

LETTER

Stabilising role of seed banks and the maintenance of bacterial diversity

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Abstract

Coexisting species often exhibit negative frequency dependence due to mechanisms that promote population growth and persistence when rare. These stabilising mechanisms can maintain diversity through interspecific niche differences, but also through life-history strategies like dormancy that buffer populations in fluctuating environments. However, there are few tests demonstrating how seed banks contribute to long-term community dynamics and the maintenance of diversity. Using a multi-year, high-frequency time series of bacterial community data from a north temperate lake, we documented patterns consistent with stabilising coexistence. Bacterial taxa exhibited differential responses to seasonal environmental conditions, while seed bank dynamics helped maintain diversity over less-favourable winter periods. Strong negative frequency dependence in rare, but metabolically active, taxa suggested a role for biotic interactions in promoting coexistence. Together, our results provide field-based evidence that niche differences and seed banks contribute to recurring community dynamics and the long-term maintenance of diversity in nature.

KEYWORDS

bacterioplankton, community dynamics, dormancy, negative frequency dependence, seasonality

INTRODUCTION

The maintenance of biodiversity is important for regulating species interactions, stabilising ecosystem functions and promoting resilience in response to perturbations. Diversity is maintained by many processes, including niche differentiation in resource use (Gudelj et al., 2010; Johnson et al., 2012; Tilman, 1982), defensive abilities (Cadier et al., 2019; Leibold, 1996; Thingstad et al., 2014) and abiotic constraints (Holt, 2009). These stabilising niche differences among species contribute to the maintenance of diversity by causing species to limit their own growth more than the growth of other species, thereby preventing competitive exclusion and allowing populations to recover from low abundances (Adler et al., 2007; Chase & Leibold, 2003; Chesson, 2000). Some stabilising mechanisms of coexistence rely on environmental fluctuations and can further increase the number of species

in a community (Chesson, 1994; Chesson & Huntly, 1997; Descamps-Julien & Gonzalez, 2005). For example, in seasonal environments, species that are favoured at different times of the year may be able to coexist in the community if they can survive through periods of unfavourable environmental conditions (Pake & Venable, 1996). Given the near-ubiquity of environmental variability, a central and unresolved question is how stabilising mechanisms promote the maintenance of diversity across the wide range of taxonomic groups and ecosystems that exist in nature.

Stabilisation from niche differences should generate negative frequency dependence (NFD) in population growth. The implication of NFD is that rare populations grow faster than common populations (Adler et al., 2007; Chesson, 2000). NFD may arise from mechanisms that promote coexistence not only in relatively constant environments, such as trade-offs in resource acquisition and

allocation, but also in temporally variable environments. In fluctuating environments, the storage effect is a coexistence mechanism that reflects the ability of species to grow well during favourable conditions while minimising losses during unfavourable conditions by ‘storing’ individuals in long-lived life stages (Chesson, 2000; Warner & Chesson, 1985). The storage effect requires that taxa differ in their responses to environmental conditions, that intraspecific limitation peaks during favourable conditions and that population growth is buffered in suboptimal environments (Angert et al., 2009; Cáceres, 1997; Pake & Venable, 1996). The storage effect may be particularly important in communities where species experience periods of extremely slow growth (Gray et al., 2019) or engage in various forms of dormancy, which are common among plants and animals, but also microorganisms (Lennon & Jones, 2011).

Support for stabilising coexistence has largely come from plant and animal communities (Adler et al., 2018; Angert et al., 2009; Cáceres, 1997; Yenni et al., 2017), while evidence for its role in complex microbial systems is less common (Zhang et al., 2009). In microbial communities, which contain a disproportionately large number of rare taxa (Lynch & Neufeld, 2015; Shade et al., 2018; Sogin et al., 2006), populations may vary widely in their stability and long-term contributions to diversity. Although rare taxa are prone to extinction (Lande, 1993), some persist for longer periods of time (Alonso-Sáez et al., 2015; Lynch & Neufeld, 2015; Newton & Shade, 2016). In fluctuating environments, many of these rare taxa can quickly respond to favourable conditions (Linz et al., 2017; Nyirabuhoro et al., 2020; Shade et al., 2014), suggesting that temporally variable opportunities for growth may be important for population persistence. While niche differences among bacterial taxa are well documented (Evans et al., 2014; Lennon et al., 2012; Meier et al., 2017), the long-term implications of these differences and their contribution to the maintenance of biodiversity in nature remain understudied.

