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ORIGINAL ARTICLE

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Drivers of bacterial beta diversity in two temperate forests

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Abstract Although the consequences of changes in microbial diversity have received increasing attention, our understanding of processes that drive spatial variation in microbial diversity remains limited. In this study, we sampled bacterial communities in early and late successional temperate forests in Northeast China, and used distance-based redundancy analysis to examine how different processes influence bacterial beta diversity and phylogeny-based beta diversity using the Bray–Curtis and UniFrac metrics, respectively. After controlling for sampling effects, bacterial beta diversity in both forests was higher than expected by chance, which indicates that the bacterial community showed strong intraspecific aggregation. Both environmental filtering and dispersal limitation contributed to bacterial beta diversity and phylogeny-based beta diversity in the two forests. However, the relative importance of these different processes varied between the two forests. In the early successional forest, dispersal limitation played a dominant role in structuring the bacterial community, whereas the effects of environmental filtering were more important in the late successional forest. Our study revealed that bacterial beta diversity and phylogeny-based beta diversity in forest communities from the same region are regulated by different forces and that the relative importance of different forces varies over succession.

Keywords 16S rRNA gene pyrosequencing · Environmental filtering · Dispersal limitation · Operational taxonomic unit (OTU) · Phylogeny

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Introduction

Understanding the processes that underlie variation in community composition (i.e., beta diversity) is a central goal in ecology. However, because different processes can result in similar patterns of beta diversity (Myers et al. 2013), determining the factors that drive beta diversity of large organisms has been proven to be difficult (e.g., Legendre et al. 2009; Kraft et al. 2011; Myers et al. 2013). This task is even more complex for microbial organisms (Ferrenberg et al. 2013). Although microbial beta diversity received increasing attention in recent years (Martiny et al. 2011; Fierer et al. 2012; Ferrenberg et al. 2013; Sokol et al. 2013; Landesman et al. 2014; Beck et al. 2015; Li et al. 2015), our understanding of the processes that underlie microbial beta diversity remains limited and controversial. However, three principal hypotheses have been proposed to explain microbial beta diversity.

The first hypothesis is that microbial distributions are random and is herein called the "random placement hypothesis". This hypothesis states that microorganisms are randomly and globally distributed (Finlay and Clarke 1999), but does not account for the effects of environmental differences and other ecological processes, such as dispersal limitation. Under this hypothesis, microbial beta diversity should have low variability across space. This hypothesis seems reasonable because most microorganisms are small and abundant and because it has received empirical support (Finlay and Clarke 1999; Finlay 2002; Chu et al. 2010).

The second hypothesis is that "everything is everywhere and the environmental selects", herein called the "environmental filtering hypothesis". This hypothesis emphasizes the role of environmental heterogeneity. Several environmental factors, such as soil pH, salinity,

carbon, and vegetation, have been found to influence patterns of microbial diversity (Fierer and Jackson 2006; Nemergut et al. 2010; Yergeau et al. 2010; Monroy et al. 2012; Landesman et al. 2014; Navarrete et al. 2015). However, the relative effect of these factors varies in different communities and regions, and this hinders our understanding of how environmental factors affect microbial diversity.

Recent studies showed that dispersal limitation can also strongly influence beta diversity of microbial communities (Martiny et al. 2011; Ferrenberg et al. 2013), because it allows historical contingencies to affect current biogeographic patterns. We call this the "dispersal limitation hypothesis". If dispersal limitation is the key driving factor of biogeogracphic patterns, spatial distance should serve as the most powerful predictor of different microbial community dynamics, because spatial distance in this case is related to the influence of historical events that have remained because of spatial isolation among populations (Ferrenberg et al. 2013).

