosion rates is
expected only if communities are maintained at or near the carrying capacity of the system for most of the exfoliation cycle. In this case, in any random sample, the probability of encountering high biomass is highest in systems that exfoliate infrequently. In Figure 6 we consider fast and slow exfoliating communities assuming the “rapid growth” or “continuous growth” models proposed by Sun and Friedmann (1999). Implied age distributions for the resulting communities show a bias towards older (and larger) biomass in slowly eroding communities only for the rapid growth model. For example, Hoppert et al. (2004) found that endolithic communities colonize carbonates within a few years following exposure by retreating glaciers. The depth and biovolume of these newly established communities were similar to those of communities in rocks exposed for ~100 years, suggesting quick growth to the equilibrium carrying capacity and subsequent maintenance for long periods.

**Figure 6: Expected biomass/age distributions for fast (blue), moderate (red) and slow (green) eroding cryptoendolithic communities assuming (a) same growth rate but variable length of steady state community, and (b) the uniform growth model proposed by Sun and Friedmann (2010). Figures to the right illustrate the distribution of young (low biomass) and old (high biomass) communities under both assumptions. Dashed line illustrates that the probability of acquiring a sample in which high biomass correlates with slow eroding communities is most likely when long exfoliation cycles accompany prolonged steady-state communities with biomass at the carrying capacity.**

**Hypothesis 3:** Cryptoendolithic microbial assemblages constitute ecological communities that are specifically adapted to a prevailing erosion rate. Both the surface renewal model and the chemostat analogy argue that the long-term growth rate (averaged over many exfoliation cycles) must match the long-term dilution rate (by erosion of the habitable zone). Logically, fast-eroding environments can only be populated by fast-growing organisms; faster growth (than competitors) would provide a selective advantage. Where erosion rates are slower, other means of competition may take precedence (e.g., ability to gather moisture; light utilization efficiency; or secretion of allelochemicals). All these selective dynamics (including the imposed erosion rate) may act simultaneously to determine community composition. Thus, we hypothesize that microbial assemblages exist that are optimally adapted to specific erosion rates. Such optimum assemblages would constitute true ecological communities in that their composition is consistent, reproducible, and co-occurring in a defined habitat, one of whose externally imposed characteristics is the erosion rate. Furthermore, given that they possess various biological mechanisms to stabilize or degrade rocks, we speculate that these communities may engineer the long-term erosion rate to maintain exfoliation rates favorable to perpetuation of the community.
Possible study outcomes that would address this hypothesis would include observation of consistent and co-occurring communities only at the highest erosion rates where colonization was observed. This would imply that erosion only becomes a dominant determinant of community composition when it is high enough that other competitive mechanisms are insignificant. Alternatively, observing that erosion rate was an integral determinant of community composition across the spectrum of erosion rates would support the speculation that communities may engineer the long-term erosion rate.

Figure 7. Proposed primary field area in the western Olympus Range, McMurdo Dry Valleys. Upper photo shows an overview of the area. Greenish rubble in the foreground is dolerite (a dark igneous rock) of the Ferrar Group; this lithology does not host cryptoendoliths. The peaks on the horizon form the western Olympus Range, and the rolling expanse of light tan- to reddish-colored bedrock that surrounds them is the proposed study region. Lower two photos show representative sandstone landscapes in the region. Lower right photo shows an erosional lag deposit that reflects lithologically-controlled variability in erosion rates. Cosmogenic-nuclide measurements near this site show that the underlying light-colored layer (a relatively weakly cemented unit) is eroding at 1.7 m/Myr, but the overlying darker layer (a sandstone of similar composition, but better cemented) is eroding at 0.2 m/Myr.

Hypothesis 4: The presence of cryptoendoliths in sandstone surfaces that have a very low geologically imposed erosion rate may set a lower limit on erosion rates. As discussed above, cryptoendolithic communities secrete byproducts that presumably cause degradation of sandstone surfaces. This implies that, even in the absence of abiotic geologic factors promoting weathering and erosion, surface degradation will still occur at some background rate set by microbial activity. This, in turn, suggests a fundamental biological control on rates of landscape evolution in arid environments such as the Dry Valleys. Our data compilation is equivocal with respect to this idea: we observed both colonized and
uncolonized surfaces at low erosion rates. The signature of a biologically-controlled background erosion rate in our proposed study would be a “floor” to the erosion rate of colonized surfaces, and erosion rates below this value observed only for uncolonized surfaces (note, however, that this relationship might be complicated by lithologic factors like the grain-size distribution or degree of cementation).

