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Metabolic insight into bacterial community assembly across ecosystem boundaries

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Abstract. The movement of organisms across habitat boundaries has important consequences for populations, communities, and ecosystems. However, because most species are not well adapted to all habitat types, dispersal into suboptimal habitats could induce physiological changes associated with persistence strategies that influence community assembly. For example, high rates of cross-boundary dispersal are thought to maintain sink populations of terrestrial bacteria in aquatic habitats, but these bacteria may also persist by lowering their metabolic activity, introducing metabolic heterogeneity that buffers the population against species sorting. To differentiate between these assembly processes, we analyzed bacterial composition along a hydrological flow path from terrestrial soils through an aquatic reservoir by sequencing the active and total (active + inactive) portions of the community. When metabolic heterogeneity was ignored, our data were consistent with views that cross-boundary dispersal is important for structuring aquatic bacterial communities. In contrast, we found evidence for strong species sorting in the active portion of the aquatic community, suggesting that dispersal may have a weaker effect than persistence strategies on aquatic community assembly. By accounting for metabolic heterogeneity in complex communities, our findings clarify the roles of local- and regional-scale assembly processes in terrestrial-aquatic meta-ecosystems.

Key words: bacteria; dispersal; dormancy; metacommunity; meta-ecosystem; terrestrial-aquatic linkages.

Introduction

The movement of material and energy across habitat boundaries is important for the structure and function of recipient ecosystems (Polis et al. 2004, Gounand et al. 2018*a*). These spatial resource subsidies can stabilize population dynamics, alter food web structure, and modify biogeochemical cycles (Polis et al. 2004, Massol et al.

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2011). However, in complex landscapes linked by spatial fluxes of resources and organisms, the process of community assembly remains less clear (Gounand et al. 2018*a*). Meta-ecosystem theory predicts that poorly adapted species dispersed across ecosystem boundaries will be eliminated from the recipient habitat via species sorting (Massol et al. 2017, Gounand et al. 2018*a*), unless resource flows sufficiently homogenize the landscape (Gravel et al. 2010). However, if generalist species are capable of tolerating a range of environmental conditions, then cross-boundary dispersal could affect community assembly in recipient habitats (Haegeman and Loreau 2014).

Habitats at the terrestrial-freshwater interface are ideal for addressing questions about meta-ecosystem ecology (Gounand et al. 2018*b*). Terrestrial ecosystems export large quantities of organic matter that support aquatic food webs, often through bacterial pathways (Berggren et al. 2010). Furthermore, many of the bacteria responsible for processing allochthonous subsidies in aquatic habitats may be derived from terrestrial ecosystems via

coupled transport with resource flows (Ruiz-González et al. 2015b). For example, in some north temperate lakes, it is estimated that nearly 10^{20} bacterial cells are transported annually from terrestrial to aquatic ecosystems (Bergström and Jansson 2000). These high immigration rates should influence the composition and activity of bacterial assemblages via metacommunity processes, such as source–sink dynamics or mass effects that overcome species sorting (Crump et al. 2012, Lindström and Langenheder 2012, Ruiz-González et al. 2015a).

Although cross-boundary flows have been well documented, the fate of terrestrial-derived bacteria in aquatic ecosystems remains unclear (Langenheder and Lindström 2019). In part, this may be because both dispersal- and niche-based perspectives overlook the range of metabolic states within microbial communities. In nature, some microorganisms may respond to favorable environmental conditions via rapid growth, while others face challenging conditions that limit or prevent growth (Lever et al. 2015). Many bacteria have evolved persistence strategies (e.g., spores, cysts, resting stages, slow growth) that buffer against harsh environmental transitions, such as those encountered when dispersed along terrestrial-aquatic flow paths (Barcina et al. 1997, Lennon and Jones 2011). By weakening the strength of species sorting, these persistence strategies may increase the apparent similarity between terrestrial and aquatic bacterial communities (Nemergut et al. 2013, Locey et al. 2019, Wisnoski et al. 2019), especially when techniques are used that lend equal weight to active, slow-growing, and dormant bacteria (e.g., DNA-based methods). As a result, the importance of terrestrial-derived bacteria in aquatic community assembly may not be fully understood when inferred from diversity patterns that do not explicitly consider the metabolic heterogeneity that exists within bacterial communities.

