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Phylogenetic Clustering Reveals Selective Events Driving the Turnover of Bacterial Community in Alpine Tundra Soils

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Abstract

Soil bacterial communities play a determining role in snow-covered ecosystems' response to global warming because of their role in nutrient recycling. However, little is known about how changes in snow-cover dynamics could affect bacterial community assembly in the short or long term. We examined the phylogenetic structure of soil bacterial communities sampled seasonally from early snowmelt (ESM) and late snowmelt locations (LSM) in temperate alpine tundra. Most of the variation in phylogenetic structure (i.e. β-diversity) was temporal rather than spatial and most observed deviations from random community assembly were towards phylogenetic clustering. Indeed, we observed phylogenetic clustering of *Acidobacteria*, *Actinobacteria*, and *α-Proteobacteria* during late winter in ESM locations, and a phylogenetic clustering of *β-*, *γ-Proteobacteria*, and *Bacteroidetes* during autumn in ESM and LSM locations probably linked to the onset of plant senescence and biomass decomposition. Interestingly, *Acidobacteria* were clustered in all LSM samples. Our study provides evidence of a high seasonal turnover of the phylogenetic structure of bacterial communities in alpine tundra soils, suggesting that climate-induced changes in snow cover can significantly alter the functioning of cold ecosystems through their filtering effects on soil bacteria communities.

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Introduction

It is predicted that alpine tundra ecosystems will be disproportionately affected by climate change due to the projected alteration of snow cover and temperature regimes (Wookey et al., 2009). Soil bacterial communities will play a key role in the response of ecosystems to global warming because of their role in nutrient cycling. Better understanding of which mechanisms drive microbial community assembly and how these will be affected by climate change is therefore of paramount importance if the fate of alpine ecosystems is to be predicted (Bryant et al., 2008).

Until recently, biological communities have been studied by considering species at the same level of dissimilarity, regardless of their phylogenetic and/or functional relatedness. However, there is now large evidence that two distinct species assemblages may be in fact very similar in terms of phylogenetic or functional composition, and that studying the phylogenetic and functional structure of communities can provide valuable insights into the evolutionary and ecological processes that drive community assembly and community response to environmental conditions (Webb et al., 2002; Lavergne et al., 2010). As a consequence, phylogenetic information has been increasingly used to infer the assembly mechanisms of biotic communities (Vamosi et al., 2009). This emerging framework of community phylogenetics enables community structure to be comprehensively described and community assembly rules to be inferred by using data of relative abundance and phylogenetic relationships between taxa (Hardy and Senterre, 2007; Münkemüller et al., 2011).

Stringent environmental filtering, i.e. the selection of taxa with specific ecological characteristics, is commonly thought to lead to the selection of closely related taxa, hence an observed pattern of phylogenetic clustering in communities. On the other hand, closely related taxa are more likely to compete for the same resources, which may result in a phylogenetic overdispersion, i.e. the recruitment of distant taxa through competitive exclusion (Webb et al., 2002). To date, the very few microbial community phylogenetics studies have suggested that phylogenetic clustering is a recurrent sign of these communities in both soil and aquatic environments, indicating that environmental filtering plays a prominent role in microbial community assembly (Horner-Devine and Bohannan, 2006; Newton et al., 2007; Bryant et al., 2008; Barberan and Casamayor, 2010). Furthermore, this phylogenetic clustering appears particularly pronounced in stressful conditions (e.g. low productivity, low organic carbon or nitrate levels) whereas overdispersion rather occurs in more favorable conditions (Horner-Devine and Bohannan, 2006). No study has yet looked at temporal patterns of phylogenetic structure of bacterial communities, although such an approach would certainly provide critical information about the extent and mechanisms of community turnover in soils experiencing environmental changes.