A leading hypothesis for the long-term maintenance of microbial diversity has been coexistence mediated by dormant seed banks (Jones & Lennon, 2010; Lennon & Jones, 2011; Mestre & Höfer, 2021; Sorensen & Shade, 2020). Dormancy can buffer microbial populations in different ways (Rittershaus et al., 2013). For example, some species form physical resting structures that protect individuals from harsh abiotic stress (de Rezende et al., 2013; Setlow, 2006). Other species may reduce mortality associated with resource limitations by shifting energetic demands from growth to maintenance energy levels (Hoehler & Jørgensen, 2013; Lennon & Jones, 2011; Lever et al., 2015). Dormancy may even protect against top-down pressure from grazers (which may be unable to digest or extract energy from starved cells or endospores) and phage (which cannot replicate due to inactive host machinery) (Bautista et al., 2015; Kearney et al., 2018; Klobutcher et al., 2006; Pernthaler, 2005). Consequently,

dormant bacteria may exhibit reduced mortality in the environment (Hoehler & Jørgensen, 2013), thereby accumulating into seed banks until conditions improve (Wörmer et al., 2019). Much insight has been gained from short-term microbial experiments and analogies with plant and zooplankton communities, but evidence from long-term field studies demonstrating how the temporal dynamics of microbial seed banks help maintain diversity in fluctuating environments is lacking.

In this study, we tracked bacterioplankton dynamics over time in a north temperate lake using high-resolution molecular data to infer ecological processes that maintain microbial diversity. Bacterial communities in fluctuating aquatic environments often exhibit recurrent, seasonal community patterns (Fuhrman et al., 2015; Gilbert et al., 2012; Shade et al., 2007; Ward et al., 2017), but the potential mechanisms that contribute to cyclical dynamics and maintain diversity in nature are poorly resolved. We characterised how persistent (and putatively coexisting) taxa respond to environmental fluctuations and used null models to assess whether stabilising biotic interactions (e.g. self-limitation, as evidenced by strong NFD) help maintain rare, but metabolically active, taxa in the community (Rovere & Fox, 2019; Yenni et al., 2017). Specifically, we compared patterns of NFD and population dynamics in the active and total portions of the community (inferred by 16S rRNA transcripts and genes, respectively) to quantify the importance of slow growth or dormancy strategies for the maintenance of diversity. Our results provide empirical evidence that stabilising biotic interactions and seed bank dynamics underlie seasonal community dynamics and play key roles in maintaining bacterial diversity in natural ecosystems.

MATERIALS AND METHODS

Study site and sampling

University Lake is a 3.2 ha meso-eutrophic reservoir located in the Indiana University Research and Teaching Preserve, Bloomington, IN, USA (39°11' N, 86°30' W). The surrounding watershed is dominated by oak, beech and maple forests. Three streams drain into University Lake, which has an estimated volume of 150,000 m³ and a maximum depth of 10 m. From April 2013 to September 2015, we took weekly water samples (1 L) from the epilimnion using a 1 m depth-integrated sampler for microbial biomass and measured environmental variables commonly associated with aquatic microbial community dynamics: total phosphorus (TP), total nitrogen (TN) and dissolved organic carbon (DOC). Microbial biomass was filtered onto 0.2 µm Supor filters (Pall, Port Washington, NY, USA) and frozen at -80°C. We quantified TP using the ammonium molybdate method (Wetzel & Likens, 2000) and TN with the second derivative method after persulfate digestion (Crumpton et al.,

1992). DOC was quantified on 0.7 μm filtrates using non-dispersive infrared (NDIR) detection on a Shimadzu TOC-V (Kyoto, Japan). We also quantified water transparency with a Secchi disk and used a Quanta Hydrolab (OTT, Kempton, Germany) water sonde to measure temperature, conductivity, dissolved oxygen, salinity and pH in the lake.

Bacterial community structure

We characterised the structure of the bacterial community using high-throughput 16S rRNA sequencing. We extracted total nucleic acids from biomass retained on 0.2 μm filters using the MoBio PowerWater RNA extraction kit and the DNA elution accessory kit. Because DNA is found in metabolically active and inactive (e.g. slow growing or dormant) individuals, we interpret sequences from this pool as the ‘total’ community. In contrast, RNA is a more ephemeral molecule that is essential for synthesising proteins; therefore, we interpret sequences from this pool as the metabolically ‘active’ subset of the community (Locey et al., 2020; Molin & Givskov, 1999; Steiner et al., 2019). We sequenced libraries (see detailed methods in Supplementary Information) and created 97% similar operational taxonomic units (OTUs). To account for variation in sequencing depth, subsequent analyses were performed on rarefied abundance data subsampled to the fewest number of reads in the time series ($N = 5979$ per sample) using R (version 4.0.5) (R Core Team, 2020).

Differential responses to environment

We evaluated whether niche partitioning occurred along with a suite of environmental variables. First, we performed a principal component analysis (PCA) on Hellinger-transformed abundances to visualise seasonal patterns of compositional trajectories. Next, we identified environmental drivers of community dynamics using redundancy analysis (RDA). Because temperature explained much of the variation in community structure in the RDA, we then looked more closely at the persistent, and potentially coexisting, subset of taxa in the community (OTUs present in $\geq 80\%$ of the DNA-based samples, Table S1) and explored how their abundances varied along the observed temperature gradient (see Supporting Information).

