lack of strain hardening is believed to contribute to the low tensile ductility of nanocrystalline metals (*25*). The most notable feature observed in the simulations is the formation of dislocation pileups: a series of dislocations being pushed toward a grain boundary by the stress, as can be seen in Fig. 3. A pileup consists of multiple dislocations queued up on the same (or nearby) slip planes, pressed toward a grain boundary by the applied stress, but held apart by their mutual repulsion. As new dislocations arrive in the rear of the pileup, their stress field helps to press the front-most dislocations into the grain boundary (Movie S1). Arrays of dislocations resembling pileups have been seen moving through copper grains as small as 50 nm (*26*). The pileup labeled "B" in Fig. 3 consists of five to six dislocations in a 35- to 40-nm-long pileup, consistent with the expected size of such a pileup at a tensile stress near 2 GPa (*9*), although the elastic fields from other nearby dislocations clearly perturb the pileup.

Several models for the Hall-Petch behavior have been suggested (*8*, *9*), and it is difficult if not impossible to distinguish between them experimentally, but these simulations provide some insight. The presence of pileups above the hardness maximum gives some credibility to the original suggestion of the Hall-Petch effect being mainly caused by pileups (*1*): For small grains, the extent of a pileup is limited and therefore the local buildup of stress in a pileup is reduced. A higher applied stress is thus required before plastic flow occurs. Estimates for grain size where the breakdown of the Hall-Petch effect occurs depend somewhat on the detailed assumptions of this model, but they fall in the range from 11 nm (*15*, *17*) to 50 nm (*27*) for copper, in agreement with the 10 to 15 nm found for the hardness maximum in the simulations. Other models focus on grain boundary sources (*28*), which certainly also play a crucial role in the simulations. Deformation twins have been suggested as dislocation obstacles in the smallest grains (*22*, *29*). Only a few twins are observed in our simulations, but a large number of stacking faults might play the same role. However, if they contributed substantially to the Hall-Petch effect, it would be seen in Fig. 1A as work hardening, because the number of stacking faults increases during the simulations. Furthermore, on the basis of the simulations, models explaining the Hall-Petch effect as stemming from increased work hardening in small grains (*30*, *31*) can certainly be excluded for nanocrystalline copper.

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Supporting Online Material

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Fig. S1
Movie S1

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Seasonal Dynamics of Previously Unknown Fungal Lineages in Tundra Soils

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The finding that microbial communities are active under snow has changed the estimated global rates of biogeochemical processes beneath seasonal snow packs. We used microbiological and molecular techniques to elucidate the phylogenetic composition of undersnow microbial communities in Colorado, the United States. Here, we show that tundra soil microbial biomass reaches its annual peak under snow, and that fungi account for most of the biomass. Phylogenetic analysis of tundra soil fungi revealed a high diversity of fungi and three novel clades that constitute major new groups of fungi (divergent at the subphylum or class level). An abundance of previously unknown fungi that are active beneath the snow substantially broadens our understanding of both the diversity and biogeochemical functioning of fungi in cold environments.

About 40% of the terrestrial environment consists of biomes that are covered by snow for varying lengths of time in the winter (*1*). Soils in these environments contain a large reservoir of organic carbon (*2*, *3*). Until recently, it was assumed that soil microorganisms were inactive during the snow-covered period. However, measurements of a high efflux of CO_2 and other greenhouse gases through the snow suggest that microbial populations can be active under the snow (*4*–*6*). These results prompted a reevaluation of whether some seasonally snow-covered environments are sinks of atmospheric CO_2 (*7*). In addition, undersnow microbial metabolism is an important biogeochemical sink for nitrogen (*8*), and the subsequent release of microbial nitrogen during snowmelt is a major contributor to high primary productivity during the short growing season in the tundra (*8*, *9*). Despite this progress, we know little about the identity or seasonal dynamics of the microbes involved.

