Sedimentary DNA can influence evolution: Establishing mineral facilitated horizontal gene transfer as a route to bacterial fitness

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ABSTRACT

Horizontal gene transfer is the one of the most important drivers of bacterial evolution. Transformation by uptake of extracellular DNA is traditionally not considered to be an effective mode of gene acquisition, simply because extracellular DNA are considered to degrade in a matter of days when it is suspended in e.g. seawater. Mineral surfaces are, however, known to preserve DNA in the environment, and sedimentary ancient DNA studies have solidified there are considerable amounts of fragmented DNA stored in sediments world-wide. Recently the age of stored DNA was increased to at least 2 ma highlighting that sediments represent a rich resource of past traits. It is well established that bacteria can acquire large kilobase DNA molecules adsorbed to mineral surfaces. Here we show that *Acinetobacter baylyi* can incorporate 60 bp DNA fragments adsorbed to a wide range of common sedimentary minerals. Our recorded transformation frequencies vary with mineral types and scales inversely with mineral surface charge and the ability of the mineral to immobilize the DNA in a liquid environment. We argue that the influence of mineral surface properties introduces interfacial geochemical processes as drivers for evolution and provide sedimentologic processes a central role in the evolutionary avenue of selection.

INTRODUCTION

Horizontal gene transfer (HGT) is recognized as the key source of accelerating genome innovation.[1] In HGT, extracellular or intracellular DNA from one species can be incorporated into a non-related species, and thereby efficiently increase genetic diversity. HGT is considered a common route to adaptation in microbes and HGT has had a significant impact on the evolution of life of both prokaryotes and eukaryotes.[2,3] HGT through conjugation and transduction are relatively well explored and conjugation is considered a key mechanism for the propagation of antibiotic resistance genes. **HGT by transformation, uptake** of extracellular DNA, is not considered an effective **mode** of **gene acquisition** as extracellular DNA degrades in a matter of days when it is suspended in e.g. seawater or a soil environment. [4-7] However, advances made in the field of sedimentary ancient DNA (SedaDNA) underlines that, DNA can be preserved for at least 2 Ma years, and the adsorption of the DNA to mineral surfaces are argued to be key for the preservation.[8] In principle, all sedimentary minerals all hold a potential to adsorb some amount of extracellular DNA. Currently there is about 0.45 Gt of extracellular DNA associated with sediments in the top 10 cm of the ocean floor, and more than 90% of that DNA extracellular. Increasing evidence suggests that bacteria can tap into the sedimentary DNA repositories for gaining fitness through uptake by transformation.[9-21] Despite this, the impact of facilitated through DNA uptake from minerals by transformation is not considered in evolutionary history.

It is becoming increasingly apparent that minerals can preserve DNA for geologic relevant timescales and that some minerals can act as vehicles shuttling DNA across time and environments. If bacteria encounter preserved DNA from past, distant or upstream environments, a transformation event can provide a cheap and effective opportunity for increasing fitness. The frequency of HGT events are rare, but in principle, the likelihood of a transformation event from mineral adsorbed DNA would be reinforced by the fact that many bacteria anchor themselves to mineral surfaces. Once a bacterial cell is anchored, the mineral can further act as a platform for distributing the newly gained trait to multiple organisms through successions of HGT. Minerals vary in surface properties, and we cannot generalize DNA retention, preservation, and potential availability for transformation across sediments or settings.

The minerals comprising sedimentary systems are diverse and they have distinct DNA adsorption capacities, which relate to the interfacial geochemical relationship between the mineral surfaces and the DNA molecules. The adsorption capacity determines how much DNA the mineral can adsorb at a given DNA concentration. The DNA-mineral affinity is often influenced by the environmental conditions such as solution pH, salinity, etc. Minerals with an overall positive surface charge and high densities of active sites such as clay edges, carbonates and oxyhydroxides are shown to have a higher DNA adsorption capacity and less dependent on solution composition than negatively charged minerals such as clay basal planes and silicate minerals. The negatively charged minerals are dependent on positively charged background ions to facilitate binding of the DNA and Atomic force microscopy has shown that the higher the charge density of the cation (ionic potential) the stronger the bond or the more immobilization of the adsorbed DNA molecule.

Effectively, bacteria can encounter mineral adsorbed DNA both on incoming sedimentary material and as historically present on site (a sedimentary deposit). DNA representing niches in an upstream environment can enter a downstream ecosystem through common sedimentary pathways, -provided the DNA-mineral bond can survive a potential change in chemical environment associated with relocation. Today, we find living bacteria in almost any niche and environment, including sedimentary deposits, representing past ecosystems.[22,23] Regardless of how contemporary microbes encounter mineral preserved DNA the mixing of modern microbes and older DNA represent a pathway for gene transfer, across a scale of time and space unrivaled by any other avenues.