Stabilising niche differences

To test if niche differences contributed to patterns of negative frequency dependence (NFD) in the community, we examined (1) whether growth exhibited negative frequency dependence overall, which is indicative

of stabilisation in the community and (2) whether rare taxa experienced stronger negative frequency dependence than common taxa (Rovere & Fox, 2019; Yenni et al., 2012, 2017). Patterns of NFD often arise from density-dependent processes, such as nutrient limitation, but density dependence will only generate NFD if species limit their own growth more strongly than they limit the growth of other species (Adler et al., 2007). In a community of relatively constant density (see Figure S1), such patterns of NFD shed light on coexistence for three reasons. First, taxa are more likely to be common in the community when they are environmentally favoured (or less disfavoured) relative to other taxa in the community. Second, taxa that experience strong intraspecific limitation during environmentally favourable periods should grow faster when rare than when common, thereby generating NFD. Third, differences among taxa in the strength of self-limitation during relatively favoured growth periods should lead to different average relative abundances in the community, implying that rare yet persistent taxa may be strongly stabilised (Rovere & Fox, 2019; Yenni et al., 2012, 2017). However, metabolically inactive individuals are less likely to engage in the biotic interactions that generate NFD.

We then calculated NFD for each OTU by comparing rates of change in relative abundance between weekly samples. We inferred the strength of NFD for a given OTU as the magnitude of the negative slope of the relationship between an OTU’s relative abundance and its per capita growth rate at each time step (t) across the time series. We calculated the relative abundance ($x_{t,s}$), of each OTU (s) as its abundance ($N_{t,s}$) in the community of s OTUs relative to the total abundance of all s OTUs ($\sum_s N_{t,s}$) at a given time step (t), such that $x_{t,s} = \frac{N_{t,s}}{\sum_s N_{t,s}}$.

From this, we then calculated the natural logarithm of the per capita growth rate of each OTU as $y_{t,s} = \log_e \left(\frac{N_{t+1,s}}{N_{t,s}} \right)$. When an OTU was absent from a sam-

ple, we replaced absences with half the abundance of the lowest detectable quantity (i.e. half a sequence read or 0.5), effectively assuming presence below the detection threshold as reported elsewhere (Rovere & Fox, 2019). To estimate the strength of NFD for each OTU, we fit simple linear regressions ($y_{t,s} = \beta_{0,s} + \beta_{1,s}x_{t,s} + \epsilon_{t,s}$), where the degree of NFD is the slope, $\text{NFD} = \beta_{1,s}$. We inferred the equilibrium frequency of an OTU (f) as its mean relative abundance (Rovere & Fox, 2019). In the end, f describes whether an OTU is common or rare, and negative slopes with greater magnitudes indicate stronger negative frequency dependence.

Stabilisation of rare bacterial taxa

We then inferred whether rare taxa exhibited stronger NFD than expected by chance. Stabilisation of rare taxa

would be supported if OTUs with lower equilibrium frequencies (smaller values of f) had more negative slopes (larger $|\beta_{1,s}|$) indicating stronger self-limitation. We eval-

uated the overall relationship between rarity and strength of NFD from the covariance between the $\log(\text{NFD})$ and $\log(f)$: a more negative covariance indicates that rarer taxa were more strongly stabilised than common taxa. To account for the fact that the expectation of this covariance is already negative, and to control for spurious statistical correlations in the temporal data due to other factors, we implemented a null model approach (Yenni et al., 2017; Rovere & Fox, 2019). We shuffled the abundances of each OTU independently, recalculated relative abundances and per capita growth rates, estimated equilibrium frequencies (f s) and negative frequency dependences (NFDs) and calculated the covariance, repeating this procedure 5000 times to generate a null distribution of covariance values ($\text{COV}[\log(f), \log(\text{NFD})]$) (Yenni et al., 2017). This procedure maintains the potential abundances detected for each OTU but erases the temporal structure of each taxon's growth dynamics, thus removing signatures of intraspecific limitation as well as any interspecific limitations correlated with the population dynamics of other OTUs. We then compared our observed covariance with the null distribution to determine the strength of asymmetry in NFD (i.e. the degree to which rare OTUs experience disproportionately stronger self-limitation than common OTUs). We quantified divergence from null distributions using standardised effect sizes ($\text{SES} = \text{mean observed covariance} / \text{standard deviation of covariances in the null distribution}$) and the ratio of observed covariance to the average covariance of the null distribution (Yenni et al., 2017). More negative SES values and larger ratios indicate greater deviations from the null expectation of equal NFD across taxa. We assessed the degree of statistical significance by calculating a p-value as the proportion of null covariance values less than or equal to our observed covariance.