We used standard methods (*10*) to estimate microbial biomass in cold soils (*8*, *11*). The results show that microbial biomass varies seasonally and reaches maximum annual levels during late winter under the snow in tundra soils (Table 1) ($P < 0.001$). This observation parallels several recent studies that have found peaks in microbial biomass in the late winter (*8*, *11*, *12*). Most of the

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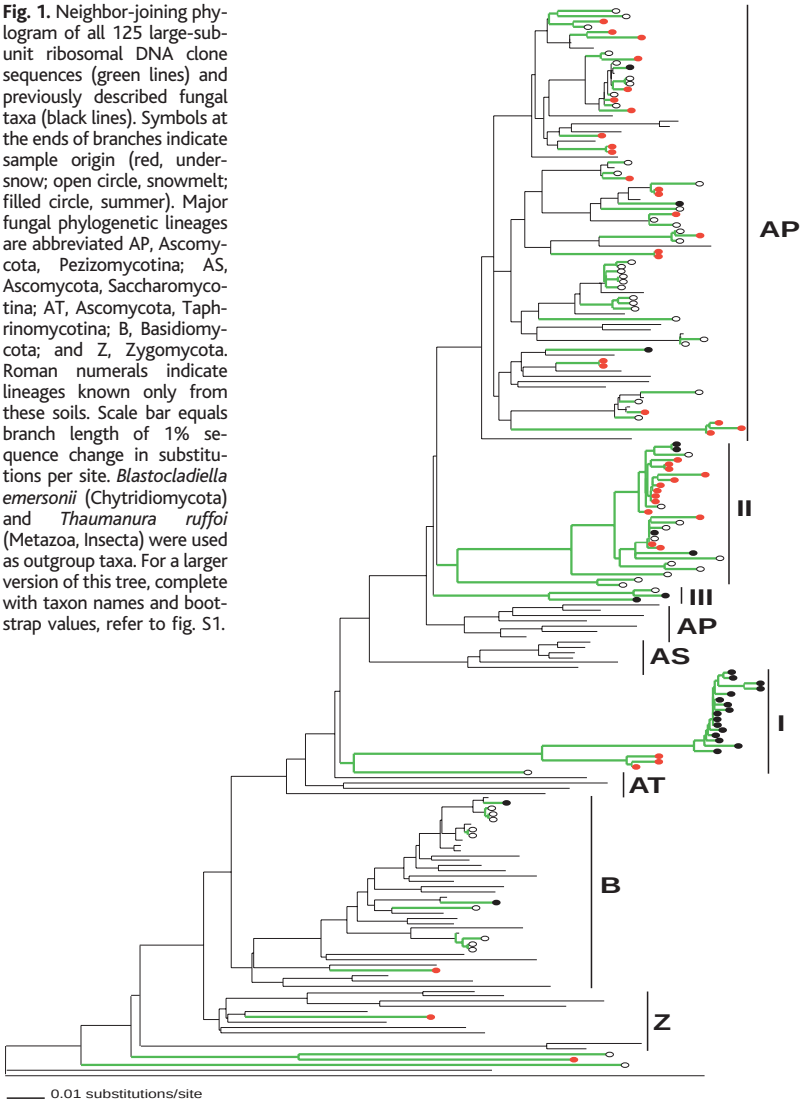

Fig. 1. Neighbor-joining phylogram of all 125 large-subunit ribosomal DNA clone sequences (green lines) and previously described fungal taxa (black lines). Symbols at the ends of branches indicate sample origin (red, undersnow; open circle, snowmelt; filled circle, summer). Major fungal phylogenetic lineages are abbreviated AP, Ascomycota, Pezizomycotina; AS, Ascomycota, Saccharomycotina; AT, Ascomycota, Taphrinomycotina; B, Basidiomycota; and Z, Zygomycota. Roman numerals indicate lineages known only from these soils. Scale bar equals branch length of 1% sequence change in substitutions per site. *Blastocladiella emersonii* (Chytridiomycota) and *Thaumanura ruffoi* (Metazoa, Insecta) were used as outgroup taxa. For a larger version of this tree, complete with taxon names and bootstrap values, refer to fig. S1.