The mechanisms and processes driving DNA uptake from mineral surfaces are still unclear. Integration of small DNA fragments in the bacterial genome is spontaneous and very simple in comparison to natural transformation of kilobase size DNA molecules (RecA-mediated). In fact, annealing at replication forks is the driving force behind transformation of bacteria with very short DNA fragments. During DNA uptake, bacteria degrade the DNA double helix and release single-stranded DNA into the cell. When the bacterial genome replicates, the released single stranded fragments can act as primers of new DNA and bind to the open chromosome near the replication fork, thereby incorporating foreign DNA in the genome of one of the daughter cells.[24] It is generally found that if an acquired gene/operon encodes beneficial traits in the host in a given environment, it will provide the host a fitness advantage, resulting in stabilization of the trait(s) in the population due to natural selection. It is clear that the DNA-mineral association is important for DNA preservation and shuttling to distant settings, but it is unclear if the DNA-mineral bond (strength, number of binding sites etc., type of bond) influences the availability of the DNA molecule to the microbe. Studies describing uptake and incorporation of mineral-adsorbed DNA have been limited to DNA that are several kilo base pairs in length. Transformation of mineral adsorbed plasmid and whole genomic DNA are shown from clays (kaolinite and montmorillonite) and iron oxy-hydroxides (goethite).[11,18] While DNA molecules are found associated with many sediments including soils [25], it is highly unlikely that the DNA will remain intact for longer timescales, owing to degradation processes such as spontaneous hydrolysis, action of nucleases and UV-mediated degradation. Common for sedimentary ancient DNA (sedaDNA) is that it is highly fragmented and degraded< 100 base pairs (bp).[26-28] The potential relevance of even short DNA for transfer was highlighted by Overballe-Petersen *et al*., showing that fragmented DNA molecules down to 20 bp could be successfully incorporated into the genome of *Acinetobacter baylyi* via transformation of suspended DNA.[29]*A. baylyi* is a naturally competent bacteria and can hence integrate DNA fragments in their genome by actively pulling DNA from their environment. The fragments

provide naturally competent bacteria with nucleotides and allows them to change their genotype. *A. baylyi* is a highly competent and recombinogenic soil bacterium, *which do not* have any sequence requirements for DNA uptake, making it an attractive target for HGT studies.[30]

Here, we explore if mineral preserved DNA can have a broad impact on the evolution of life as suggested by Sand and Jelavic.[31] We tested if fragmented DNA (60 bp) adsorbed to a broad range of environmental relevant minerals can be transferred via uptake to *A. baylyi*. We inquired if the DNA-mineral association, besides being relevant for DNA preservation, also play a role for transformation efficiency, i.e. will a DNA strand loosely associated with a mineral surface be faster to incorporate than a DNA strand tightly adsorbed -if at all? A difference in uptake associated with DNA-mineral associations can have implications to which environment would enhance our proposed evolutionary pathway.

We used *A. baylyi* and relevant soil minerals such as iron oxides and hydroxides (hematite and goethite); clays (kaolinite and mica); carbonates and non-clay silicates (quartz) to evaluate their potential in facilitating DNA uptake by bacteria. We synthesized short DNA molecules of 60 bp encoding the *trpE* gene, adsorbed these fragments to the mineral surfaces of iron oxyhydroxides (hematite and goethite); clays (kaolinite and mica); carbonates and a non-clay silicate (quartz). We allowed transformation to occur in the presence of nutritionally deficient and rich conditions. The minerals display a broad range of DNA adsorption capacities and we link the strength of DNA-mineral association to uptake frequency by considering the mobility of the mineral adsorbed DNA as well as overall mineral surface charge and local charge densities. It was observed that minerals with a net negative charge like quartz and mica were the most efficient for transformation whereas hematite and goethite with a strong positive charge could bind DNA with a high affinity were the poorest DNA donors.

RESULTS AND DISCUSSION

Uptake by transformation

The experimental strategy and protocols used for DNA adsorption and horizontal gene transfer experiments are depicted in Figure 1.

