Resurrecting host–microbiome interactions: combining resurrection ecology and microbiome transplants to test temporal local adaptation

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Abstract

Host-associated microbiomes can influence fitness, respond rapidly to environmental change, and potentially contribute to host adaptation. Yet, determining whether host–microbiome associations evolve adaptively over ecological timescales remains challenging because historical host genotypes and their associated microbial communities are rarely available for experimental comparison. Resurrection ecology offers a means of recovering historical host genotypes from dormant propagules, while microbiome transplantation provides an experimental approach for testing the effects of microbial communities on host performance. Combining these approaches could enable direct tests of temporal local adaptation in host–microbiome associations. Freshwater *Daphnia* provide a promising model because their dormant eggs can persist in lake sediments, allowing historical host genotypes to be resurrected. However, the microbiota associated with dormant eggs may originate from multiple sources, including ancestral hosts, lake water, and surrounding sediment, complicating the recovery of historically associated microbial communities. We outline a framework combining sediment archives, host resurrection, microbiome characterisation, and reciprocal transplantation experiments to test whether historical and contemporary hosts perform better with microbiomes from their respective time periods. We discuss the conceptual predictions, methodological challenges, and experimental controls required to distinguish temporal local adaptation from microbial environmental effects, host-genotype specificity, and changes in community composition. This framework could extend resurrection ecology beyond host evolution to experimentally investigate the historical evolution of host–microbiome interactions.

1. Introduction

Microbiomes influence host nutrition, development, immune function, stress tolerance, and survival, making host–microbiome interactions important components of ecological and evolutionary processes (Foster et al., 2017; Koskella et al., 2020). Microbial communities can respond rapidly to environmental change, potentially modifying host responses to changing ecological conditions. However, demonstrating that these associations evolve adaptively over time requires more than documenting changes in microbiome composition or correlations between microbial communities and host performance. It requires experiments that distinguish adaptive changes in host–microbiome associations from environmental filtering, ecological turnover, and non-adaptive temporal variation.

Research on *Daphnia* provides a strong foundation for investigating these questions. Laboratory experiments have shown that associated microbiota can affect host survival, growth and reproduction, with effects depending on environmental conditions such as food availability (Sison-Mangus et al., 2015; Callens et al., 2016). Other studies have characterised bacterial community composition and potential functional capacities, including genes associated with nutrient acquisition and metabolism (Cooper et al., 2020), while experiments using natural and laboratory-derived inocula demonstrate that microbial communities and their effects can differ between field and laboratory settings (Houwenhuyse et al., 2023; 2025). A recent synthesis by Gurung et al. (2026) revisited whether *Daphnia magna* possesses a core microbiome, identifying recurring associations with particular taxa, especially *Limnohabitans planktonicus* in laboratory cultures. However, these associations were less consistent in field-grown animals, leaving the extent of a stable core microbiome—and the degree to which commonly associated bacteria are host-selected rather than environmentally acquired—an open question (Gurung et al., 2026; Freese and Schink, 2011). Thus, although the structure and function of *Daphnia* microbiota are increasingly well characterised, the origins and persistence of host–microbe associations remain important uncertainties.

Resurrection ecology provides a powerful approach for addressing this challenge. By reviving dormant organisms preserved in natural archives, researchers can compare historical and contemporary genotypes under controlled conditions, testing

evolutionary responses to environmental change (Burge et al., 2018; Weider et al., 2018). In freshwater ecosystems, dormant eggs of *Daphnia* can preserve historical genetic variation within lake sediments, enabling comparisons between past and present populations. When combined with long-term environmental monitoring, these archives offer opportunities to investigate how populations have responded to anthropogenic pressures, including eutrophication and climate change.