Alpine landscapes are characterized by strong seasonal dynamics and marked mesotopographical gradients, which determine highly contrasting snow cover regimes and plant communities between nearby locations (Körner, 1999; Litaor et al., 2002; Choler, 2005; Edwards et al., 2007). These highly dynamic, fragmented environments therefore provide unique conditions to assess the effects of changes in snow cover on soil microbial communities. Despite their significance, bacterial communities remain so far poorly characterized in alpine tundra. Lipson and colleagues re-

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ported strong seasonal variations of bacterial phylogenetic composition and structure (Lipson and Schmidt, 2004; Lipson, 2007), but considered only areas with shallow winter snowpack, precluding assessing the response of bacterial communities to changes in snow cover regimes. On the other hand, a few other studies described the significant effect of snow cover regimes on the seasonal variations of bacterial community (Bjork et al., 2008; Zinger et al., 2009), but did not assess their phylogenetic structure. A fine-tuned evaluation of the mechanisms driving bacterial community assembly in response to global change therefore remains to be done. In the case of alpine ecosystems, this involves linking the temporal turnover of different bacterial clades and their phylogenetic structure to changing environmental conditions that occur both seasonally and spatially.

In this study, we analyzed the phylogenetic turnover (β-diversity) of bacterial communities at the two extremes of a snow cover/mesotopographical gradient, namely Early and Late Snow Melt locations (hereafter ESM and LSM). Based on a Small Sub-Unit of the ribosomal RNA (SSU) sequence data set obtained previously (Zinger et al., 2009), we provided a robust analysis showing that bacterial phylogenetic β-diversity is strongly influenced by temporal fluctuations of the environment, and identified key seasons and bacterial clades responsible for the phylogenetic turnover of bacterial communities.

Material and Methods

STUDY AREA, SAMPLING, AND LIBRARY CONSTRUCTION

The study area is located in the Grand Galibier massif (southwestern Alps, France, 45°05′N, 06°37′E). The site displays a mesotopographical gradient that comprises an ESM location (a windblown ridge that remains snow-free most of the year) and a LSM location (a flat depression where snow accumulates). The characteristics of these sites have previously been described (Zinger et al., 2009). Briefly, ESM locations are characterized by an inconsistent winter snowpack and by long periods of soil freezing (six months per year approximately). LSM locations exhibit a long-lasting, deep, and insulating snowpack almost eight months per year, which leads to a fairly constant winter soil temperature around 0 °C. Plant cover in LSM is dominated by low stature species, such as *Carex foetida* (Cyperaceae) and *Salix herbacea* (Salicaceae), which must cope with a shorter growing season. Plant cover in ESM locations is more discontinuous and dominated by *Kobresia myosuroides* (Cyperaceae), a stress-tolerant turf graminoid, and *Dryas octopetala* (Rosaceae), a dwarf shrub. The upper soil layer in ESM locations (Alpine Ranker) has a higher soil organic matter (SOM) content than in LSM locations (Stagnogley enriched in clay), but the carbon stock is lower due to shallower soils. Soil pH is stable and higher in ESM throughout the year (pH $>$ 6.5), except in winter when ESM soils become more acidic (pH $\approx$ 5) than LSM soils (pH $>$ 6) (Zinger et al., 2009).

The sampling strategy has been described in a previous study. Briefly, samples were collected in 2005 on 24 June, 10 August, 10 October, and in 2006 on 3 May. The soil DNA extraction, Polymerase Chain Reactions (PCRs), clone libraries' construction, and sequencing have been described (Zinger et al., 2009). We obtained eight SSU libraries, one per date/location. We conserved 2111 sequences for analysis. The accession numbers of the SSU sequences used in the present study are FJ568339 to FJ570564. All statistical analyses were performed using the computing environment R (R Development Core Team, 2009).

TAXONOMIC ANALYSIS AND PHYLOGENETIC STRUCTURE

The taxonomic assignment of SSU sequences was done using the Ribosomal Database Project (Cole et al., 2003). The multiple alignments were performed using the ClustalW algorithm (Thompson et al., 1994). Phylogenetic trees were inferred by neighbor-joining and maximum likelihood (based on a generalized time reversible model of nucleotide evolution) using the phangorn package (Schliep, 2011). Both methods yielded matrices of pairwise Molecular Operational Taxonomic Unit (MOTU) distances that were highly correlated for all bacteria phyla (Mantel tests, p-value $<$ 0.001]. Here we only present results based on Neighbor-Joining (NJ) trees.