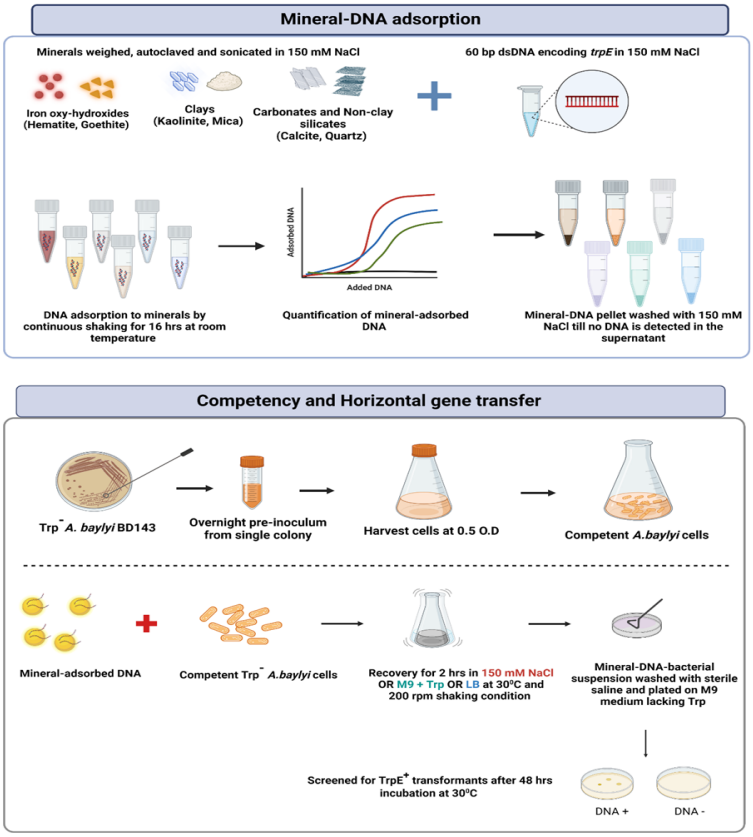

Figure 1: Schematic outlining the experimental strategy used for preparation of mineral-DNA complexes for adsorption as well as competent cell preparation and mineral-facilitated horizontal gene transfer.

DNA adsorption

The minerals provided distinct adsorption capacities of the 60 bp DNA fragments encoding *trpE* in the 150 mM NaCl solution. The adsorption to goethite, kaolinite, mica, calcite and quartz plateaued at higher DNA equilibrium concentrations indicative of monolayer adsorption (Fig. 2 and S1). Goethite had the highest maximum adsorption capacity of ~45 µg/mg, followed by hematite with a maximum adsorption capacity of 10 µg/mg. Kaolinite adsorbed a maximum DNA concentration of ~ 4 µg/mg whereas calcite, mica and quartz adsorbed the lowest amount of DNA per mg of mineral (0.1-0.2 µg/mg). Goethite, kaolinite, calcite and mica were fitted to a Langmuir isotherm. Hematite and quartz, conformed well to a Freundlich isotherm with no surface saturation. For most of the minerals, we aimed to add a concentration of DNA to the transformation experiments where the mineral was not yet fully saturated with DNA and we used the adsorption isotherms as guides to select the DNA:mineral ratio applied in the transformation experiments. The mass of mineral (mg), DNA concentration (µg/mL), amount of DNA adsorbed (µg/mg) and the adsorption parameters in the experiments are given in Table S2.