Research plan. To summarize, the purpose of this proposal is to explore these hypotheses with a well-designed survey of erosion rates and microbial communities in sandstone regions of the high-elevation western Dry Valleys. Here we describe our plan for this survey.

Field area in the Western Olympus Range, McMurdo Dry Valleys. The primary habitat of cryptoendolithic microbial communities in the Dry Valleys is the extensive outcrop area of sandstones at elevations between ca. 1000-2000 meters above sea level. These rock units, generally referred to collectively as Beacon Group sandstone, include several mappable formations that vary in grain size, sedimentary structures, depositional environment, and mechanical properties, but share the common property of being nearly pure quartz arenite sandstones. We propose to carry out this study in a region of extensive sandstone outcrop in the western Olympus Range, between Wright and Victoria Valleys (Figure 7). This region comprises a gently rolling plain of sandstone outcrop punctuated by steep-sided, flat-topped peaks. Extensive geologic mapping in this region indicates that the last regional ice cover occurred more than 12.5 million years ago; ice extent changes since that time have most likely been limited to small-scale advances and retreats of permanent snowfields and glacierets located in the lee of some of the peaks (Lewis et al., 2006, 2007). A variety of geologic evidence from the western Dry Valleys indicates that the climate has been similar to present polar desert conditions since approximately 13.5 Ma (Marchant et al., 1993a,b; Denton et al., 1993; Sugden and Denton, 2004; Lewis et al., 2006, 2007). This region lies at a similar elevation to, and includes areas with similar aspect and lithology to, well-described cryptoendolithic sites such as Linnaeus Terrace and Battleship Promontory.

We selected this region because the large outcrop area of Beacon Sandstone includes a high diversity of geomorphic environments, spanning a large range in slope, aspect, wind exposure, and lithology. Our overall plan depends on sampling sandstone surfaces with a wide range of erosion rates, and a geomorphically diverse environment increases the likelihood that we can achieve this. Our previous cosmogenic-nuclide measurements from sites in the proposed field area (included in the compilation in Figure 5) show erosion rates between 0.15 – 2 m/Myr, which covers nearly the entire range of sandstone surface erosion rates observed in the Dry Valleys. As in physiographically similar parts of the Dry Valleys, surfaces colonized by cryptoendolithic communities appear to be common (for example, the sample shown in the center panel of Figure 4 is from this area).

Specifically, our field plan includes one field season operating from a tent camp established on one of the permanent snowfields in the western Olympus Range, most likely near Mts. Electra or Circe. This location permits easy foot access to several square miles of topographically and lithologically diverse Beacon sandstone surfaces.

Survey design. Our basic approach to survey design will be as follows. In the field, we will seek to collect samples from a wide range of geomorphic and lithologic environments, attempting to cross gradients in slope, aspect, exposure to sun and wind, and lithology. As a working hypothesis, we anticipate that if erosion rates are primarily controlled by geological and microclimatic factors, spatial variation in erosion rates will have a spatial scale of hundreds of meters or greater. Thus, we expect the spacing of sample sites to reflect this approximate scale. At each site that we identify based on its geomorphic environment, we anticipate that we will see smaller-scale – meters to decimeters – variation in microbial colonization and rock surface appearance. Thus, we will attempt to capture landscape-scale variation in geomorphic context in the overall spacing of our sampling locations, as well as outcrop-scale variation in microbial habitat and diversity, by collecting multiple samples from apparently colonized and apparently uncolonized surfaces at each location. Our governing assumption is that this approach of maximizing variance in the field-observable characteristics of sample sites will result in a high diversity of erosion rates and microbial community characteristics. We also note, however, that it is important to keep in mind that other factors, presumably most significantly the degree of sun exposure and the availability of surface moisture, will certainly affect microbial communities independently of any erosion rate effect. It would
presumably be possible to control for these effects by collecting detailed information about environmental parameters at each site – and we will collect these data in the field – but, as discussed above, choosing sites with optimal characteristics for cosmogenic-nuclide erosion rate measurements (horizontal, snow-free, and with a clear sky view) will have the effect of standardizing some of the important parameters and simplifying this problem.