In this study, we explored microbial community assembly along a hydrological flow path of a small reservoir. In this type of system, inputs from the terrestrial landscape occur upstream in the riverine zone, directional surface flow orients the passive dispersal of bacteria through the lacustrine zone, and emigration occurs over the impoundment (Thornton et al. 1990; Fig. 1). We hypothesized that dispersal maintains terrestrial-derived bacteria in the reservoir, promoting local (α) diversity and homogenizing among-site (β) diversity at the terrestrial-aquatic interface, but that these taxa may not be metabolically active. Due to species sorting, we hypothesized that only a subset of the immigrating terrestrial bacteria become metabolically active members of the aquatic community.

METHODS

Study system

University Lake is a meso-eutrophic reservoir located in Griffy Woods, Bloomington, Indiana, USA (39.189° N, 86.503° W; Fig. 1). Created in 1911, the 3.2-ha impoundment has an operating volume of 150,000 m^3. With a maximum depth of 10 m, University Lake is fed by three streams that drain mature oak–beech–maple forest. The underlying geology is Harrodsburg limestone on ridgetops and Borden siltstone/shale in valleys. The thin unglaciated soils surrounding the reservoir are Brownstown-Gilwood silt loams.

Bacterial community structure

We collected surface-water samples along a longitudinal transect through University Lake in July 2013, filtering epilimnetic biomass from 200 mL of water onto 0.2 µm Supor Filters (47 mm diameter; Pall, Port Washington, New York, USA). We characterized composition of the active and total portions of the bacterial communities by sequencing 16S rRNA genes (DNA) and transcripts (RNA), respectively. While sequences recovered from the DNA pool can come from active or inactive individuals, sequences from the RNA pool are commonly used to make inferences about active microorganisms given that rRNA transcripts have short half-lives and that ribosomes are required by cells for protein synthesis (Molin and Givskov 1999, Bowsher et al. 2019, Locey et al. 2019, Steiner et al. 2019). Sequences were processed in mothur (v. 1.41.1; Schloss et al. 2009) and 97% similar operational taxonomic units (OTUs) were created using the OptiClust algorithm (Westcott and Schloss 2017). See Appendix S1 for detailed methods.

Quantifying patterns of diversity along the flow path

We analyzed within sample (α) and among sample (β) diversity along the flow path. We estimated α-diversity using rarefaction with the iNEXT R package (Hsieh et al. 2016), following singleton-correction for sequence data (Chiu and Chao 2016). We used Hill numbers (^qD) for a given order, q, to weigh common and rare species using the equation $^qD = \left(\sum_{i=1}^{S} p_i^q \right)^{\frac{1}{1-q}}$, where p_i is the relative abundance of species $i = 1, \ldots, S$. The value ^qD is the number of equally abundant species that would yield the observed value of a diversity metric, such as richness ($q = 0$), Shannon's index ($q = 1$), or Simpson's index ($q = 2$), in each aquatic sample. When different values of q are plugged into the equation for ^qD, Hill numbers at higher orders (q) increasingly reflect the most common species because larger exponents reduce the influence of rare taxa in the metric. We measured β-diversity between soil and aquatic samples as the average similarity (1 − Bray-Curtis) of each aquatic sample to the three soil samples using the vegan package in R (Oksanen et al. 2019). To detect molecule-specific trends in α- or β-diversity along the flow path, we used multiple regression. With aquatic α- or β-diversity as the response

Fig. 1. University Lake, a reservoir located on the Indiana University Research and Teaching Preserve in Bloomington, Indiana, USA. Points indicate sampling locations along the terrestrial-aquatic transect, from upstream soils, through the stream inlet, across the lacustrine zone, and over the dam. Image source: Google Earth.

variable, we tested for the effects of molecule type (treating RNA vs. DNA as a categorical variable) and flow-path distance (a continuous variable in meters) on diversity. We included an interaction term to detect differences in slopes between DNA and RNA samples along the flow path.