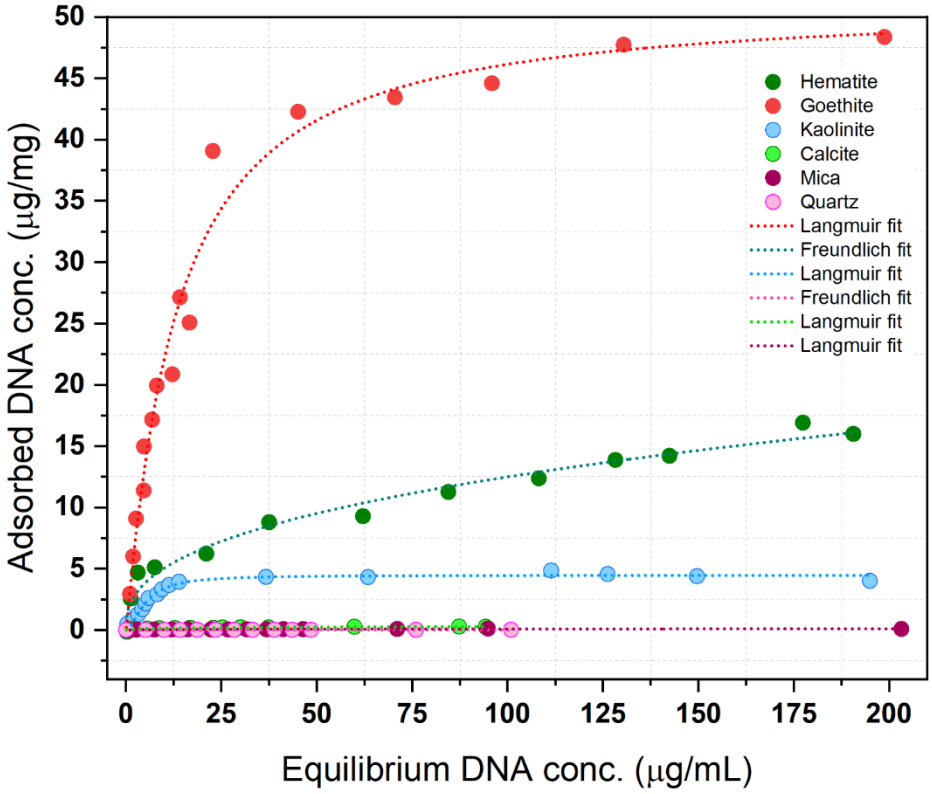

Figure 2: Equilibrium adsorption of salmon sperm DNA to minerals in saline under physiological conditions. Serially increasing concentrations of salmon sperm DNA (0-200 µg/mL) were mixed with sonicated mineral suspensions in 150 mM NaCl at pH 7. After incubation for 16 hrs, the amount of adsorbed DNA was estimated using absorbance at 260 nm for the indicated minerals. Langmuir or Freundlich fitting was performed to generate the adsorption isotherms for each DNA-mineral pair. The data are representative of three experiments and are plotted as mean.

Transformation

The transformation efficiency of *trpE* DNA into *A. baylyi* was estimated by screening the transformants on M9 agar plates lacking exogenous tryptophan. As shown in Figure 3, different minerals resulted in different transformation efficiencies. Cells incubated with 10 ng/µL suspended DNA served as the control. The transformation efficiency of *A. baylyi* ranged from 0.1 to 4 cells/µg DNA and was strongly dependent on the mineral type. The negatively charged minerals, quartz and mica, which had the lowest DNA adsorption capacity and the weakest DNA-surface interactions, displayed the highest uptake efficiency. The strongly positively charged hematite, which had the highest DNA adsorption capacities and were able to immobilize the adsorbed DNA, resulted in the lowest transformation efficiency. Natural environmental settings are a mix of nutritionally rich and poor conditions. To test the effects of nutrient supply on the efficiency of transformation, we allowed the cells to recover either in saline (150 mM NaCl), M9 supplemented with tryptophan, or LB, and plated them on M9 agar lacking tryptophan to score for transformants. We observed that the transformation efficiencies were the lowest when cells were grown in saline and were the highest for M9 and LB media, demonstrating that nutritionally rich conditions further facilitate DNA uptake owing to more energy available. Transformation by short DNA fragments is dependent on annealing at the replication forks. In nutritionally rich media, cell division will be higher than in nutritionally poor conditions. Rapidly growing cells have chromosomes with multiple replication forks , offering a high probability and faster uptake frequency of integration of DNA fragments in the bacterial genome.[32] We measured cell viability to access if the presence of any of the minerals would compromise cell health and hence influence transformation efficiency. With the

exception of goethite and hematite, no significant reduction in the cell viability was observed for the minerals (Figure S2). The growth pattern was consistent when the cells were cultured in either saline (150 mM NaCl), M9 supplemented with tryptophan or LB. Growth was observed only when *A.baylyi* was plated on M9 agar supplemented with tryptophan, owing to its prototrophic nature.