Seed bank dynamics

Given the hypothesis that seed banks are important for the maintenance of bacterial diversity in nature, we analysed the temporal dynamics of buffered population growth, a key criterion of the storage effect. First, we examined whether the seed bank served as a reservoir of taxonomic diversity by comparing the ratio of total richness to active richness at each time point in the time series, where larger ratios indicate that the total community had higher α -diversity than the active subset of the community. To quantify the dynamic nature of the seed bank, we fit an autoregressive integrated moving average model, $\text{ARIMA}(0,0,1)$, with temperature and water

transparency as environmental covariates. We then computed 95% confidence intervals using the 'forecast' R package. Second, we sought to determine whether seed bank dynamics were more important for the maintenance of rare or common taxa in the community. To do so, we developed a reactivation metric based on the recovery of sequences in the DNA and RNA pools over time. For each OTU, a reactivation score is calculated as the number of times an OTU was present (i.e. detected in the DNA pool) but likely in an inactive (i.e. absent from the RNA pool) state at time point t , yet active (present in the RNA pool) at the subsequent time point $t + 1$. Based on this, our interpretation is that OTUs with higher reactivation scores are more reliant on the seed bank for long-term persistence in the community, while OTUs with a lower reactivation score tend to remain in the active state. We used non-linear regression to analyse the relationship between the average relative abundance of active OTUs (excluding zeroes) and their reactivation score to determine whether seed banking was more important for maintaining rare taxa than common taxa in the bacterioplankton community.

We compared observed patterns of reactivation to null models of community dynamics to characterise differences in the seed bank strategies among putatively coexisting taxa. While some microbial taxa engage in stochastic reactivation (Buerger et al., 2012), other taxa emerge from dormancy in a responsive manner, usually through the interpretation of environmental cues (Lennon & Jones, 2011; Lennon et al., 2021). To generate the range of seed bank dynamics expected under stochastic reactivation, we created null models ($n = 1000$) by randomly redistributing observed DNA counts of each OTU across the time series, keeping total observed counts for each OTU constant to preserve the relationships among common and rare taxa in the community. We then randomly distributed observed activity (i.e. $\text{RNA} > 0$) for each OTU among samples where the OTU was present (i.e. $\text{DNA} > 0$). We quantified the standardised effect size (SES) for each OTU relative to the null distribution. We interpreted $|\text{SES}| > 2$ to indicate seed bank transitions significantly different from random chance.

RESULTS

Differential responses to environment

Bacterial community dynamics were related to environmental variability, with taxa differentially favoured at different times of the year. During the summer months, the community followed a recurrent successional trajectory (Figure 1a). This trajectory was strongly aligned with seasonal trends in temperature (Figure 1b). Across longer timescales, interannual variation in pH was associated with compositional differences in the active

bacterial community during winter months. Within an annual cycle, the persistent OTUs ($n = 82$) demonstrated temporal partitioning in their maximal growth rates in the active portion of the community (Figure 2, Table S1). The relative abundances of persistent taxa also varied in response to changes in water temperature, with some OTUs increasing in abundance with warmer temperatures, others increasing with cooler temperatures and others showing a hump-shaped abundance relationship with temperature (Figure S2).

Stabilising biotic interactions

Persistent taxa exhibited stabilising NFD, which varied in strength depending on each taxon's mean relative abundance in the community (Figure S3 and S4). NFD was significantly stronger for rare taxa than common taxa, but only in the active portion of the community ($p = 0.0002$; $SES = -4.07$, covariance ratio = 1.08), not in the total community ($p = 0.221$; $SES = -0.777$, covariance ratio = 1.01) (Figure 3). In other words, the total community showed nearly the same degree of stabilisation ($|SES| < 2$, covariance ratio ~ 1) as the null communities.

Seed bank dynamics

Our data suggest that seed banks of dormant or slow-growing individuals contribute to the maintenance of diversity. Over the course of our study, total richness ranged from 1.2 to 2.0 times higher than the richness of the active portion of the community (Figure 4). Furthermore, this discrepancy between total and active richness exhibited seasonality, demonstrating a time-varying role for the bacterial seed bank. The seed bank played a weaker role (i.e. active and total richness were more similar in magnitude) during the summer, while proportionally higher diversity was found in the seed bank over winter, when growing conditions were presumably less optimal due to reduced temperatures and less solar radiation (Figure 4). After accounting for temporal autocorrelation, we found that increased water temperature and transparency significantly predicted a reduction in the seed bank ratio ($MA1 = 0.31 \pm 0.09SE$, intercept = $1.53 \pm 0.02SE$, temperature = $-0.11 \pm 0.02SE$, Secchi depth = $-0.09 \pm 0.02SE$; $AIC = -96.08$). In addition, the OTUs that exhibited more reactivations from the seed bank were also the taxa that were, on average, consistently rare when active in the community (intercept = $0.21 \pm 0.07SE$, $\alpha = 1.25 \pm 0.097SE$) (Figure 5). Compared to null models of stochastic reactivation for persistent taxa, 52 OTUs had reaction patterns indistinguishable from random, 18 had fewer reactivations than expected by random chance and 12 were determined to always be active (Figure S5). Thus, multiple seed-banking