To study bacterial phylogenetic structure, we used two different approaches. First, we used the framework provided by Rao's quadratic entropy (Hardy and Senterre, 2007). We computed the Q_{st} index (β-phylogenetic diversity; Villéger and Mouillot, 2008), which measures how communities are structured, taking into account taxa phylogenetic relationships and their local abundances, according to Villeger and Mouillot (2008) as recently implemented by de Bello et al. (2010). We computed Q_{st} between two locations, between dates, and between dates and locations. Significance of Q_{st} estimates was assessed with 10,000 permutations of phylotypes across the phylogenetic tree (see above). Second, we computed the nearest taxon index for each location (hereafter NTI), which quantifies the degree of phylogenetic clustering of taxa given their patterns of presence/absence and their phylogenetic relationships (Webb et al., 2002). The NTI of each community was defined as [$-$(MNND $-$ MNNDnull)/SD(MNNDnull)], where MNND is the mean phylogenetic distance of species to their nearest neighbor in the phylogenetic tree (Webb et al., 2002). MNNDnull is the mean MNND for the same communities after randomly permuting taxa across the phylogenetic tree 9999 times, and SD(MNNDnull) is the standard deviation of these permuted MNND values. As defined here, a positive NTI indicates phylogenetic clustering within a given community, whereas a negative value indicates phylogenetic overdispersion in the local community. These analyses were carried out with the R package picante (Kembel et al., 2010).

Results

To assess the relative effect of time (seasons) and space on the phylogenetic structure of bacterial communities, we partitioned the phylogenetic β-diversity between different locations, different sampling dates, and the interaction between season and location. As shown in Figure 1, β-diversity was much greater between seasons than between sites; a pattern consistent across bacterial clades. This result indicates that much of the turnover of bacterial communities occurred over time rather than across sites, resulting in an even greater spatiotemporal variation in the phylogenetic structure of bacteria communities.

The phylogenetic structure of bacterial communities was then evaluated by using the NTI. We found an overall pattern of phylogenetic clustering all year round for both ESM and LSM sites (Table 1, annual effect). Phylogenetic clustering was consistent

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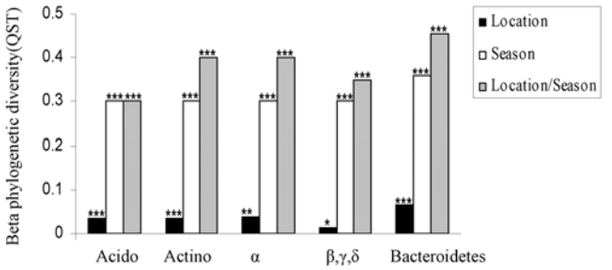


FIGURE 1. Phylogenetic β-diversity of early snowmelt (ESM) and late snowmelt locations (LSM). Q_{st} was estimated using the total phylogenetic tree. Significance of Q_{st} estimates was assessed by comparison with a null model obtained with 9999 permutations. Significance code: ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, +: $P < 0.1$.

throughout the sampling dates for LSM but only for October and May in ESM (Table 1). The temporal variations of the most abundant bacterial phyla/subphyla were also assessed with patterns of NTI (Fig. 2). In ESM, bacterial communities showed no significant phylogenetic clustering in June and August (Fig. 2, part A). However, phylogenetic clustering was observed for *Bacteroidetes*, *β-γ-δ Proteobacteria* in October; *Acidobacteria*, *Actinobacteria*, and *α-Proteobacteria* in May. In LSM, *β-γ-δ Proteobacteria*, *Bacteroidetes*, and *Actinobacteria* displayed phylogenetic clustering in October (Fig. 2, part B). Finally, *Acidobacteria* showed significant phylogenetic clustering all year round, and are likely to have been the main cause of the overall annual phylogenetic clustering in LSM (Table 1).

We also characterized the distribution of bacterial orders for the major phyla (Fig. 3). *Acidobacteria SD1* phylotypes largely dominate in LSM libraries, but only in May and October in ESM. The *β-Proteobacteria* phylotypes were more abundant in ESM than LSM, with an increase in October due to the *Burkholderiales* order. *Pseudomonadales* (*γ-Proteobacteria*) and *Flavobacteriales*/*Sphingobacteriales* (*Bacteroidetes*) phylotypes also display a peak in October libraries.

Discussion

Recent research has documented how bacterial communities of alpine tundra soil respond to snow cover regime (e.g. Bjork et al., 2008; Lipson and Schmidt, 2004; Lipson, 2007; Zinger et al., 2009), but the mechanisms driving the assembly of microbial communities remain poorly understood. We have previously reported that ESM and LSM have contrasting and seasonally variable bacterial communities (Zinger et al., 2009). Here, we provide new insights into the factors responsible for their spatial and seasonal variation by looking at their phylogenetic structure.