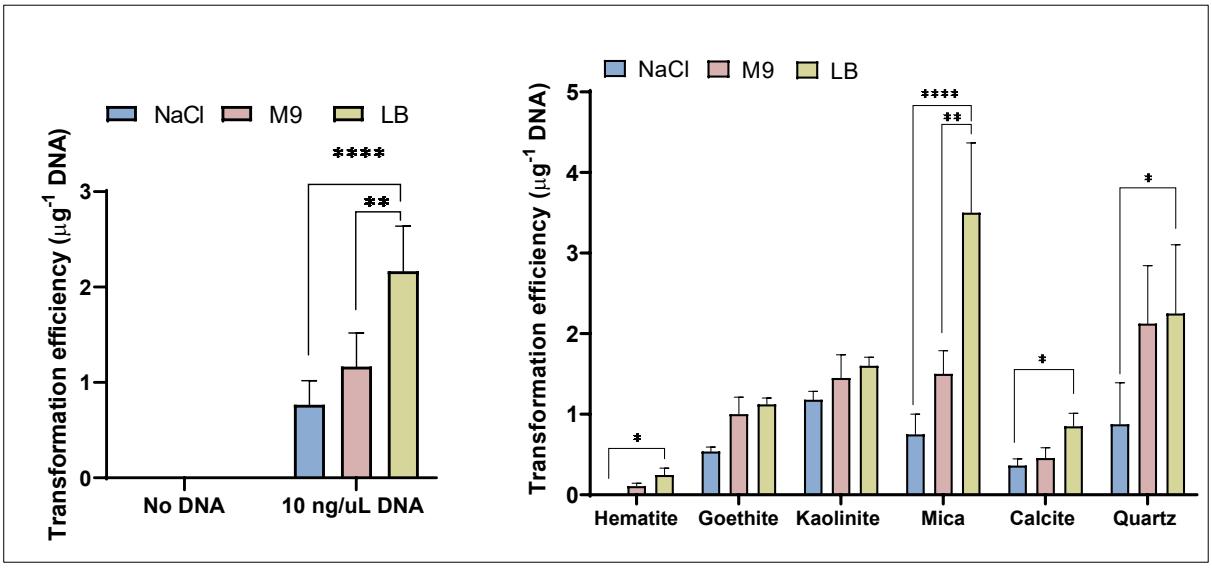

Figure 3: *A. baylyi* is transformed by mineral-adsorbed DNA under nutritionally poor and rich conditions. Competent *A. baylyi* cells were exposed to 60bp *trpE*$^{+}$ DNA fragments adsorbed to different minerals as indicated. Recovery of the cells was performed in either saline (150 mM NaCl), M9 supplemented with tryptophan or LB medium for 2 hrs. The transformants were screened using M9 lacking tryptophan and reported as transformation efficiency per µg DNA obtained using (a) Free DNA and (b) Mineral-adsorbed DNA. The data are representative of three biological replicates and are plotted as mean ± S.D. Statistical analysis was performed using two way ANOVA.

Translating to a natural setting

The uptake efficiency of the 60 bp fragments (0.1-4 cells/µg DNA) in our setup is small relative to reported rates of mineral adsorbed plasmids and whole genomes. Previous reports have shown that transformation frequencies of *Bacillus subtilis, Pseudomonas stutzeri* and *Acinetobacter calcoaceticus* declined with decreasing molecular size of DNA.[33,34] The transformation efficiency of *B. subtilis* by sand-adsorbed chromosomal DNA was 50 times higher when compared to free DNA.[9] On the other hand, other soil bacteria such as *P. stutzeri* and *A. calcoaceticus* showed the same transformation frequencies irrespective of whether chromosomal DNA was adsorbed to sand or free.[10,12].

Despite the low transformation frequencies observed with small and fragmented DNA, it is important to consider the potential for DNA recombination based on the DNA content present in the environment. Majority of the environmental DNA is fragmented and exists in various degradation stages.[16,35,36] It was shown that DNA fragments of up to 20 bp can successfully transform bacteria and that the mechanism of such DNA incorporation is different from the classical homologous recombination of large DNA molecules. Gigatons of fragmented DNA and the simple integration mechanism of annealing to replication forks in bacteria means that short and damaged DNA can virtually integrate in any cell. For the long-term evolutionary impact of genetic changes, the frequency of integration does not play a key role. It is the selective advantage that determines whether the genetic change will get established in the population or not.

DNA-mineral associations and proposed effect on uptake frequency

The rate of uptake scaling with mineral surface charge is in line with interfacial geochemical principles. In general, a direct interaction between a positively charged mineral surface site and a negative phosphate backbone group would facilitate a stronger bond than an association to a negatively charged surface site - mediated by the Na^+ ion in this case. A mineral surface is rarely homogeneous and all surfaces used in this study, but quartz, have different types of site chemistries and composition (Supporting). Mineral surface charge is in general considered important for adsorption, but DNA adsorption dynamics to mineral surfaces has been shown to be related to local charge densities more so than overall surface charge. Atomic force microscopy provides information of which sites on a particular surface the DNA associates with and fast scanning in liquid gives insight to the mobility of the adsorbed DNA. Visualizing DNA- a molecule with a topography of about 2 nm- we need a flat surface and we chose three representative surfaces: (10.4) calcite, mica and (001) hematite in the 150 mM NaCl solution (discussion on choice in methods). The calcite surfaces display charge dense step edges and terraces that are overall positively charged. Mica is atomically flat and has a permanent negative charge. The hematite 001 is the most stable hematite face in nature and represents a general trend for DNA adsorption on iron oxides terraces.