We also analyzed taxon-level trends along the flow path. To make inferences about species sorting on terrestrial-derived bacteria (defined as the OTUs detected in soil samples), we measured changes in their relative abundances in the aquatic DNA and RNA pools. We assumed that terrestrial taxa that were disfavored in the aquatic habitat were either never detected in the active aquatic community (i.e., they were detected in the DNA, but not RNA, pool), or they became rarer in the active aquatic community along the flow path. In contrast, we assumed taxa that were favored in aquatic sites became more common along the flow path. If we detected a terrestrial OTU in at least 75% of the aquatic RNA samples, we inferred that the taxon was metabolically active in the aquatic community, but results were robust to different thresholds (Appendix S1: Fig. S2).

Furthermore, to determine whether aquatic samples were nested subsets of the soil samples (e.g., due to mass effects or species sorting favoring habitat generalists) or exhibited compositional turnover due to the gain and loss of OTUs (e.g., due to species sorting favoring habitat specialists), we partitioned β-diversity into its nestedness and turnover components from the Sørensen family of metrics (Baselga 2010) and classified OTUs based on their habitat specificity. All statistical analyses were conducted in R (version 3.5.2; R Core Team 2018).

Results

Patterns of bacterial diversity along the flow path were strongly influenced by metabolic heterogeneity (Fig. 2a, $R^2 = 0.83$, $P < 0.001$), as shown by significant differences in slope and intercept of the multiple regression model (Table 1). In the total aquatic bacterial community (DNA), richness was highest near the terrestrial-aquatic interface and declined toward the dam. In comparison, the active (RNA) aquatic richness was lower and less variable along the transect. Differences in α-diversity between active and total portions of the community were highest near the terrestrial-aquatic interface (e.g., subtracting the RNA term (1,170) from the intercept (1,497 OTUs) of the $q = 0$ model indicates there were 78% fewer taxa in the active subset near the terrestrial-aquatic interface; Table 1). Across different orders of Hill numbers, diversity differences were greatest when rare and common taxa were equally weighted ($q = 0$), as might be expected if immigrant or dormant taxa were rare. When dominant taxa were weighted more heavily ($q = 1, 2$), the active portion of the community still had lower diversity overall (significant RNA terms), but differences in the decay of diversity became less distinguishable between the two portions of the community as stronger emphasis was placed on the dominant taxa (distance × RNA interaction; Table 1).

Metabolic heterogeneity also had strong effects on β-diversity (Fig. 2b). Similarity between terrestrial and aquatic samples was highest near the terrestrial-aquatic interface and decreased toward the dam ($R^2 = 0.78$, $P < 0.001$). However, maximum similarity to soils and the rate of decay in similarity differed between the total and active portion of the community. Near the stream inlet, similarity

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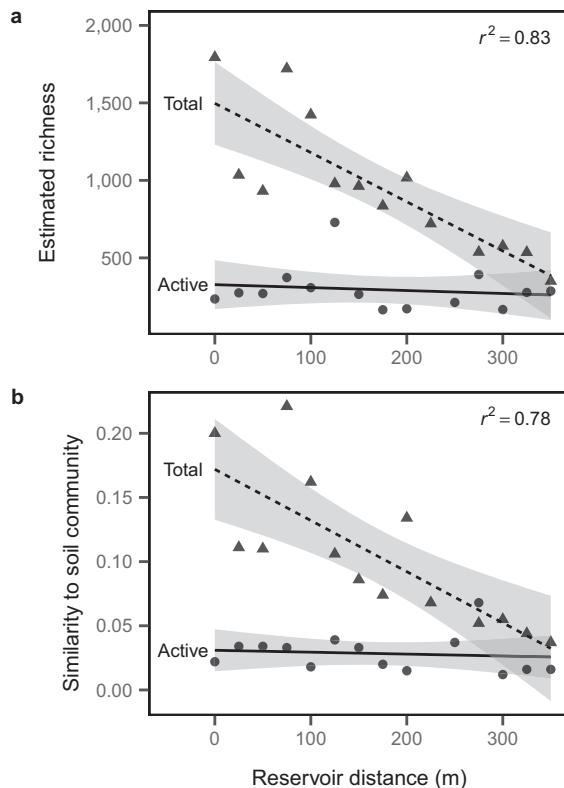
FIG. 2. Terrestrial influence on aquatic microbial diversity. (a) Estimated alpha diversity (richness, ^1D) in the active (circles) and total (triangles) aquatic communities along the reservoir transect. (b) The average similarity to the soil samples for active and total aquatic communities declines with distance away from the terrestrial-aquatic interface (0 m).