It is clear that each of the three above-mentioned hypotheses represent different ecological and evolutionary processes, and may explain patterns of beta diversity in different microbial communities. Ultimately, these processes interact to generate and maintain microbial diversity. However, quantifying the relative role of each of these processes on microbial beta diversity remains a challenge. Recently, variation partitioning methods have been applied to detect the relative importance of different processes on beta diversity (Legendre et al. 2009; Yergeau et al. 2010; Myers et al. 2013). Environmental filtering is likely to play a significant role if the beta diversity pattern is mostly explained by environmental factors, whereas dispersal limitation is likely to exert a dominant influence if the beta diversity pattern is mostly explained by spatial factors. The unexplained variation in beta diversity may result from local stochasticity (Legendre et al. 2009), unmeasured environmental and spatial factors (Borcard et al. 2004), or sampling effects that result from variation in gamma diversity (i.e., regional species pool; Chase and Myers 2011; Kraft et al. 2011; Myers et al. 2013). The first two factors are widely recognized; however, the importance of species pool composition influence on beta diversity is only just beginning to be examined for macroorganisms (Kraft et al. 2011; DeCaceres et al. 2012; Myers et al. 2013) and are still poorly understood for microorganisms (Ferrenberg et al. 2013). In a recent study on beta diversity in temperate and tropical forests, Myers et al. (2013) demonstrated that differences in species pool can explain a high proportion of the beta diversity pattern for macroorganisms, such as trees. Clearly, there are obvious differences between macroorganisms and microorganisms, such as size and abundance; therefore, it is important to test whether the species pool also significantly affects microbial beta diversity.

It is evident that the three above-mentioned hypotheses and the processes that can drive microbial beta diversity are not mutually exclusive. However, the relative importance of different processes on microbial beta diversity remains largely controversial (Nemergut et al. 2013). In this study, we tested the three hypotheses to determine the relative contribution of environmental filtering and dispersal limitation on bacterial beta diversity and phylogeny-based beta diversity in two temperate forests in Northeast China, one early and one late successional forest. To study beta diversity, we followed the approach described in Myers et al. (2013), who examined beta diversity of macroorganisms. We first tested the random placement hypothesis, which predicts that bacteria are randomly distributed. We determined the beta diversity of bacteria in both forests and evaluated whether the diversity differed from a null model generated by randomly sampling from the species pool in each forest. If the observed beta diversity in the two forests does not significantly differ from the expectation of the null model, the random placement hypothesis cannot be rejected. This would indicate that bacterial beta diversity in the two forests was not influenced by specific processes. Rejection of the null model would indicate that bacterial beta diversity was influenced by processes such as environmental filtering or dispersal limitation (Myers et al. 2013). Second, we used variation partitioning analyses to disentangle the relative importance of environmental filtering and dispersal limitation on bacterial beta diversity and phylogeny-based beta diversity. We also tested the influence of the species pool on bacterial beta diversity by evaluating the species pool. If the species pool had a similar influence to what has been reported for macroorganisms, the unexplained variation of bacterial beta diversity would significantly decrease after incorporating the effects of the species pool into the model (Myers et al. 2013). Finally, we tested whether the relative contributions of environmental filtering, dispersal limitation, and species pool on bacterial beta diversity and phylogeny-based beta diversity were similar in the two forests.

Methods

Site description and soil sampling

To determine which processes drive bacterial beta diversity in temperate forests, we sampled soil from two forests in Northeast China in June 2010. Both forests are mixed forests with broad-leaved deciduous tree and conifers, but at different successional stages; an early successional forest (approximately 80 years) and a late successional forest (approximately 300 years). *Pinus koraiensis* and *Tilia amurensis* were the common tree species in the late successional forest, whereas *Betula platyphylla* and *Populus davidiana* were common in the early successional forest. We selected a 150 m × 150 m plot for each forest, and collected soil samples at a regular grid at intervals of 30 m (Li et al. 2014). In total, 36 soil samples were collected from each forest. To collect soil samples, we first removed the litter on the

forest floor, and then used a PVC core (5 cm diameter) to remove soil up to 10 cm depth. Each field-moist sample was homogenized and sieved to 4 mm and then divided into two subsamples within 48 h of sampling. One subsample was kept at 4 °C for measuring soil properties; the other subsample was stored −80 °C for DNA extraction.

Bacterial community composition analysis

We followed the protocol described in Li et al. (2005) but with a few modifications to extract the DNA from the soil samples. Primers 27F and 534R, which included a sequencing adapter (454 Life Science's A or B), were used to amplify the variable region V1–V3 of 16S rRNA. During sequencing, an 8-base pair barcode was included in the 534R primer for sample multiplexing. Amplicons amplified with one set of barcoded primers were pooled, and equimolar concentrations were pyrosequenced at the Institute for Bioinformatics and Evolutionary Studies (IBEST; University of Idaho, Moscow, ID, USA) on a Roche FLX 454 automated pyrosequencer.