First of all, we observed a strong spatio-temporal β-diversity, with temporal variations within a location being much more important than the effect of the habitat itself (Fig. 1). This result contrasts with our previous observation, where higher effect of the habitat was observed (Zinger et al., 2009), and may be explained by the difference of taxonomic scale considered in both studies. Indeed, Zinger et al. (2009) used a molecular fingerprinting technique that provides a global picture of local microbial communities. Although consistent, fingerprinting techniques suffer, however, from a lack of resolving power and are inadequate to assess the phylogenetic relationship among taxa (Bent and Forney, 2008), which may preclude the detection of variations at finer taxonomic scales contrary to both molecular and statistical analyses used here. This apparent contradiction suggests that snow cover regimes may select for major bacterial clades (e.g. *Acidobacteria*, *Actinobacteria,* and *α-Proteobacteria*) amongst which sub-clades respond rapidly to temporal changes in soil climate, snow cover, and vegetation phenology. Additionally, the higher temporal β-diversity observed here might be due to winter samples, for which we previously observed drastic changes in bacterial community composition (Figs. 2 and 3).

Our results concur with previous studies in showing that bacterial communities generally show a tendency to be phylogenetically clustered and support the general conception that environmental filtering is a main driver of microbe community assembly (e.g. Horner-Devine and Bohannan, 2006; Barberan and Casamayor, 2010). This may be especially true in soils, where organisms are able to feed across multiple trophic levels, which is likely to promote taxa coexistence rather than competitive exclusion (Setälä et al., 2005). Alternatively, the spatial scale considered here may be too large for the detection of biotic interactions occurring at much lower scales (microhabitat). In our case, soil pH is probably one of the main drivers responsible for the observed phylogenetic clustering. Large-scale surveys of soil from different habitats already showed that bacterial diversity patterns were largely related to soil pH (Fierer and Jackson, 2006; Chu et al., 2010). Our results support this effect and further suggest that it stems from the apparent resistance of the *Acidobacteria SD1*, *SD2*, and *SD3* groups (Fig. 2; Fig. 3, part A). *Acidobacteria* also displayed phylogenetic clustering in other alpine acidic soils (Bryant et al., 2008; Lipson and Schmidt, 2004; Lipson, 2007), but, however, appeared overdispersed in ESM during vegetation season (Fig. 2, part A), with soil pH > 6.5. This supports the idea that phylogenetic structure of bacterial communities tends to be overdispersed in more favorable environmental conditions (Horner-Devine and Bohannan, 2006), as predicted by theory (Webb et al., 2002).

One could have expected to observe higher phylogenetic clustering in ESM, where environmental conditions may be considered harsher than LSM sites, due to sparser plant cover, higher temperature shifts, and complex organic matter, but it was not the case (Table 1, Fig. 2). First, LSM and winter ESM soils are more acidic

TABLE 1

Nearest taxon index (NTI) metrics of overall bacterial communities in early snowmelt (ESM) and late snowmelt locations (LSM). NTI positive index values present phylogenetic clustering and negative values indicate phylogenetic overdispersion. The NTI was calculated from a phylogenetic tree comprising all phyla. Significance code: ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, +: $P < 0.1$.

Time	ESM	LSM
Annual	2.08 *	3.10 ***
June	−0.20	4.29 ***
August	1.40 +	5.25 ***
October	3.71 ***	7.30 ***
May	7.30 ***	3.20 ***