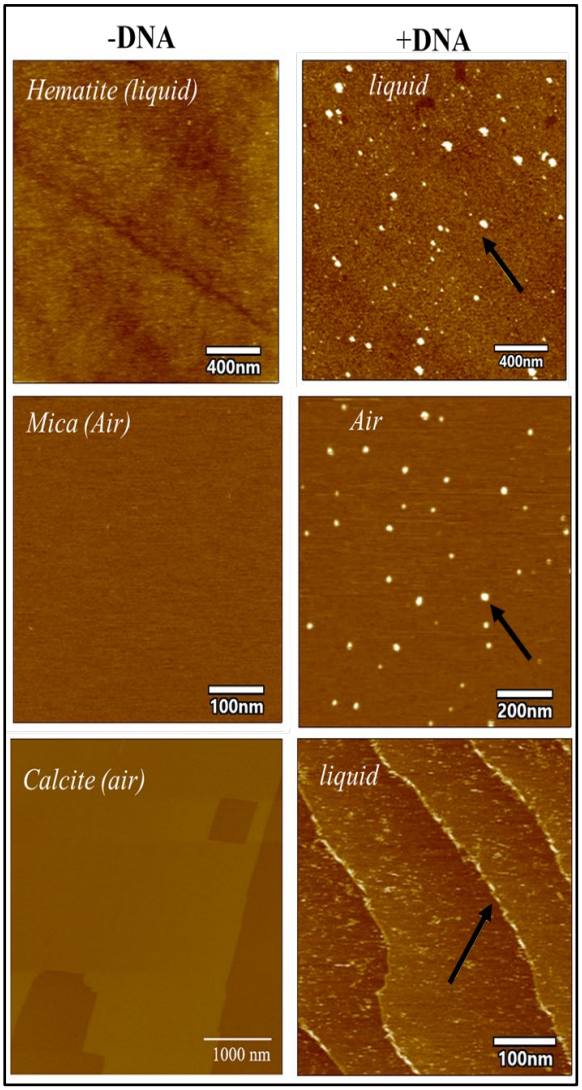

Figure 4: Atomic Force imaging in liquid shows DNA conformation on the mineral surfaces with varying charges. 60bp DNA fragments were allowed to bind to (a) hematite crystal; (b) mica and (c) calcite crystal in the presence of 150 mM NaCl at pH 7 and imaged in liquid or air conditions. (Liquid: Hematite, calcite; Air: Mica). Black arrows indicate DNA.

To visualize biomolecules with AFM in liquid conditions, the molecules need to be adsorbed strong enough - i.e. have enough anchor points to the surfaces- for the AFM probe to scan the molecules. If biomolecules have too few anchor sites, and / or are too loosely bonded, the AFM tip will merely move the molecule and cannot display a scan of the full molecule. The negatively charged mica surface did not provide a charge landscape facilitating a bond to the negatively charged DNA backbone that allowed us to image the DNA in liquid. Drying the sample and scanning in ambient air did reveal adsorbed molecules highlighting the DNA and the surface had formed a weak association. At the hematite surface, the DNA is readily and stably attached, owing to its positive surface charge. The interaction between DNA and hematite was strong enough to be visualized even under liquid conditions (Fig 4 and Fig S3). The calcite surface displayed its characteristic step edges and terraces and the DNA molecules aligned along the positively charged step edges. Most of the DNA was found to be associated with the step edge whereas a few DNA molecules were observed on the negatively charged calcite terraces. The DNA adsorbed on the step edges did not move during imaging in liquid conditions whereas the DNA adsorbed to the terraces moved during imaging. The AFM was able to scan the moving DNA strands on the terraces highlighting that the DNA here was strongly bonded than at the mica surfaces. In light of how the DNA-mineral association influences mobility of the adsorbed DNA, we find the amount of surface binding sites and the bond strength may well explain the differences we observed in the uptake efficiencies.