Raw bacterial sequence data were obtained using Mothur v1.12.2 (Schloss et al. 2009). After removing the tag and primer sequences, sequences were trimmed and parsed into different samples. The high-quality sequences (with scores >25) were filtered to obtain sequences that were 200–550 nt long. Uchime v4.1 was used to perform chimera detection (Edgar et al. 2011). Based on the Silva SSU 16S rRNA reference database (v108; Pruesse et al. 2007), the unique sequences were then identified. A random subset of a maximum of 1000 sequences from each sample was used for the following analysis; for samples with less than 1000 reads, all reads were included. Mothur v1.12.2 (Schloss et al. 2009) was used to conduct operational taxonomic unit (OTU) clustering with a 0.03 cutoff, which estimates species-level bacterial biodiversity. Acidobacteria, verrucomicrobia, bacteroidetes, and chloroflexi were the dominant phyla in both forests. Detailed descriptions of the techniques used for gene pyrosequencing and bacterial community composition can be found in Li et al. (2014). The sequences obtained in this study were uploaded and made available at the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under accession number SRP028799 (Biosample numbers SAMN02222467–SAMN02222628). Because OTUs with one sequence have a disproportionately large influence on beta diversity relative to their actual abundances, we pruned OTUs with only one sequence. In total, we recorded 2881 OTUs in the late successional forest and 2931 OTUs in the early successional forest; 1219 OTUs were identical in both forests. Bacterial community comparisons (beta diversity) were performed using the abundance-based Bray–Curtis and phylogeny-based UniFrac metrics.

Environmental factors

Soil factors

The soil factors described below were measured for all samples and used in the analyses (Table S1). Organic carbon (OC) was measured using a HT1300 TOC analyzer (Analytik jena, Germany). Total nitrogen (TN) and total sulfur (TS) were measured using a 2400II CHN elemental analyzer (PerkinElmer, USA). Soil C/N was computed using OC and TN values. Soil pH was determined using a glass electrode at a 2.5:1 water:soil ratio. Total phosphorus (TP) was measured by the Mo–Sb Anti-spectrophotometric method, and total potassium (TK) was detected by flame atomic absorption spectrophotometer. Aluminum ion (Al^{3+}) was measured by colorimetry. Hydrogen cation (H^{+}) concentration was measured by the potassium chloride extraction-titration method. Cation exchange capacity (CEC) was determined by the ammonium acetate method. Soil texture (% sand, silt, and clay) was determined based on hydrometer analyses.

Vegetation

To quantify the effect of vegetation, we censused all trees with a diameter at breast height ≥1 cm within 10 m around each soil sample and summed tree species richness, abundance, and basal area. The area within 10 m was measured, because trees do not tend to interact beyond 10 m (Wang et al. 2010).

Spatial factors

We used spatial eigenfunctions generated from Principal Coordinates of Neighbor Matrices (PCNM) across the coordinates of all samples in each forest as spatial factors. The PCNM factors represent the complete spatial structure among all samples better than the coordinates of all samples or the polynomials of the coordinates (Borcard et al. 2004). For each forest, 25 PCNM eigenfunctions with positive eigenvalues were included in analysis.

Statistical analyses

Observed and predicted beta diversity were compared using the approach described in Myers et al. (2013) and Ferrenberg et al. (2013). In brief, a null model approach was applied to compare the observed bacterial beta diversity to the expected beta diversity generated by randomly sampling from the species (i.e., OTU) pool in each forest. The species (OTU) pool was defined as the total OTU number and total abundance of each OTU among all samples in each forest. We used the abundance-based Bray–Curtis metric to calculate the dissim-

ilarity among all samples as observed beta diversity in each forest. We then randomly sampled each OTU from the species (OTU) pool in each forest while controlling for the relative abundance of each OTU in the OTU pool and the total abundance in each sample. We ran 9999 simulations of the null model and computed a standardized effect size (i.e., beta deviation) by calculating observed beta diversity minus the mean expected beta diversity, which was then divided by the standard deviation of expected beta diversity. A beta deviation of zero indicates a random distribution of bacteria, whereas a positive beta deviation indicates an aggregated distribution of bacteria, and a negative beta deviation indicates an even distribution of bacteria (Myers et al. 2013). We then used multivariate dispersion tests (Anderson 2006) to test the difference of bacterial beta diversity, beta deviation, and phylogeny-based beta diversity between the late and early successional forests.