$k = 2.57 \times 10^{-3} \pm 3.6 \times 10^{-4}$, $r^2 = 0.81$, $P < 0.001$) with distance from the stream inlet (Fig. 3a). However, 13% of taxa present in soils were detected at least once in the active aquatic community. Of the soil-derived taxa detected in at least 75% of active aquatic samples, 18 declined along the transect, but 11 were maintained at high relative abundances in the active aquatic community (Fig. 3; see Appendix S1: Tables S1, S2 for list of taxa).

DISCUSSION

Our results support the hypothesis that the importance of dispersal for community assembly across ecosystem boundaries depends on the metabolic activity of dispersers in the meta-ecosystem. Along a terrestrial-aquatic flow path, the influence of terrestrial bacteria on aquatic bacterial α- and β-diversity was highest near the terrestrial-aquatic interface. This pattern, consistent with terrestrial immigration playing an important role in aquatic community assembly (i.e., mass effects), was weaker in the active portion of the aquatic community than the total aquatic community. Specifically, both α-diversity and similarity to soils were substantially lower in the metabolically active portion of the aquatic community (Table 1; Fig. 2), suggesting a hidden role for species sorting in the aquatic habitat that was only apparent when incorporating metabolic information. In fact, most terrestrial-derived taxa were not detected in the active aquatic community and decayed exponentially away from the terrestrial-aquatic interface (Fig. 3a). Altogether, our findings are consistent with the hypotheses that most terrestrial-derived taxa fail to colonize aquatic habitats and that only a small number of habitat generalists may be able to colonize aquatic environments from nearby terrestrial landscapes. Our study also highlights the utility of incorporating information on metabolic heterogeneity to gain insight into the structure and dynamics of spatially heterogeneous metacommunities and meta-ecosystems.

Metabolic heterogeneity informs aquatic community assembly

Inferring community assembly processes from diversity patterns is challenging because species can be present in a habitat for reasons other than habitat suitability (e.g., high dispersal, persistence traits). Accounting for metabolic heterogeneity helps distinguish favorable from suboptimal habitats by detecting the responses of actively growing organisms (e.g., Muscarella et al. 2016), providing insight into the fate and potential functions of dispersers in recipient ecosystems. The frequent detection of terrestrial bacteria in aquatic ecosystems has led to the view that dispersal is a dominant process structuring aquatic diversity, but our results suggest that local aquatic environments still impose harsh biotic or abiotic filters on the metabolically active subset of the aquatic community (Fig. 2). Thus, the

to soils was more than fivefold higher in the total community than in the active portion (intercept $= 0.172 \pm 0.014$ [mean $\pm$ SE], $\beta_{RNA} = -0.141 \pm 0.020$), and similarity to soils declined linearly toward the dam ($\beta_{distance} = -4.0 \times 10^{-4} \pm 6.83 \times 10^{-5}$, $\beta_{distance \times RNA} = 3.9 \times 10^{-4} \pm 9.61 \times 10^{-5}$). In contrast, the active portion remained dissimilar to terrestrial soils along the entire transect (Fig. 2b). These patterns of β-diversity were not purely driven by nestedness, as both the active portion and the total aquatic community exhibited turnover relative to soil samples (Appendix S1: Fig. S3), and 71% of the active aquatic OTUs were not detected in the soil samples (Appendix S1: Fig. S4).