The uptake efficiency was highest for quartz, mica and kaolinite. The quartz and the mica and kaolinite basal planes will absorb the majority of the DNA through a Na^+ bridge. From the AFM images, it is clear that the DNA is highly mobile and weakly adsorbed and could be argued to be easily accessible for uptake. The DNA adsorbed on the positively charged clay sites (edge sites and kaolinite octahedral planes) would be stronger bonded and following out logic - available for uptake at a slower rate. Goethite, calcite and hematite can provide a direct electrostatic bond to DNA. The majority of the DNA adsorbed to calcite is adsorbed strongly (in the sense that it is immobilized) which, following our hypothesis, could explain the low uptake frequency. We cannot address though, if the DNA removed by the bacteria was dominantly the small number of mobile strands associated with the terraces. Goethite and hematite are nanoparticles and contain a range of different crystal faces and surface sites. In general, goethite has a higher number of active sites than hematite and is more positively charged, which is also showed by our zeta potential and adsorption data where goethite has a much higher adsorption capacity for DNA than hematite (4 times higher). Goethite has been shown to adsorb DNA though direct electrostatic bonds (Inner-sphere).[37] Goethite is naturally hydroxylated and wetted by water at all pH values but the dominant crystal face of hematite (001) is slightly hydrophobic at natural pH values that will change the DNA-mineral bond character. Molecular dynamics simulations have shown that hydrophobic graphene would bond via the base pairs through π–π stacking [38] and hydrogen bonding.[14,39,40] Freeman shows that hydrogen binding through amines provides a strong bond and in the case of calcite, in fact can lead to fragmentation of the strand because of loss of intra helix hydrogen bonds as a result of the bond to the surface.[41] Surface hydrophobicity can also lead to enhanced associations between surfaces and bacteria and essentially facilitate a lower mobility of bacteria adsorbing to the hematite.[42]

Drivers for uptake efficiency

Bacterial transformation in mineral systems have been shown to be affected by adsorption of competency signaling molecules, altered expression of competency genes, by membrane damage enhancing permeability and reduction of motility. [19,43,44] Huang *et al.*, found that kaolinite and montmorillonite inhibited the transformation of *B.subtilis* by adsorbing a key signaling molecule of competency. They also found that high goethite cell ratios caused membrane damage which facilitated uptake of foreign DNA in *B. subtilis.*[18] Similar effects were observed for magnetite and nano-Al_2O_3 which increased transformation of antibiotic resistance genes in *E. coli* by altering membrane permeability.[43,44] In addition, flagellar motility was reduced through bacterial association with phyllosilicate minerals causing downregulation of competency genes and reduced transformation.[19] In our study, we added cells at maximum competence to the mineral suspension. We cannot rule out that the competent bacteria could have lost some competency because of adsorption of the signaling molecules on the mineral surfaces over the course of 2 hrs of incubation. However, we are not convinced

that adsorption of signaling molecules is the (only) reason for the low efficiency observed for hematite. Across the literature, goethite, in general, has a higher adsorption capacity than hematite for organic compounds [45] and if the bacteria lost competence because of adsorption of signaling molecules, we would assume goethite to adsorb more signaling molecules than hematite. We did observe a slight reduction in the viability when bacteria were exposed to goethite and hematite, which suggests low cell numbers compared to the other minerals. However, high transformation frequency for goethite is possibly due to goethite-induced enhanced membrane permeability, allowing more DNA molecules to enter the bacteria.

Overall, our results demonstrate that the transformation frequencies vary with the mineral types. The uptake rate scales inversely with binding capacity/binding strength. While DNA-mineral interactions play a major role in the release of DNA to the bacteria, it is also possible that the minerals affect the expression of competency genes in *A. baylyi* as well and the minerals with a high adsorption capacity adsorbed more of the competency genes. On the other hand, DNA uptake can also be enhanced because of membrane damage and especially for goethite, bacterial membranes are shown to be compromised upon interaction. Again, if the iron oxides induced membrane damage, we would expect a high uptake rate. Taken together, we find it most plausible that the DNA-mineral interactions are the main driver of the measured uptake efficiency (and in the case of hematite, bacterial affinity may decrease motility).

From a fundamental point of view, it is interesting to unravel the reason behind the differences in uptake rate provided by the different minerals. However, assigning certain minerals to be more efficient at facilitating HGT may be redundant because of the ease of incorporation and availability of DNA fragments in the environment. Owing to the universality of the mechanism behind the uptake of short and fragmented DNA, its integration can in essence occur in any cell. Therefore, it can be reasonable to assume each time a cell encounters short and degraded DNA there is a probability, although small, that the cell is transformed. In that light, environments prone to enable mineral facilitated HGT are tied to environments that store DNA and essentially are able to preserve DNA across time and space.