To measure the effect of environmental and spatial factors, distance-based redundancy analysis was conducted to partition variation in observed bacterial beta diversity, beta deviation, and phylogeny-based beta diversity (UniFrac) into different fractions explained by environmental and spatial factors (Myers et al. 2013). Environmental factors included soil and aboveground biotic factors. Because there was strong collinearity among particular environmental factors, we first removed environmental factors that were highly correlated with other factors ($r > 0.6$) and then performed forward selection ("forward.sel" function in the R package packfor 0.0–8) to select environmental factors with a significant effect on beta diversity, beta deviation, and phylogeny-based beta diversity. Similarly, forward selection was also applied to the PCNM variables. The explanatory environmental and PCNM variables retained in forward selection were then used to partition variation ("varpart" function in the R package vegan 2.0–10; Oksanen et al. 2012) in observed beta diversity, beta deviation, and phylogeny-based beta diversity into fractions of variation explained by environmental, spatial, and spatially structured environmental factors for each forest. All analyses were conducted in R 2.15.2 (R Development Core Team 2012).

Results

According to the Bray–Curtis metric, observed beta diversity was high and similar in both forests (multivariate dispersion test, $F = 0.22$, $P = 0.64$). Beta deviation was strongly positive in the two forests (Fig. 1). These results indicate that there is strong intraspecific aggregation of most bacterial OTUs. However, the beta deviation was marginally higher in the late successional than in the early successional forest (Fig. 1; multivariate dispersion test, $F = 2.98$, $P = 0.08$), which indicates that bacteria showed a slightly stronger aggregated pattern in the late successional forest.

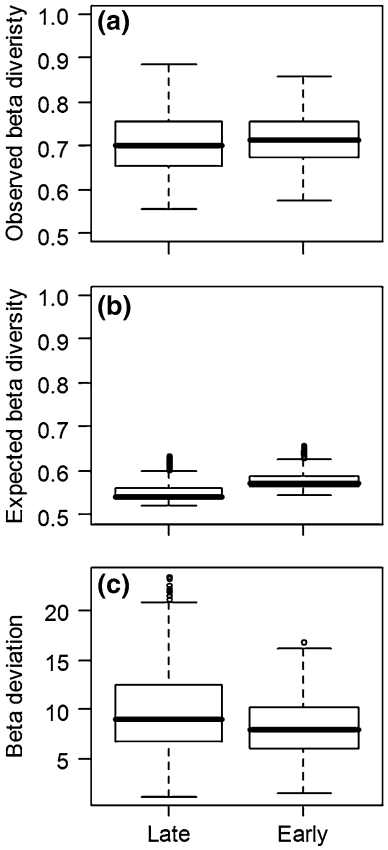

Fig. 1 *Box* plot of the abundance-based Bray–Curtis dissimilarity (beta diversity) of a late and an early successional forest. **a**, **b**, and **c** are shown as observed beta diversity, expected beta diversity, and beta deviation of soil bacterial communities, respectively. The *bottom* and *top* of each box represent the first and third quartiles, respectively. The *whiskers* represent values outside the *upper* and *lower* quartiles

Both environmental and spatial factors explained a large percentage of variation in beta diversity and beta deviation in both forests. The unexplained variation in the early successional forest (33.2 % for beta diversity and 35.5 % for beta deviation) was lower than that in the late successional forest (59.1 % for beta diversity and 66.2 % for beta deviation; Fig. 2). Thus, in both forests, the unexplained variation did not decrease as expected after accounting for the effect of species (OTU) pool. Environmental factors explained a larger fraction of the beta diversity and beta deviation in the late successional forest, whereas spatial factors contributed more in the early successional forest (Fig. 2). The environmental factors that were significantly related to beta diversity and beta deviation also differed between the two forests (Table 1). For example, pH explained 18.5 % of total variation in beta diversity and 17.4 % in beta deviation in the late successional forest, whereas Al^{3+} accounted for 20.6 % of total variation in beta diversity and 16.4 % in beta deviation in the early successional forest.