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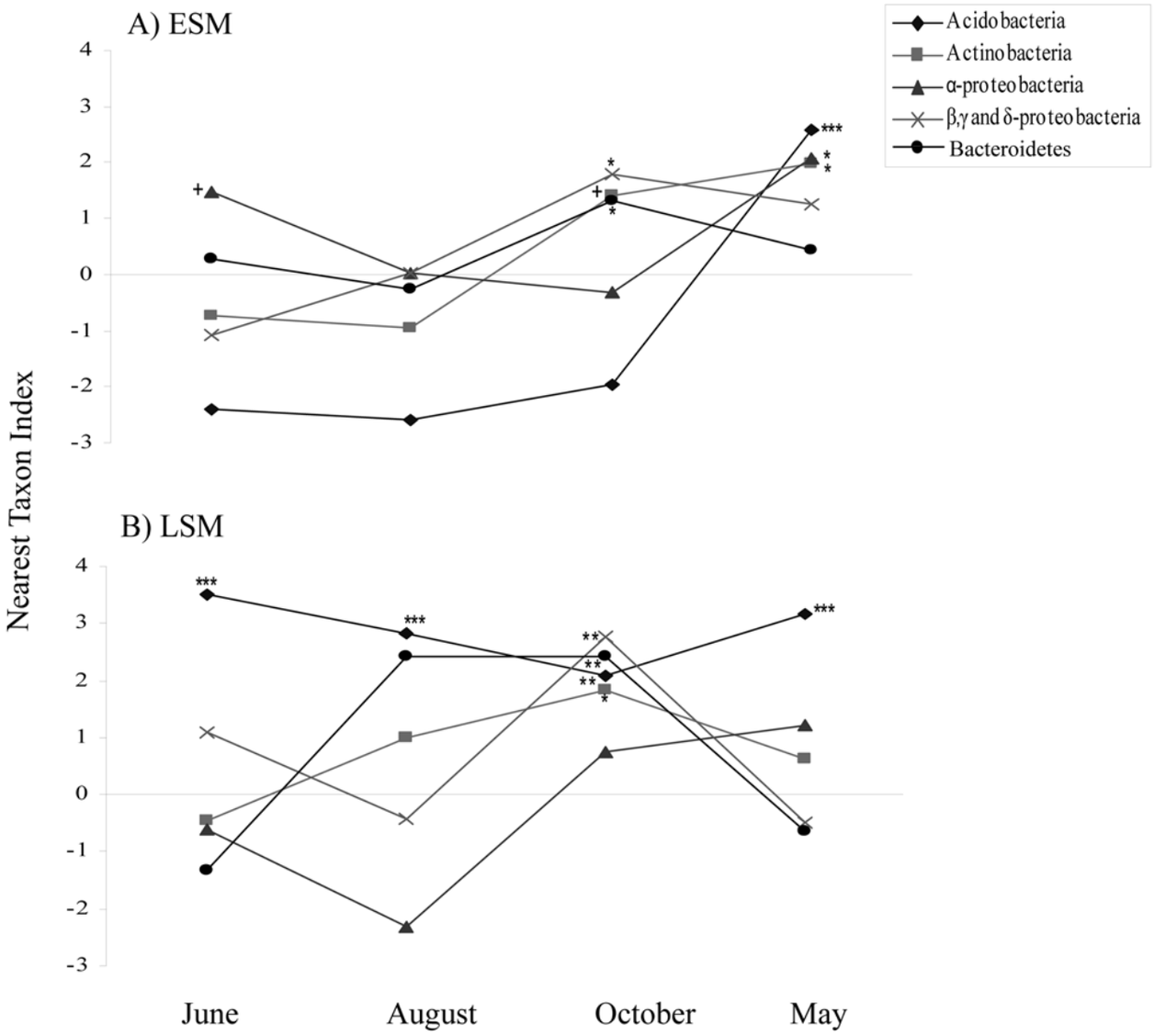


FIGURE 2. Seasonal variation in the phylogenetic structure of bacterial communities. (A) ESM and (B) LSM. A phylogenetic tree was obtained for each taxon. The significances of NTI estimates are as in Figure 1.

(soil pH < 6). Soil pH may therefore overwhelm the effect of other conditions that are yet less stressful (e.g. higher nutrient availability or temperatures). Second, Goldfarb et al. (2011) recently showed that the addition of complex carbon compounds in soils, such as lignin, cellulose, or tannins, reduces phylogenetic clustering of bacteria when compared with the addition of labile C (i.e. glycine or sucrose). They attributed this result to the higher functional redundancy of organisms able to thrive on labile C-pools. We then believe that high NTI values could be due to highly diversified phyla in terms of C-substrates that are yet highly similar phylogenetically when labile C is not limited (e.g. *α-Proteobacteria*, *Bacteroidetes*), as suggested previously (Horner-Devine and Bohannan, 2006).