Table 1. Microbial biomass estimated using standard methods for tundra soils (*10*, *12*) for undersnow, snowmelt, and summer soils from alpine tundra soils. Biomass levels were highest under the snow and showed a significant decline thereafter ($P = 0.0006$; one-way analysis of variance). Ratio of active fungal-bacterial biomass (F/B ratio) was determined using microscopic counts of fluorescein-diacetate–positive bacteria and fungi. Data were converted from biovolume to biomass before ratios were calculated (*11*). Three spatial replicates were combined for the F/B ratio measurements.

Sample origin	Microbial biomass (μg C/g soil)	F/B ratio
Undersnow	363 ± 18	14.9
Snowmelt	244 ± 21	7.0
Summer	125 ± 32	6.6

biomass in these soils is fungal, especially in the winter (Table 1). Given their known physiological functions, the dominance of fungi in winter helps explain previous observations that microbial growth in the winter is fueled by decomposition of organic polymers and phenolic compounds. In contrast, the summer microbial community at the same sites depends mostly on simple compounds associated with root exudates and microbial turnover for growth (*11*). This difference in the biogeochemical function of the summer and winter microbial communities led us to explore the phylogenetic relationships between them.

To characterize the diversity of the winter, spring, and summer fungal communities, we used DNA sequence–based methods (*10*, *13*). Whole-community DNA was extracted and ribosomal gene libraries were constructed. A phylogenetic analysis of 125 fungal clone sequences revealed an abundance of Ascomycota (Fig. 1). Two other fungal phyla, the Basidiomycota and Zygomycota, accounted for only 10% and <1% of the sequences, respectively. These results differ from studies of forest soils, which show a dominance of Basidomycota (*14*, *15*). This analysis also shows that a large number (40%) of the sequences clustered into unique groups within the Ascomycota that are distantly related to any previously described and sequenced species. To confirm this result, we performed a more focused Bayesian analysis (*16*) that included representatives of all of the described subphyla and classes within the Ascomycota (*17*) (fig. S2). Many unique lineages were sampled within each group, and within-group sequence divergences were high (17 to 28%), indicating that we have discovered several new major groups of fungi. On the basis of previous taxonomic assessments (*17*), these groups may constitute new subphyla or classes, potentially greatly expanding the known higher order diversity of fungi. Whereas novel lineages are commonly found in similar environmental studies of bacteria and archaea (*13*), few studies have described hidden diversity within the fungi. One recent study hinted at this hidden fungal diversity (*18*), but did not show the depth or breadth of diversity reported here.

A comparison of fungal community composition between the winter (beneath the snow) and spring (during snowmelt), and between spring and summer (which is warmer and dry), revealed substantial overlap between winter and spring but a nearly complete turnover between spring and summer (Fig. 2). The shift in community composition was largely attributable to the presence of a large number of sequences from the novel Group I clade in the summer that were absent at other times of the year, and the abundance of novel Group II sequences that were present mainly in the winter and spring. Nonrandom shifts in community composition coupled with changes in soil moisture, temperature, and carbon availability (*11*) imply that the sampled fungal sequences probably differ functionally, an inference supported by the large genetic difference between Group I and II sequences. Similar seasonal shifts have been observed for bacteria in alpine soils sampled from the same sites (*19*), suggesting that the tundra soil microbial communities are dynamic during periods of rapid environmental change and that one-time, static, surveys may underestimate microbial diversity.

These seasonal changes in fungal diversity have implications for our understanding of the global importance and biogeochemical functioning of seasonally snow-covered environments. The discovery of subphylum and class-level ascomycetes is a step toward exploring the relationship between fungal diversity and biogeochemical function in the field. However, further elucidation of their roles in nature may require new culturing approaches or metagenomic studies that allow the linkage of functional and ribosomal RNA genes.