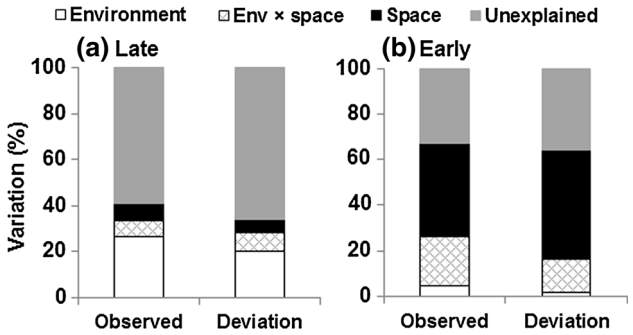

Fig. 2 Abundance-based Bray–Curtis dissimilarity (beta diversity) of soil bacterial communities in a late (**a**) and an early (**b**) successional forest. The percentage of variation explained by environmental and spatial factors is shown

The results of the weighted UniFrac metric were also similar to those found in the Bray–Curtis metric analysis; environmental factors contributed more than spatial factors in the late successional forest, whereas spatial factors contributed more than environmental factors in the early successional forest (Fig. 3).

Discussion

In this study, we aimed to discriminate among three competing hypotheses that represent different ecological processes and mechanisms that can explain bacterial beta diversity and phylogeny-based beta diversity in two temperate forests. Although the random displacement hypothesis explained soil bacterial diversity in some regions (Finlay and Clarke 1999; Finlay 2002; Chu et al. 2010), we found no support for this hypothesis in our study, because observed beta diversity in both forests was significantly higher than predicted by this hypothesis. This result was also confirmed by the large amount of variation in bacterial beta diversity in our study that was explained by both environmental and spatial factors.

Many studies have demonstrated that environmental factors, such as those related to resources and habitat quality, are important in influencing bacterial community diversity (e.g., Fierer and Jackson 2006; Nemergut et al. 2010; Yergeau et al. 2010; Monroy et al. 2012; Landesman et al. 2014). In our study, environmental factors significantly affected bacterial beta diversity in both forests, but the specific effects of these factors differed between the two forests. For example, pH has been shown to be an important factor that explains variation in bacterial diversity between different regions or at different spatial scales (Yergeau et al. 2010; Griffiths et al. 2011; Landesman et al. 2014). In our study, pH was strongly correlated with bacterial beta diversity and phylogeny-based beta diversity in the late successional forest, but it did not explain variation in the early successional forest. It is important to note that, although we measured a variety of soil factors, it may be possible that unmeasured environmental factors, such as soil salinity

Table 1 Variation in observed beta diversity and deviation (Abundance-based Bray–Curtis metric), and phylogeny-based beta diversity (Weighted Unifrac metric) explained by significant environmental and spatial variables used in the distance-based redundancy analyses in late and early successional forests

Variables	Abundance-based Bray–Curtis				Weighted UniFrac	
	Observed		Deviation			
	Late	Early	Late	Early	Late	Early
Environment: soil						
pH	0.19**		0.17**		0.26***	
Total phosphorus	0.10*					
Total nitrogen						0.06*
Total sulfur	0.06*		0.11*			0.06*
Total potassium		0.06*				
AL^{3+}		0.21***		0.16**		
$H+$						
Space: PCNM eigenfunctions						
PCNM1	0.14**		0.14**		0.09*	
PCNM2		0.10**		0.10**		
PCNM3						0.13**
PCNM4		0.09*		0.10*		0.08*
PCNM5		0.09**		0.08*		0.07*
PCNM10						
PCNM11		0.05*		0.05*		
PCNM13		0.04*		0.05*		
PCNM14		0.08*		0.09**		
PCNM16						
PCNM18		0.05*		0.05*		
PCNM19		0.08*		0.08*		0.04*
PCNM22						
PCNM24		0.04*		0.04*		0.05*

*, **, and ***, represent $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively

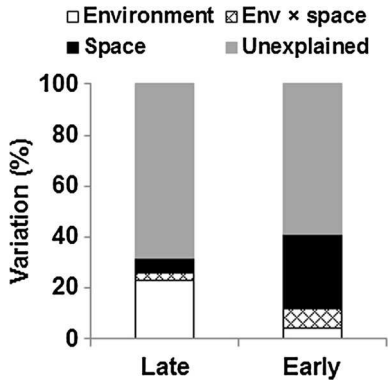

Fig. 3 Phylogeny-based beta diversity using the weighted UniFrac metric of soil bacterial communities in a late and an early successional forest. The percentage of variation explained by environmental and spatial factors is shown

and heavy metals, could be responsible, at least in party, for the variation that we could not explain. It may be that the importance of soil factors were underestimated in our study, and future studies should attempt to examine a more complete set of soil factors.