Microbiome transplantation provides a complementary experimental tool (Villegas et al., 2026). Reciprocal transplantation can test whether microbial communities originating from different hosts or environments have differential effects on host fitness. For example, experiments with *Daphnia magna* have shown that microbiome composition can alter host responses to environmental stressors, including hypoxia, and that the consequences of microbiome manipulation can depend on host genotype and environmental conditions (Coone et al., 2023; Callens et al., 2016). More recent work comparing natural and laboratory-derived microbial inocula further demonstrates that microbiome provenance can influence host responses to combined stressors, underscoring the importance of testing microbial effects in ecologically relevant contexts (Houwenhuyse et al., 2025).

Despite these advances, and to the best of our knowledge, resurrection ecology and microbiome transplantation have never been integrated into a framework designed to test whether host–microbiome associations have adapted during historical environmental change. Combining the two approaches would allow researchers to compare historical and contemporary hosts and microbial communities, testing whether their effects on host fitness depend on their temporal origin. We propose that this integration could establish a framework for microbial resurrection ecology, in which historically associated microbial communities are recovered, characterised, and experimentally tested alongside resurrected hosts (Fig. 1).

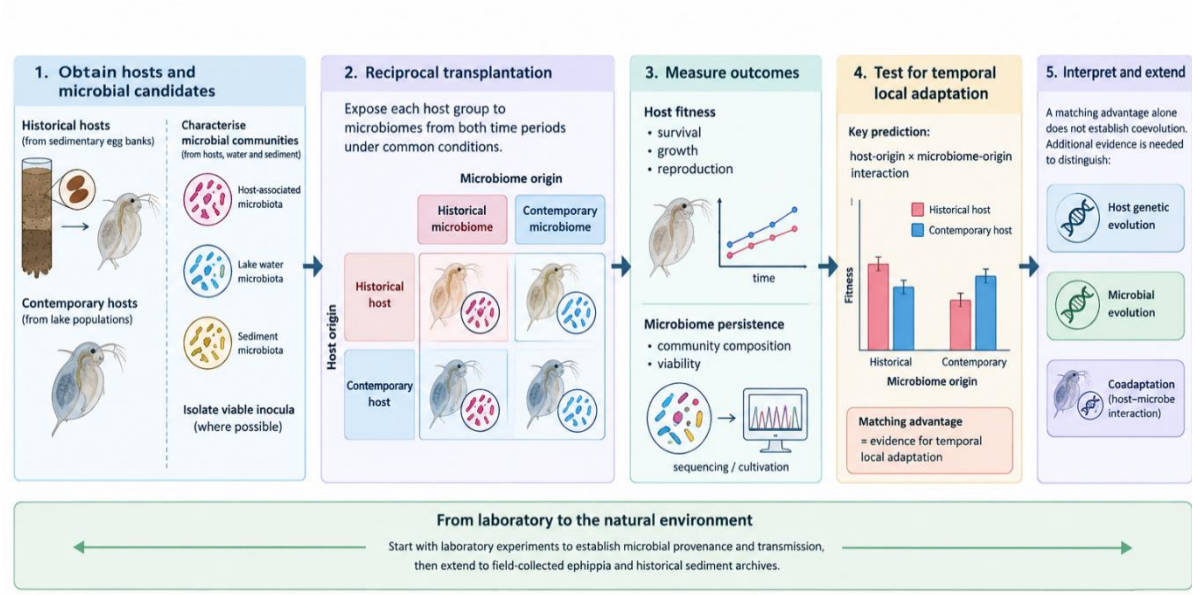


Figure 1. Framework for testing temporal local adaptation in host–microbiome associations. Historical and contemporary *Daphnia* hosts are paired with microbial communities from different time periods in reciprocal-transplant experiments, following characterisation of candidate microbiota from hosts, lake water, and sediment; host fitness and microbiome persistence are measured under common conditions. A host-origin × microbiome-origin interaction consistent with a reciprocal matching advantage would support temporal local adaptation, while distinguishing host evolution, microbial evolution, and coadaptation requires further evidence, with experiments progressing from controlled laboratory tests to field-collected ephippia and historical sediment archives.