We detected a small number of habitat generalists (defined as OTUs present both in soil samples and in the active portion of the aquatic community), but the majority of terrestrial soil taxa did not appear to colonize the aquatic community. Most taxa present in both soil and aquatic communities were never detected in any active aquatic sample (~82% of taxa remained inactive), and these inactive taxa accounted for roughly 4.5% of all reads in the total reservoir community. The richness of these taxa declined exponentially (first-order decay,

TABLE 1. Output from multiple regression models.

Order (q)	Diversity	Term	Estimate	SE	t-Statistic	P
0	richness	intercept	1,497	100.6	14.88	<0.0001
0	richness	distance	−3.176	0.4976	−6.381	<0.0001
0	richness	RNA	−1,170	142.3	−8.222	<0.0001
0	richness	distance × RNA	2.985	0.7003	4.263	0.0003
1	Shannon	intercept	153.7	19.41	7.921	<0.0001
1	Shannon	distance	−0.2941	0.096	−3.062	0.0053
1	Shannon	RNA	−123.9	27.46	−4.513	0.0001
1	Shannon	distance × RNA	0.2457	0.1352	1.818	0.0815
2	Simpson	intercept	55.44	6.47	8.57	<0.0001
2	Simpson	distance	−0.0783	0.032	−2.446	0.0221
2	Simpson	RNA	−36.78	9.151	−4.019	0.0005
2	Simpson	distance × RNA	0.0402	0.045	0.8918	0.3813

Notes: Model coefficients are shown for active and total α-diversity along the transect examined at different levels of q, representing equal weighting of rare and common taxa ($q = 0$), proportional weighting ($q = 1$), and biased weighting toward common taxa ($q = 2$). In these models, intercepts represent estimates of total diversity at each order near the terrestrial-aquatic interface, with the RNA term capturing the reduced diversity in the active subset. With increasing order, the distance × RNA interaction becomes weaker, signifying that diversity decays at similar rates in the active and total communities as common taxa are increasingly weighted.
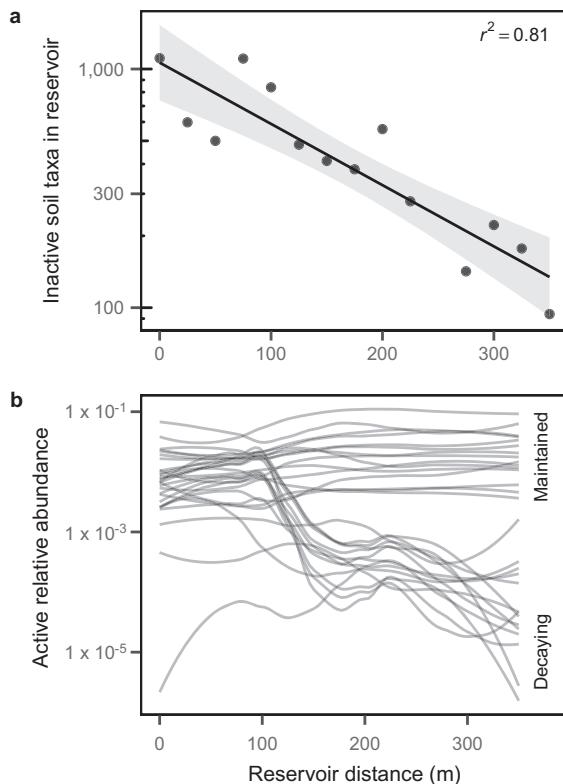
FIG. 3. Fate of terrestrial-derived taxa in the reservoir. (a) Number of taxa detected in soils but never detected in active aquatic samples declines exponentially away from the terrestrial-aquatic interface with a first-order decay constant $k = 2.57 \times 10^{-3}$. Note that the y-axis is on a logarithmic scale. (b) Taxa detected in at least 75% of active aquatic samples either decay in abundance along the transect or are maintained. We used local polynomial regression (LOESS) to visualize relative abundances for each operational taxonomic unit (OTU) along the transect.

strength of species sorting on terrestrial-derived bacteria in aquatic habitats may increase with metabolic activity levels of cross-boundary dispersers.