It is well established that vegetation, an important biotic environmental factor, can also impact microbial diversity (e.g., Stephan et al. 2000; Kowalchuk et al. 2002; Prescott and Grayston 2013). In our study, we found no significant effect of vegetation on bacterial beta diversity and phylogeny-based beta diversity. Possible reasons may include that (1) there were no top-down effects on microbial diversity, which was also observed in several other studies that found undetectable or only minor relationships between plant and microbial diversity (Kielak et al. 2008; Bardgett and Wardle 2010); and (2) the summary statistics we used (species richness, abundance, and basal area) did not represent above-ground plant factors well. Many researchers have argued that the identity of plants within a community and factors, such as plant species composition, have a more important impact on the diversity of other trophic levels than plant diversity or abundance per se (Smalla et al. 2001; Kowalchuk et al. 2002; Bardgett and Wardle 2010; Bezemer et al. 2010).

The importance of spatial factors for influencing microbial diversity is increasingly recognized; they may even have a stronger effect than environmental factors, which emphasizes the important role of dispersal limitation in influencing microbial diversity (Martiny et al. 2011; Ferrenberg et al. 2013). Our results showed that the spatial factors were most dominant in the early successional forest, which indicates that there was a strong effect of dispersal limitation in influencing bacterial diversity in this forest. We speculate that bacteria experienced weak competition at the beginning of secondary succession, and that this resulted in ecological equivalence (Leibold and McPeek, 2006). However, environmental filtering was more important in the late successional forest. Several researchers have suggested that dispersal limitation may play a dominant role in influencing community assembly within successional stages, whereas environmental filtering may be more important during successional transition periods (Ellner and Fussmann 2003; Cadotte 2007; Ferrenberg et al. 2013). This indicates that the late successional forest we analyzed might be in a transition stage (e.g., from early to late succession). Alternatively, it is possible that other factors, such as disturbance, differed between the two forests that we studied. In the late successional forest, we observed some small-scale disturbances, such as treefalls via wind or senescence (Wang et al. 2009), which may have increased small-scale habitat heterogeneity.

Although both environmental and spatial factors contributed to bacterial beta diversity and phylogeny-based beta diversity in the two forests, some variation in bacterial beta diversity and phylogeny-based beta diversity remained unexplained. Unexplained variation in beta diversity can arise from local stochastic processes, unmeasured environmental and spatial factors, and sampling effects, because of variation in gamma diversity (i.e., the regional species pool). After controlling for sampling effects, we found that the amount of unexplained variation was similar in both forests. These results indicate that the unexplained variation in bacterial beta diversity in our study may have resulted from stochastic processes and unmeasured environmental and spatial factors, but that it was not caused by sampling effects. These results differ from those of studies that focused on macroorganisms. For example, Myers et al. (2013) found that the regional tree species pool explained a high proportion of the variation in beta diversity of tree species in both tropical and temperate forests. The difference in our results may be due to bacterial richness (OTU richness, nearly 10,000) being much higher than tree species richness (several hundred). More studies are needed to explore whether our results could be extrapolated to other microbial communities.

It is important to note that our analyses were only conducted in two forests, and data on soil microbes in more forests, such as forests in different successional stages, should be collected and analyzed in further studies to confirm the results found here. Moreover, we focused on a relatively local scale; the maximum distance between samples within each forest was only 1000 m. We only sampled soil in one tree community in each of the two forests. The costs of the method we used (pyrosequencing of the bacterial 16S rRNA gene) prevented sampling more communities in each forest. Consequently, the amount of variation that exists among different tree communities that originate from a single forest remains to be examined. Finally, we emphasize that different OTUs within the bacterial community may be functionally redundant, and trait-based analyses may provide important additional information about community assembly processes (Oliver 1996). Further studies should consider functional similarity among these bacterial OTUs.

In this study, we conducted a comprehensive analysis on the drivers of bacterial beta diversity and phylogeny-based beta diversity in two temperate forests. The bacterial community showed strong intraspecific aggregation, and both environmental filtering and spatial factors contributed to bacterial beta diversity and phylogeny-based beta diversity in the two forests, whereas sampling effects caused by differences in regional species pools had minor effects. Dispersal limitation played a dominant role in structuring the bacterial community in the early successional forest, whereas environmental filtering was more important in the late successional forest. Drivers of bacterial beta diversity and phylogeny-based beta diversity may influence ecosystem processes, and a better understanding of the processes that underlie bacterial beta diversity and phylogeny-based beta diversity, and where and when influence of these processes may change will be vital for understanding ecosystem function.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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