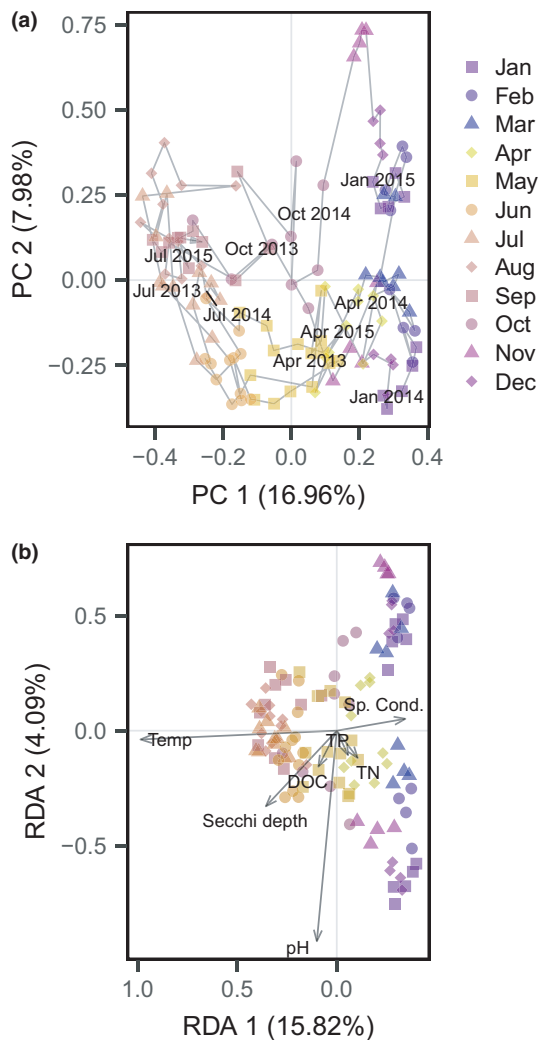


FIGURE 1 Seasonal dynamics of the active bacterial community in University Lake. (a) The compositional trajectory of the active community (determined by high-throughput sequencing of 16S rRNA transcripts) shows strong seasonality, but the community remains relatively static over winter. The first two axes of the principal component analysis (PCA) depict summer/winter differences (PC1) along the major axis and slight inter-annual differences in winter composition (cool colours) along the minor axis (PC2). The summer successional trajectory (warmer colours) is highly repeatable across years. (b) Constrained ordination using redundancy analysis (RDA) shows the environmental drivers of community structure along with strong correlates of individual taxa in the community. This analysis reveals that differences in pH explain variation in winter composition among years

strategies appear to promote long-term persistence in the community.

DISCUSSION

Our findings from a multi-year survey support the view that biodiversity was maintained by stabilising mechanisms, including niche differentiation and seed bank dynamics, that generated negative frequency dependence (NFD) in a natural bacterioplankton community.

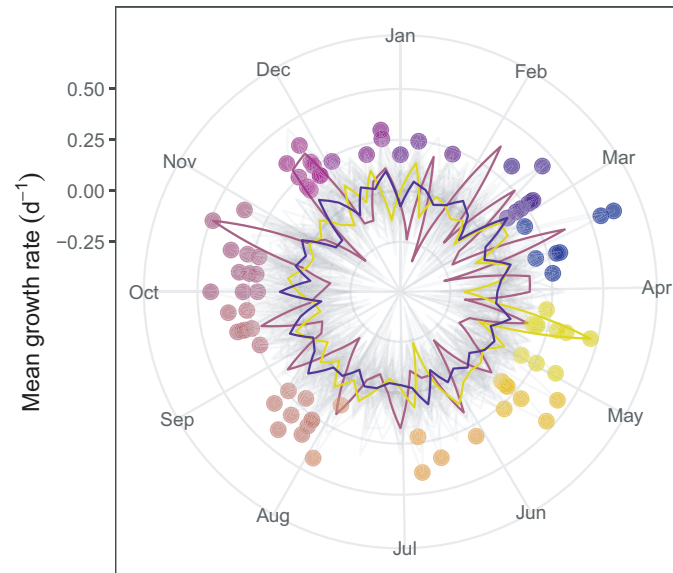


FIGURE 2 Temporal partitioning of maximum growth rate among persistent bacterial taxa in University Lake. Lines represent the mean daily growth rate for each taxon over the time series. Points indicate the maximum growth observed for each bacterial taxon (OTU). Overall, the 82 persistent OTUs have maximum growth rates at different seasons of the year. Points are colour coded such that warmer colours correspond to spring and summer months and cooler colours correspond to winter months. Coloured lines trace out the growth dynamics of three individual taxa with different environmental responses (blue = OTU 1, Betaproteobacteria; yellow = OTU 17, Actinobacteria; mauve = OTU 18, Gammaproteobacteria). More taxonomic details can be found in Table S1