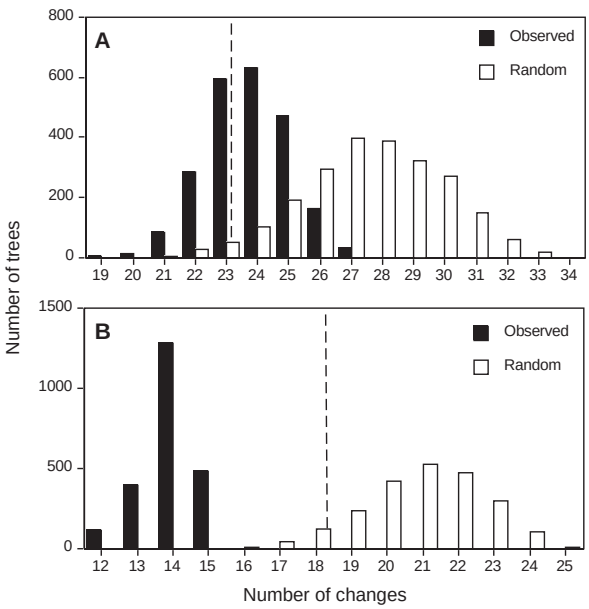

Fig. 2. Frequency distributions showing the number of changes required to describe the covariation of fungal lineage with season. Observed distributions are based on trees in the posterior probability distribution from Bayesian analysis (observed) and distribution of randomly generated trees from MacClade (random). Dashed lines indicate the 95% lower confidence limit for the randomized data. (**A**) Comparison of winter and spring communities ($P > 0.05$; not significant). (**B**) Comparison of spring and summer communities ($P < 0.001$).

Nevertheless, the presence of previously unknown, higher order lineages of fungi in tundra soils suggests that the cold, snow-covered soils may be an underappreciated repository of biological diversity.

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Synchroneity of Tropical and High-Latitude Atlantic Temperatures over the Last Glacial Termination

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A high-resolution western tropical Atlantic sea surface temperature (SST) record from the Cariaco Basin on the northern Venezuelan shelf, based on Mg/Ca values in surface-dwelling planktonic foraminifera, reveals that changes in SST over the last glacial termination are synchronous, within ±30 to ±90 years, with the Greenland Ice Sheet Project 2 air temperature proxy record and atmospheric methane record. The most prominent deglacial event in the Cariaco record occurred during the Younger Dryas time interval, when SSTs dropped by 3° to 4°C. A rapid southward shift in the atmospheric intertropical convergence zone could account for the synchroneity of tropical temperature, atmospheric methane, and high-latitude changes during the Younger Dryas.

Ice core gas records (*1*, *2*) demonstrate that the atmospheric concentration of methane, which is thought to be dominantly derived from tropical wetlands (*3*, *4*), rose and fell within decades of the Greenland deglacial warming and cooling events (*5*, *6*). Because the atmosphere integrates globally, the methane signal suggests that a large part of the terrestrial tropics responded in kind with North Atlantic changes (*3*). Proxy temperature records from tropical ice cores also show a deglacial signal similar to the Greenland records, although dating issues and local effects complicate interpretation of the observed signals (*7*). Evidence for a thermal response in tropical surface waters during the Younger Dryas (YD) chronozone, the most prominent of the deglacial events, is more ambiguous; high-resolution Pacific sea surface temperature (SST) records show either a small (<1°C) cooling (*8*) or no response (*9*), whereas a record from the Tobago Basin in the southeastern Caribbean indicates what has been interpreted as an antiphased response (*10*), with a small warming during the YD.

The Cariaco Basin, on the northern Venezuelan shelf, is a unique repository of tropical paleoclimate records (*11–17*). The combination of shallow sills (<150 m), permanent anoxia below ~300 m, and high sedimentation rates (0.3 to > 1 mm/year) has produced nearly continuous, annually laminated, unbioturbated sediments for the past 14,700 years (*12–14*). The presence of annual varves in the deglacial portion of the Cariaco sequence makes it possible to develop an independent chronology that can be directly compared to ice core records (*18*, *19*).

Today, the Cariaco Basin has two distinct seasons: a cool dry season in (boreal) late winter, when the northeasterly trades are directly overhead and coastal upwelling and high productivity dominate; and a warm wet season in late summer, when the intertropical convergence zone (ITCZ) is

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