**Sampling.** Rock samples will be collected in the field using aseptic precautions (flame sterilized implements) and ethanol or bleach wiped gloves. At the time of sampling, replicate small subsamples (1-5 g) of each rock will be transferred to gas tight vials and sealed for later water content determination. Separate subsamples (~1-2 g) will be crushed and extracted in buffer for determination of adenosine triphosphate (ATP) content (providing a relative assessment of community metabolic state and total biomass). A subsample will also be split off for cosmogenic-nuclide analysis; this requires no special handling. Rocks will be transferred to large sterile Whirlpack bags and temporarily stored in the dark at temperatures ≤ 0 °C (using coolers or lockers buried below the snow surface). We propose two helicopter flights during the field season for sample transfer to -20 °C freezers in McMurdo. Samples will be ultimately shipped to Hamilton College at the same temperature (with dessicant containing overpacks to avoid moisture accumulation).

**Erosion-rate measurements.** The first stage of our analytical approach will be cosmogenic-nuclide analysis of all samples to establish the range and distribution of surface erosion rates. We will use the cosmogenic nuclide 21 Ne, which is a stable noble gas that is relatively easy and straightforward to measure at expected (high) concentrations for our proposed field area. Sample preparation for this analysis involves extracting ~0.5 g of quartz by crushing, and etching it with HF to remove surface contamination. A ~150 mg aliquot is then degassed for ~15 min at 1100° C by laser heating under vacuum. Ne is separated from the evolved gas and introduced into a static vacuum, sector field mass spectrometer. After sample preparation is complete, each analysis requires ~1.5 hrs. At present, BGC has one analytical system capable of a throughput of ~50 21 Ne analyses/week, and in summer 2012 a second system will be commissioned (recently funded by NSF I&F; EAR-1050479; PIs Balco and David Shuster). We anticipate that we will collect, and analyse for 21 Ne, approximately 100-150 samples.

**Microbial community characterization.** Based on the results of the erosion rate survey, we will select a subset of colonized and uncolonized surfaces that span a range of erosion rates for microbial community characterization, as follows.

**DNA recovery and biomass quantification.** Subsamples of approximately uniform mass and cross sectional depth will be recovered aseptically from each rock and crushed in a sterile stainless steel compression cell (to be fabricated in the machine shop at Hamilton). After homogenizing, samples will be split. Half of the crushed material will be used for DNA extraction. The other half will be used for Kjeldahl nitrogen determination as a proxy for total biomass (after Sun and Friedmann, 1999).

**Molecular characterization of cryptoendolithic communities.** Terminal restriction fragment length polymorphism (TRFLP) will be used to profile the microbial diversity in each rock sample. To screen broadly we will use fluorochrome labeled universal primers targeting the V4-V8 regions of the SSU rRNA gene of bacteria, archaea and eukaryotes (e.g., Amaral-Zettler et al. 2011). Resulting amplicons will be digested using two or more restriction enzymes. The size (molecular weight) of the labeled digest fragments will be determined by electrophoretic separation and comparison to standard masses (e.g. LIZ-500 Applied Biosystems). The resulting TRFLP patterns will be used to quantitatively assess differences in community composition. The normalized TRFLP peak areas will be used to create Euclidean distance matrices that describe the dissimilarity of community profiles for each gene digest. Communities of similar composition result in similar TRFLP patterns and have minimum Euclidean distances. Clone libraries will be constructed from select samples that represent dominant community types and sequenced for phylogenetic assignment to nearest related organisms. Finally, TRFLP, erosion rate and geochemical data for each sample will be statistically analyzed to determine which environmental parameters best correlate with the abundance of specific taxa and best predict community structure and diversity. The McCormick lab has recently used this same approach to describe depth dependent shifts in microbial community composition in a meromictic lake and in Antarctic marine sediments (McCormick et al. 2011).
Observations of rock degradation by cryptoendolithic communities. We will prepare a thin section of each sample selected for microbiological analysis. Although this will not be an initial priority, this will enable later quantification of changes in rock density and/or chemistry through image analysis and/or ion beam techniques.

Quantification or control of other parameters expected to control population structure. In the field we will collect data on slope, aspect, exposure geometry, surface hardness (most likely by Schimdt hammer or an equivalent technique) and any observables that may be related to water availability (e.g., persistence of snow; proximity to permanent snowfields; wind exposure). In the laboratory, we will collect data on mineralogy, grain size data, and sedimentary structure.

Potential challenges. In this section we highlight several issues that may complicate our goal of determining the relationship between cryptoendolithic microbial communities and sandstone surface erosion rates. These are important issues, and we considered them carefully in preparing this proposal. However, we argue that based on available evidence, none of these represent insuperable obstacles.