Exponential decay of soil-derived bacteria in aquatic ecosystems

Dispersing across an ecosystem boundary is likely a harsh transition for many bacteria (Monard et al. 2016). Although most active aquatic taxa were also detected in nearby soils, only a minority of taxa present in soils were common in the active aquatic community (Fig. 3). The exponential decay of metabolically inactive terrestrial taxa away from the terrestrial-aquatic interface also resembles diversity declines near river margins (Power et al. 2004). This exponential loss could be due to physical factors (e.g., settling or volumetric dilution) or biotic interactions (e.g., consumption, competition, or lysis following reactivation) that are not offset by reproduction. While our study captured a snapshot in time, if these inactive organisms remain in the system with the potential to reactivate, they could influence community dynamics if environmental conditions change in their favor. Future studies that differentiate activities at a finer resolution (e.g., slow growing, dormant with the potential to reactivate, or even dead) (Carini et al. 2016, Lennon et al. 2018) could further illuminate the fate of cross-boundary dispersers in meta-ecosystems. In general, the exponential decay suggests that terrestrial influences on aquatic bacterial diversity may be localized near ecosystem boundaries.

Nevertheless, a subset of taxa detected in soils were active in the aquatic community. Some became less common along the transect, which could reflect sorting along a riverine-to-lacustrine environmental gradient, or a reduction in mass effects (Fig. 3b). These decaying taxa included representatives from the Actinobacteria

(*Arthrobacter*, *Micrococcus*, *Solirubrobacter*), Bacteroidetes (*Flavobacterium*, *Pedobacter*), and Proteobacteria (α: *Bradyrhizobium*, *Sphingomonas*; β: *Duganella*, *Comamonas*; and γ: *Pseudomonas* sp.), some of which are abundant and ubiquitous in soils (Delgado-Baquerizo et al. 2018). In contrast, taxa maintained in the active aquatic community may have wide niche breadths allowing them to be habitat generalists, or they may be of aquatic origin (e.g., dispersed by floods, animals, or wind, but our soil sampling locations were chosen to minimize this possibility). These potential habitat generalists included taxa belonging to the Actinomycetales, Bacteroidetes (order Sphingobacteriales), Proteobacteria (α: order Rhizobiales, β: family Comamonadaceae, γ: *Acinetobacter*), and Verrucomicrobia (class Spartobacteria). In sum, most terrestrial-derived bacteria may possess persistence strategies that allow them to persist on the periphery of aquatic ecosystems, but habitat generalists that cross ecosystem boundaries could influence aquatic bacterial community assembly.

Metabolic heterogeneity in metacommunities and meta-ecosystems

Our work provides empirical evidence that accounting for metabolic heterogeneity may improve our understanding of metacommunity and meta-ecosystem processes (Massol et al. 2017, Wisnoski et al. 2019). Cross-boundary dispersal can expose organisms to harsh environmental conditions, against which they may be buffered through metabolic flexibility (e.g., slow growth, dormancy). While generalists may be able to colonize a range of habitat types in meta-ecosystems (Haegeman and Loreau 2014), specialists that disperse across ecosystem boundaries may require coupling with resource subsidies or persistence strategies that buffer against suboptimal conditions. Metabolically explicit community assembly also has implications for ecosystem functioning in a spatial context. While high dispersal is predicted to impede ecosystem functioning by creating species-environment mismatches (Leibold et al. 2017), these effects may be reduced if dispersers are metabolically inactive and minimally affect recipient communities. Thus, metabolic heterogeneity may be an important link for understanding the relationships between individuals, communities, and ecosystems across spatial scales.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2968/suppinfo

Data Availability

Raw sequencing data can be found at NCBI (BioProject PRJNA547598) and all R code for analyses and figures is archived in a GitHub repository on Zenodo (https://doi.org/10.5281/zenodo.3588541).

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