Repository of DNA in sediments

It is clear that we have large amounts of extracellular DNA associated with sediment across our sedimentary systems - and clay minerals are able to store much more DNA than e.g. quartz. . The adsorption capacity of DNA and subsequent strength of the DNA-mineral complex is dominated by a charge-dependent process and thus the rate and extent of adsorption of dissolved DNA to minerals depends largely on the type of mineral and the pH of the bulk phase. That also entails that the DNA adsorption capacity and mobility of the strand on e.g. quartz change with the environmental conditions. Once adsorbed, on a mineral surface, the mineral has the potential to shuttle the DNA relatively safely to different environments. For DNA to be transported on mineral surfaces and maintain adsorbed, a strong adsorption appears to provide better survival of the complex. If we consider that mineralogy and mineral surface characteristics play a role for DNA adsorption, preservation and as uptake efficiency setting containing minerals with a high DNA adsorption capacity and/or high preservation potentials would consequently support mineral facilitated HGT more so than others, -although the uptake efficiency may be low. It can be argued that the uptake efficiency is not of major importance for long-term evolutionary outcomes simply because of the large amount of fragmented DNA present in the environment as argued by Pettersen et al.[46] Consequently, as we are able to transform mineral adsorbed DNA from all tested minerals – even at low nutrient conditions we claim that mineral facilitated horizontal gene transfer provide a cheap option for bacteria to gain fitness. Following integration in the primary recipient bacteria, in this case *A. baylyi*, the traits can be further disseminated by means of both vertical gene transfer and HGT, not limited to transformation which would propagate the gained advance effectively.

Significance and scenarios of implications for evolution of bacterial life

Expanding our interpretations from this study following the principles of interfacial geochemistry, mineral facilitated HGT can be considered relevant across a broad range of sedimentologic deposits and environments. Bacteria can inhabit historic deposits and acquire old traits. DNA molecules shuttled to distant environments on mineral surfaces could also be utilized both close to and far from the DNA-mineral complex formation. However, as local microbes adapt to the flux of available genes not much would be left in terms of new traits, unless there is a disturbance distal to the catchment. We anticipate that abrupt changes such as landslides, flooding, or even a new meander on a river can cause new niches to open and e.g. provide a flux with different coded traits. It is in such scenarios of stress the requirement for new traits is in high demand and is when shortcuts to fitness are important and is when membrane permeability enhances uptake capacity.

The requirement for DNA fragments to be incorporated are much less than for larger DNA molecules and the small fragments are easily and naturally taken up and annealed in the replication fork.[24] However, horizontal transformation of plasmid DNA from mineral surfaces my not be as easy as for fragments, but it has shown to be occurring in a lab setting. Set in an environmental and sedimentologic context, transformation of plasmids adsorbed to minerals would mainly occur during mineral deposition or during sediment transport rather than from old DNA in historic deposits. Regardless, we find that DNA encoding beneficial traits favored by selection can be acquired from minerals from a broad range of geologic and environmental settings and end up in highly diverse members of bacterial communities.

We argue that fitness acquired by mineral facilitated horizontal gene transfer can have vast implications for the evolution of organisms that can acquire genes through transformation. Discussing fitness in terms of a fitness landscape, the fittest populations (i.e. they are adapted to their local environment) are found at the summit and the less fit are in the valleys. If a fit population experiences a change in the environmental conditions or depositional setting, it can lose its fitness and move down the landscape toward the valley. However, changes in the geological setting are thought to remodel the fitness landscape by building bridges between summits enabling a population to by-pass the valley.[47] Mineral facilitated HGT offers populations a pathway to retain or obtain fitness during a change in the environmental conditions and for catalyzing "the evolutionary flight" to reach the next summit. In this scenario, a geologically provided sedimentary and environmental setting for preserving DNA would enhance the adaptive potential for obtaining fitness.

CONCLUSION

We demonstrate that mineral-adsorbed 60 bp *trpE*$^{+}$ DNA can transform an auxotrophic *A. baylyi* strain with an absolute requirement for exogenous tryptophan into a prototrophic strain that can synthesize tryptophan endogenously. We find that minerals with different surface properties can adsorb fragmented and damaged DNA to varying extents. Iron oxyhydroxides were the most efficient adsorbers of DNA followed by clay and silicate minerals. We argue that mineral-facilitated HGT provides a mechanism for rapid adaptations and we speculate that it would provide an efficient path to fitness when there is an abrupt change in the environmental conditions or other evolutionary drivers associated with a shift in the provenance of incoming sediments.

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CONFLICT OF INTEREST

The authors report no conflicts of interest.

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