Complex exposure histories. The term “complex exposure” denotes a surface exposure history that violates the steady-erosion assumption used in calculating an erosion rate from a cosmogenic nuclide concentration. In the Dry Valleys, the most likely form of complex exposure would be shielding of a sample site by a frozen-based, non-erosive, glacier or permanent snowfield for a significant fraction of its history. In this case, the surface nuclide concentration might not have reached equilibrium with the erosion rate. Several lines of evidence show that this scenario is unlikely for our proposed field area.

Skin depth and time scale mismatch. Equation 2 involves the important assumption that the surface erosion rate has remained steady for long enough to attain nuclide production-erosion equilibrium. One can represent this as an effective half-life for equilibration with a new erosion rate; this depends on the erosion rate, and for the rates observed in the Dry Valleys is ~0.25-2 Ma. On the other hand, microbial colonization and exfoliation are believed to take place on a depth scale of order 1 cm and corresponding time scale of order 10 ka. Thus, our erosion rate measurements reflect a significantly longer averaging time than our observations of microbial communities. Whether or not this time/depth scale mismatch presents a significant obstacle to our study depends to a large extent on our results. For example, in the end member case where cryptoendolith community structure depends entirely on a geologically imposed erosion rate, this scale mismatch would not at all affect our ability to quantify the community structure-erosion rate relationship. In an opposite theoretical case where cryptoendolith communities had only been present for 10,000 years at any of our sites, we might observe that community structure was related to modern environmental variables, but not to long-term erosion rates. As there exists abundant evidence for the long-term presence of cryptoendolithic communities in the Dry Valleys (Friedmann and Weed, 1987), we view this latter possibility as unlikely. In addition, although the age of any extant community may not significantly exceed 10,000 years, the genetic composition of that community likely reflects a much longer legacy, having persisted through many exfoliation cycles with selection acting on time scales commensurate with those at which erosion is measured. To summarize, we view this issue as a potential complicating factor that we will have to keep in mind during data analysis, but scenarios in which it entirely precludes our study appear unlikely.

Broader impacts: undergraduate research and education: In summary, this project uses straightforward, robust, and well-established methods to investigate simple hypotheses. In our view, however, these hypotheses are nevertheless extremely interesting from both a geological and biological perspective. Thus we view this project as an ideal example of research that is both accessible to undergraduate training and experiential education and also likely to produce broadly significant results. In short, it is an ideal platform for undergraduate research. In keeping with this idea, we have structured this project as a collaboration between a scientist at a research institution (Balco) and a faculty member at a primarily
undergraduate-focused college (McCormick) in which a significant fraction of the research will be done by undergraduates. Our field plan will involve one UC-Berkeley undergraduate working with Balco, and three Hamilton undergraduates working with McCormick, participating in fieldwork in the Dry Valleys, presumably during the winter of their junior year. The analytical work will take place in the following summer, and we have budgeted travel funds for undergraduates at each location to travel to the other and participate in both the geochemical and microbiological measurements. Our goal is not only to learn something new about the fundamental way in which microbial communities interact with geomorphic processes, but also to use this study as a vehicle for communicating the design and execution of interdisciplinary research design to undergraduate students.

The PIs have very different background and training and bring a high degree of inter-disciplinarity to the project. Balco is a research scientist specializing in geologic and geomorphic applications of cosmogenic-nuclide geochemistry and low-temperature thermochronometry. He has spent six field seasons in Antarctica, including one in the proposed field area. McCormick teaches in both the Biology and Geoscience departments at Hamilton College and has built a strong web of interdepartmental collaborations with all the science departments. His research interests lie in microbial ecology and environmental geomicrobiology. Including his current students, McCormick has mentored or co-advised 59 research students since he started teaching at Hamilton College in 2003 (28 Senior Thesis Students 18 summer research students and 13 independent studies). Of the 28 thesis students that Mike mentored, 10 proceeded to graduate school in sciences and 7 to medical school (61% in science related fields). McCormick has worked in Antarctica on two cruises of the N.B. Palmer. Together, these PIs have demonstrated ability to complete significant research and also mentor and train students to enable them to pursue careers in science.