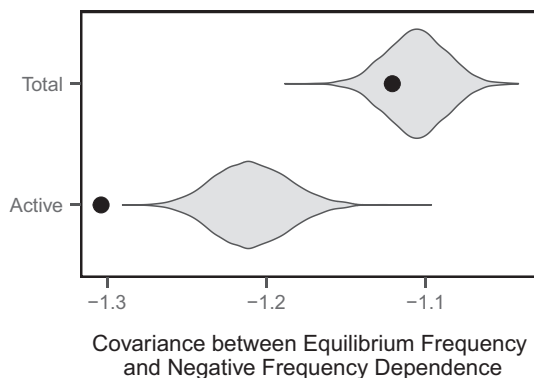


FIGURE 3 Negative frequency dependence (NFD) among persistent bacterial taxa ($n = 82$) was significantly stronger for rare than common taxa only in the active portion of the community. The degree of asymmetry in NFD is determined by the covariance between the equilibrium frequency of each OTU and its strength of NFD; negative covariance indicates that rarer taxa exhibit stronger NFD. Compared with expected covariances from a null distribution, the standardised effect size (SES) of the observed covariance in the active portion of the community was -4.07 , while the SES of the total community was -0.78 . The overall strength of NFD (observed NFD/mean NFD) was 1.08 in the active portion and 1.01 in the total community. The metabolic state on the y -axis indicates whether the NFD comparison is for the active portion of the community (inferred from 16S rRNA transcripts) or the total portion (inferred from 16S rRNA genes, i.e. DNA)

High-resolution sampling revealed recurrent seasonality in community dynamics, driven by taxon-specific responses to annual environmental fluctuations. Our results also showed that the maintenance of diversity may be enhanced by life-history strategies, such as slow

growth or dormancy, that buffered rare taxa from local extinction during environmentally unfavourable periods (e.g. winter) and facilitated re-establishment when conditions improved. These apparent niche differences and seed bank dynamics contributed to stabilising biotic interactions (e.g. stronger intra- than interspecific limitation) among rare, but metabolically active, taxa in the community.

Negative frequency dependence in microbial communities

We found evidence for stabilisation through negative frequency dependence (NFD). While documented in some plant and animal assemblages (Harpole & Suding, 2007; Rovere & Fox, 2019; Yenni et al., 2017), observations of NFD in complex microbial communities are uncommon. Our study revealed disproportionately strong NFD for rare taxa, offering an explanation for why some taxa appear to stably persist at low relative abundances in nature (Alonso-Sáez et al., 2015; Lindh et al., 2015), potentially as members of the ‘rare biosphere’ (Lynch & Neufeld, 2015; Shade et al., 2018; Sogin et al., 2006). Our approach also identified stabilising mechanisms operating among metabolically active rare taxa that were not detectable from the dynamics of the total bacterial community (Figure 3). Ignoring this metabolic heterogeneity can obscure inferences of underlying ecological processes (Wisnoski et al., 2020), which would have gone otherwise undetected in this study as well.

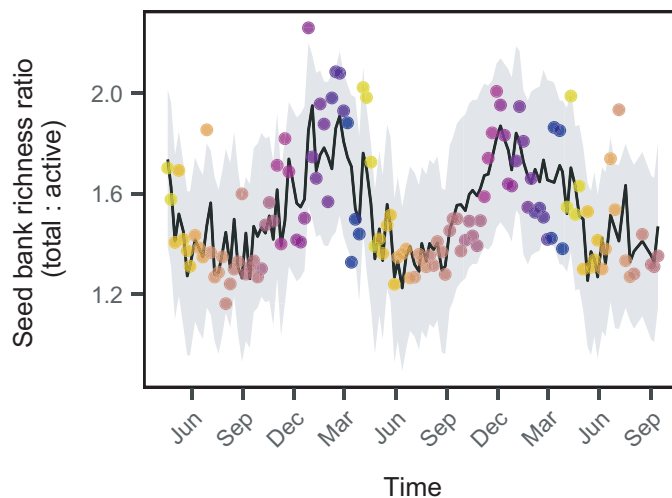


FIGURE 4 Seasonal importance of the seed bank for bacterial diversity in University Lake. Richness was much higher in the total community, relative to the active community, during the fall and winter months. The active and total communities converged over the summer, indicated by values on the y -axis closer to 1. Warmer colours correspond to spring and summer months, while cooler colours correspond to winter months. The line is a fit from an ARIMA model with temperature and water transparency (two seasonal variables) as covariates. Shaded regions are 95% confidence intervals