During the growing season, (i.e. June and August), root development and the resumption of root exudation increases soil heterogeneity and nutrient availability. One should therefore expect the overdispersion of bacterial communities due to either niche diversification following more intense competitive interactions for resource acquisition. Although only ESM bacterial communities tended to follow this pattern at the community level (Table 1), this trend was not that clear when considering each phylum separately (Fig. 2, part A), except for *Acidobacteria*, for the reasons explained above. The clustering of LSM communities is again mainly due to *Acidobacteria*. However, *α-Proteobacteria* tended rather to be overdispersed, especially in August, during the peak of standing biomass. This clade usually increases in abundance in the rhizosphere or with the addition of labile-C (Fierer et al., 2007). *α-Proteobacteria* seems therefore to be subjected to competitive interactions for root exudates and other labile C pools during the growing season.

Interestingly, we found strong a phylogenetic clustering of β-, γ-, *δ-Proteobacteria*, *Bacteroidetes*, and *Actinobacteria* com-

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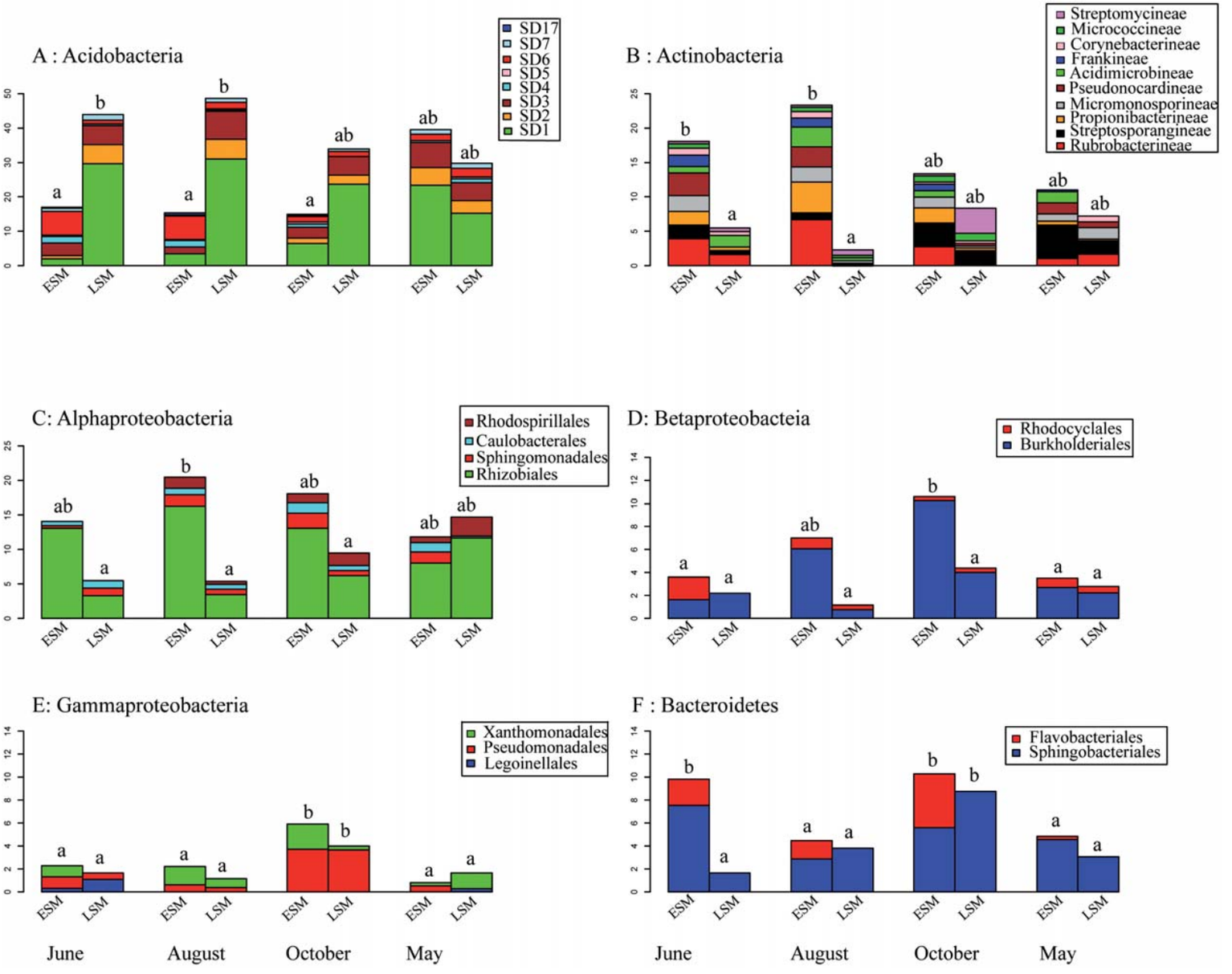