The proposed research will not only provide cutting edge projects for summer and senior undergraduate research, it will also provide rich material for investigative laboratories in courses taught at Hamilton. For example, clones isolated from libraries could be analyzed and sequenced by students in each of the following courses: Bio 115 (Fundamentals and Frontiers) an advanced thematic introductory course for incoming freshman with a strong background in biology, Bio 221 (Microbiology)– an introductory microbiology course taught from an environmental microbiology perspective, and Geo 260 (Geomicrobiology) - a course taught in the Geosciences Department that introduces students to the historic and contemporary interactions between microbial life and Earth’s geochemistry. McCormick is also developing a new project based 300 level course to be introduced in Spring 2013 entitled Molecular Methods in Geomicrobiology. The large collections of TRFLP and clone sequences obtained in this project would provide ideal material for team-based projects. Beyond learning a variety of molecular approaches to assess community diversity, students will be introduced to statistical methods that provide insight into the influence of environmental factors on community structure (e.g., ordination techniques such as principal coordinate analysis or canonical correlation analysis). Development of the Dry Valleys field site as a common platform for studying the links between biogeochemical dynamics and microbial community structure will help students appreciate the adaptations of life in extreme environments and ultimately ask questions about the intimate interplay of genes and geochemical landscapes across evolutionary time.

Results of prior research

Extending the record of Antarctic landscape evolution into the Pliocene with Ne-21 measurements (Balco and D. Shuster, ANT-0838958, 6/1/2009-5/31/2010, $47,265); Systematic analysis of landscape evolution and surface ages in the southern Transantarctic Mountains (J. Putkonen, Balco, and Shuster, ANT-0838968, 9/01/2009-present, $247,684).

These related projects comprise a research program focused on understanding current and former landscape-forming processes in the Transantarctic Mountains using a combination of geomorphic observations, sediment-transport data, and cosmogenic-nuclide measurements. This environment is of interest because, largely due to the lack of free water and geomorphically active biota, landscape-forming processes are fundamentally different from those elsewhere on Earth. Key findings include:
1. Quantifying both present and long-term rates of sediment transport and surface degradation, which show a striking, and surprising, contrast between relatively active sediment transport and surface disturbance processes and extremely slow rates of long-term landform degradation.

2. The common landscape-forming process of penetrative creep is largely absent.
3. Rates of erosion and sediment transport processes are extremely patchy, resulting in the close juxtaposition of relatively active surfaces with surfaces that have been stable for millions of years. The overall landscape appearance strongly reflects these extreme contrasts in the rates of erosion and surface modification.

4. Rates of landscape-forming processes were different during the relatively warm climate of the Pliocene: in most cases faster and more active, but in some cases slower. However, they remained extremely low relative to other environments.

Publications related to these awards on which Balco is a co-author (see References Cited section) include Morgan et al. (2010a, 2010b; student author); Balco and Shuster (2009a, 2009b) and Putkonen et al. (2012).

Collaborative Research in IPY: Abrupt Environmental Change in the Larsen Ice Shelf System, a Multidisciplinary Approach - Marine Ecosystems. (McCormick, M.L. and multiple co-PIs, ANT-0732917, 9/15/07-present, $160,127)

This grant is a component of the "LARISSA" project (Larsen Ice-Shelf System, Antarctica), a large interdisciplinary undertaking which aims to assess ice-ocean-ecosystem interactions during the current period of climate change in the Larsen ice-shelf system along the east coast of the Antarctic Peninsula. Specifically, our project aimed to 1) characterize the geochemistry and microbial community diversity in a cold seep discovered in the Larsen B embayment shortly after the 2002 break up of the Larsen B ice shelf; and 2) assess the long term influence of ice shelf loss on the benthic microbial communities of the eastern continental shelf of the AP. Unfortunately, both attempts to reach the Larsen B cold seep were unsuccessful due to unnavigable sea ice conditions (cruises NBP10-01 and NBP12-03). Despite this setback, alternate sampling undertaken during NBP10-01 permitted us to characterize microbial community composition in various Antarctic environments (including marine sediments, contaminated soils of Palmer Station and whale bones) using identical methods to those described in this proposal. To date, this project resulted in 5 Senior Theses (Bucceri, 2011, Garrett, 2011, Taylor, 2011, Seamen, 2012, Pallen, 2012; see References Cited section). During NBP12-03, which concluded only six weeks prior to this writing, we addressed our second objective with rigor, conducting a biogeographic study of sediment microbial community composition and pore water chemistry along a 160 km near-shore to mid-shelf transect. Over 800 sediment samples were collected for microbial community analysis and over 4500 samples for geochemical analysis.