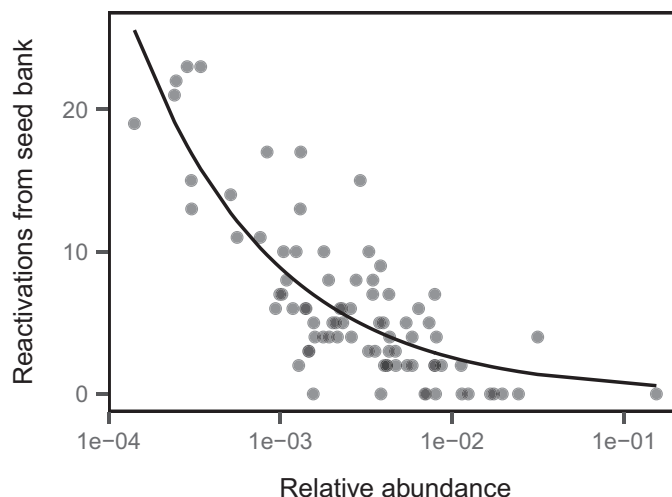


FIGURE 5 Rare taxa showed more seed bank transitions than common taxa. For the 82 persistent taxa identified over the time series, OTUs that were (on average) rare in the active portion of the community had a higher number of reactivations from the seed bank, while more common taxa had fewer reactivations. The line is a negative exponential fit from a nonlinear regression

Stronger NFD among rare taxa is also important for coexistence in plant and animal communities, but the magnitude of this effect varies across taxonomic groups (Rovere & Fox, 2019; Yenni et al., 2017). For example, NFD is less asymmetric for herpetofauna than plant or mammal communities (Yenni et al., 2017) possibly due to higher evenness (Rovere & Fox, 2019). Compared with macro-organismal systems, the degree of NFD asymmetry in our highly uneven bacterial community was moderate based on the covariance ratio (covariance ratio = 1.08), suggesting that coexistence among rare taxa may be weak, that alternative null models ought to be developed for microbial systems or that additional processes are important for maintaining diversity in our study system. Nevertheless, our results provide critical

evidence that active bacteria mediate the biotic interactions responsible for generating stronger NFD among rare taxa in the community ($SES = -4.07$, $p < 0.001$). Consistent with prior work showing that rare taxa may be disproportionately active in freshwater bacterial communities (Jones & Lennon, 2010), our study demonstrates that rare, metabolically active bacteria may also be critical for the long-term maintenance of bacterial diversity.

Dynamic microbial seed banks

Seed bank dynamics are thought to maintain diversity in fluctuating environments. In particular, seed banks provide a demographic buffering effect that satisfies

one criterion of the storage effect. Evidence for coexistence via the storage effect comes largely from communities of desert annuals (Angert et al., 2009; Pake & Venable, 1996), grasslands (Adler et al., 2006), tropical trees (Usinowicz et al., 2012), zooplankton (Cáceres, 1997) and marine fish (Secor, 2007). In most microbial studies, the role of seed banks for coexistence has been inferred from short-term observations, but here we provide temporal evidence that bacterial seed banks may be important for community dynamics and the maintenance of diversity over longer, multi-annual timescales. In the temperate climate of our study lake, different taxa showed maximum growth rates at different times of the year, coinciding with seasonal transitions in environmental conditions (Figure 2), and contrasting active and total community dynamics suggested buffered population dynamics (Figures 3–5). Bacterial taxa may also exhibit more fine-grained differences in temporal niches than can be characterised by peak activity (e.g. see Figure S2), which may be a somewhat conservative estimate of temporal niche differences. Nevertheless, our data provide evidence that two out of the three criteria for a storage effect (differential responses to the environment and buffered population dynamics) are likely operating in the community.

The third criterion of the storage effect is that there is covariance between environmental conditions and competition. Documenting this pattern, especially in highly diverse communities, has proven to be a challenging endeavour. Our study demonstrated that species experienced greater self-limitation (consistent with stronger intraspecific than interspecific competition) when they were more common in the active community (and were thus more likely favoured by the environment or less negatively affected by it) (Figure 3, Figure S2). We also found that diversity was maintained during less favourable growth environments (Figure 4). But it is unclear whether environmental fluctuations in this system generate the covariance between environment and competition necessary to fully invoke the storage effect (Chesson, 2000; Miller & Klausmeier, 2017). Theoretical models indicate that the storage effect is more likely to evolve when species' generation times are much shorter than the timescale of environmental fluctuations (Miller & Klausmeier, 2017), a scenario that is well aligned with bacterioplankton living in a highly seasonal north temperate lake. Such conditions may also favour dormancy strategies that respond to seasonal cues (Brendonck & De Meester, 2003; Lennon et al., 2021), in contrast to stochastic dormancy transitions (Buerger et al., 2012). Indeed, we found a subset of microbial taxa that reactivated significantly less often than would be expected by chance (Figure S5) as might be expected if bacteria in the lake respond to more predictable seasonal cues. More broadly, putatively coexisting bacteria appear to rely on a range of seed banking strategies (Lennon et al., 2021), ranging from environmentally responsive, to stochastic,

to a weak reliance on dormancy for persistence (Figure S5).