FIGURE 3. Relative abundance of bacterial phyla and class. (A) *Acidobacteria*, (B) *Actinobacteria*, (C) *α-Proteobacteria*, (D) *β-Proteobacteria*, (E) *γ-Proteobacteria*, and (F) *Bacteroidetes*. Significant differences between the two studied locations and seasons are indicated by small letters.

munities in both ESM and LSM in October, which is likely to be related to plant senescence and the onset of biomass decomposition. For *Actinobacteria*, this clustering was concomitant with the increase of the genus *Thermomonaspora* from the *Streptosporangiaceae* family, (data not shown); representatives of this genus are known to harbor lignin and cellulose degrading enzymes (Tuncer and Ball, 2002). For the other mentioned phyla, the increase of *Pseudomonadales*, *Burkholderiales*, *Flavobacteriales*, and *Sphingobacteriales* (Fig. 3, parts B, D, E, F) orders were concomitant with clustering. These orders comprise heterotrophs associated with the degradation of complex organic matter (Cottrell and Kirchman 2000). Moreover, *β-Proteobacteria* and *Bacteroidetes* have been related to the high carbon mineralization rate (Fierer et al., 2007) and become more abundant in tannin-/lignin-rich environments (Goldfarb et al., 2011). The shift of nutrient resources from simple molecules secreted by root exudates to complex substrates contained in plant litter may thus contribute to this phylogenetic clustering, as different enzymatic pathways could be particular to certain taxa.

In May, the shift of soil pH in ESM induced a phylogenetic clustering of *Acidobacteria*, according our previous findings (Zinger et al., 2009). But the analyses presented here revealed other significant changes of the phylogenetic structure of bacterial communities in ESM. Indeed, both *α-Proteobacteria* and *Actinobacteria* were phylogenetically clustered (Fig. 2, part A). This feature cannot be attributed to soil pH given those taxa did not show any particular pattern in LSM. Rather, such a change is likely to be the result of long freezing periods, a flush of mineral nutrients (Baptist and Choler, 2008), and/or the absence of plant activity. The clustering of *Actinobacteria* is again due to the *Streptosporangiaceae* family probably involved in litter degradation (see above). In contrast, the clustering of *α-Proteobacteria* cannot be identified at the order level, and suggests that the environmental filtering applies at finer taxonomic resolution.

The temporal variations results provide further support for the recently proposed conceptual model of copiotrophic/oligotrophic lifestyles (Fierer et al., 2007). This model suggests that certain phyla display dominant trophic behavior. Copiotrophs (*β-Proteobacteria, Bacteroidetes*) display a high temporal variability in population size, driven by substrate availability, while oligotrophs (*Acidobacteria*) display low variability and are outcompeted by copiotrophs in high-resource environments. Although the methodology used here does not enable abundance to be quantified empirically, we found that the phylogenetic composition of *Acidobacteria* typically reflects oligotrophic behavior, while the increase of *β-Proteobacteria* and *Bacteroidetes* after litter fall is consistent with their copiotrophic lifestyle.

The bacterial community's composition and phylogenetic structure respond very quickly to environmental changes, even after drastic events such as plant senescence (autumn) and soil pH drop (late winter). Such a dynamic suggests that alpine soil bacterial communities display strong resilience/resistance capacities probably due to the presence of clades differing in their ecological lifestyle. Resistance of bacterial communities seems to occur in LSM soil, given that specific clades dominate all year-round probably selected to cope with harsh conditions. In contrast, the phylogenetic turnover is high in ESM soils suggesting a high functional diversity. Changes in snow cover regimes may lead to a durable acidification of ESM soils, as in LSM, with the concomitant decrease on functional diversity. It is worth pointing out that even in this extreme case, specific clades would be recruited for the organic matter degradation in autumn as we observed in LSM soils. Further work is needed to consider the scenario of reduction of snow cover and the concomitant soil alkalinization in LSM.

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