In addition, we cannot rule out the potentially strong contribution to NFD by another non-mutually exclusive class of fluctuation-dependent mechanisms. Namely, relative nonlinearity in competition can promote coexistence if species differ in their responses to competition in ways that benefit their competitors (Hallett et al., 2019; Letten et al., 2018; Yuan & Chesson, 2015). For example, nonlinear species interactions can generate stabilising oscillations in the community that allow species to recover from rarity, such as when fluctuations provide a competitive release for species even in environmental conditions where they are not intrinsically favoured (Hallett et al., 2019). While our data cannot provide definitive proof of the specific coexistence mechanisms operating in the community, the documented patterns are consistent with the criteria needed for a temporal storage effect.

Seasonal reoccurrence in bacterial communities

Seed banks may also have more general implications for bacterial community dynamics. The persistence of taxa with temporal niche differences could contribute to the repeatability of summer community dynamics in the active portion of the community (Hellweger et al., 2008) by favouring overwinter survival (Figure 4). For example, we found that the seed bank exhibited seasonality, such that diversity stored in the seed bank was maximised when environmental conditions (e.g. water temperature, resource/consumer densities) were least favourable for bacterial growth (Neuenschwander et al., 2015). This pattern is consistent with the notion that dormant seed banks help buffer individuals from harsh environmental conditions. In addition, transitions from inactive to active metabolic states were more frequently detected among taxa that were rare when active. Analogous to the methodological challenges of finding and identifying dormant individuals in non-microbial seed banks (e.g. plants), detection limits may affect the classification of metabolically active bacteria. Nevertheless, our reactivation metric should capture rapid shifts in the metabolically active portion of the community. Overall, our results suggest that recurrent environmental cues regulate active community dynamics by favouring different taxa at different times of the year, and that seed banks are important for maintaining these seasonal community trajectories at multi-annual timescales.

Future directions and conclusions

Our study provides empirical evidence consistent with the theory that niche differences and seed bank dynamics stabilise bacterial communities and maintain

diversity in nature. In a naturally fluctuating lake environment, we demonstrated key differences in the diversity, dynamics and stabilisation between the active and total subsets of the bacterial community, but an ultimate goal is to tighten the mechanistic links between rates of ribosomal RNA transcription and in situ growth rates for individual taxa (Newton & Shade, 2016; Papp et al., 2018) or through other techniques that involve the physical sorting of cells based on metabolic activity prior to sequencing (Couradeau et al., 2019; Reichart et al., 2020). While our results showed that stabilising mechanisms generated NFD in the community, an important next step is to quantify the strengths and directions of the multiple fluctuation-independent and -dependent coexistence mechanisms that may be operating in diverse microbial communities (Ellner et al., 2019; Hallett et al., 2019; Letten et al., 2018).

A grand challenge at the intersection of microbial and community ecology is to extend the experimental investigations of microbial coexistence in the laboratory (Letten et al., 2018; Zhang et al., 2009) into systems reflecting the high diversity and complex interaction networks of most natural microbial communities. It will require careful experimentation and clear consideration of scale to account for issues such as sampling biases and immigration that deviate from clear alignment with coexistence theory. For example, it is important to incorporate the timescale of microbial responses to fluctuations in relation to the sampling frequency. Likewise, it may also be important to consider the dispersal of terrestrial bacteria into aquatic ecosystems (Crump et al., 2012), since immigration could contribute to inferences made about local processes. However, previous work in our study system revealed that most terrestrial-derived bacteria were metabolically inactive, most likely reflecting the abrupt environmental transitions that accompany cross-ecosystem dispersal (Wisnoski et al., 2020). Thus, the lack of asymmetric NFD we observed in the total community could arise in part from allochthonous inputs of inactive bacteria that decouple local population growth rates from relative abundance. Nevertheless, by focusing on the dynamics of metabolically active bacteria, our approach uncovered stabilising biotic interactions that may have otherwise been obscured by metabolic heterogeneity in the total community.

In conclusion, we show that stabilising biotic interactions and the ability to engage in dormancy or slow growth strategies play important roles in maintaining microbial diversity in a natural ecosystem over a multi-year timescale. In particular, strong NFD offers a new explanation for why the majority of bacterial taxa persist at low average relative abundances in nature (Lynch & Neufeld, 2015). Our work builds on inferences about the roles of microbial dormancy (and other persistence strategies) obtained from shorter timescales and provides evidence that dormancy is an important buffer against

local extinction over longer timescales. More generally, our work demonstrates the importance of stabilisation in microbial systems, offering new insight into the long-term maintenance of microbial diversity.

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AUTHORSHIP

JTL designed the study and coordinated data collection. NIW performed statistical analyses and wrote the first draft of the manuscript. Both authors contributed substantially to edits and revisions.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13853>.

DATA AVAILABILITY STATEMENT

Sequence data are available on NCBI SRA (BioProject PRJNA664410), and the remaining data and code to reproduce all analyses are available on Zenodo (<https://doi.org/10.5281/zenodo.5087753>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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