The central challenge is that recovering a historical host does not necessarily recover its historical microbiome. This distinction is especially important for *Daphnia*, whose dormant eggs are enclosed within ephippia and may encounter microorganisms from several sources during egg formation, burial, and hatching. Given the potential for host-associated communities to change rapidly following transfer from the field to laboratory conditions, and the uncertainty surrounding the distinction between host-associated and environmentally acquired bacteria, resolving these sources is a prerequisite for interpreting reciprocal microbiome transplant experiments.

2. What does temporal local adaptation mean for host–microbiome associations?

Local adaptation conventionally occurs when organisms achieve higher fitness in their native than in foreign environments (Kawecki & Ebert, 2004). For host–microbiome associations across time, the equivalent question is whether hosts perform better with microbiomes from their own historical period.

A reciprocal transplant of historical and contemporary hosts and microbiomes tests this prediction. The key test is a host-origin × microbiome-origin interaction: the effect of microbiome origin on fitness depends on host origin (Koskella & Bergelson, 2020).

Three outcomes are informative. Temporal matching occurs when historical hosts perform better with historical microbiomes and contemporary hosts with contemporary microbiomes, consistent with temporal local adaptation. Microbiome main effects occur when one community benefits both host groups, suggesting general differences in microbial effects rather than temporal matching. Host-specific or asymmetric effects occur when benefits depend on host genotype or particular temporal combinations, potentially reflecting genotype-specific compatibility, evolutionary lag, or changing microbial effects (Kawecki & Ebert, 2004; Koskella & Bergelson, 2020).

A matching advantage does not, by itself, establish coevolution. It could arise through host evolution, microbial evolution, or changes in their interaction. Stronger claims of coadaptation require evidence of coordinated changes in host and microbial traits, ideally supported by experiments separating host-genetic from microbiome-mediated effects (Koskella & Bergelson, 2020; Douglas & Werren, 2016).

This distinction matters because microbial communities can change through ecological processes without microbial evolution, while host adaptation can indirectly alter microbiome composition by changing the host environment. Fitness measurements should therefore be combined with characterisation of host genotypes and microbial communities, treating temporal matching as evidence consistent with adaptation rather than proof of coevolution (Koskella & Bergelson, 2020).

3. Resurrection ecology provides the temporal framework

Sediment archives containing dormant *Daphnia* eggs offer a means of recovering hosts from different historical periods. By isolating eggs from dated sediment layers and hatching them under controlled conditions, researchers can compare resurrected historical genotypes with contemporary populations (Burge et al., 2018; Weider et al.,

2018). The availability of long-term ecological monitoring can help relate these comparisons to historical environmental change.

However, historical host resurrection and microbiome resurrection are distinct methodological problems. Dormant eggs can preserve viable host embryos, but the microorganisms detected on or within an egg may not all represent the host's original microbiome. DNA sequencing alone cannot distinguish viable microorganisms from dead cells or extracellular DNA, nor can it establish whether detected microorganisms were transmitted by the mother, acquired from lake water during egg formation, or associated with the egg after burial (Emerson et al., 2017; Capo et al., 2022).

This distinction is supported by experimental work on *Daphnia* diapause. Mushegian et al. (2018) found that microorganisms associated with the ephippial exterior could contribute to normal growth and reproduction after hatching, whereas microorganisms from inside the ephippium alone were insufficient under their experimental conditions. Their findings demonstrate that the environment can provide functionally important microorganisms during emergence from dormancy.

Consequently, the historical microbiome of a resurrected host should not be assumed to be equivalent to the microbial community recovered from its dormant egg. Instead, researchers must establish the provenance, viability, and functional relevance of candidate microbial inocula before interpreting their effects in reciprocal transplantation experiments.

4. Identifying the origins of microbiota associated with dormant eggs

A major challenge for microbial resurrection ecology is distinguishing host-associated microorganisms from those acquired from the environment. Three potential sources are particularly relevant to *Daphnia* ephippia: maternal host-associated microbiota, lake-water microorganisms encountered during ephippium formation, and sediment-associated microorganisms acquired after burial (Figure 2). These sources may contribute differently to the microbiota of dormant eggs and emerging offspring, and their relative contributions and persistence remain uncertain.

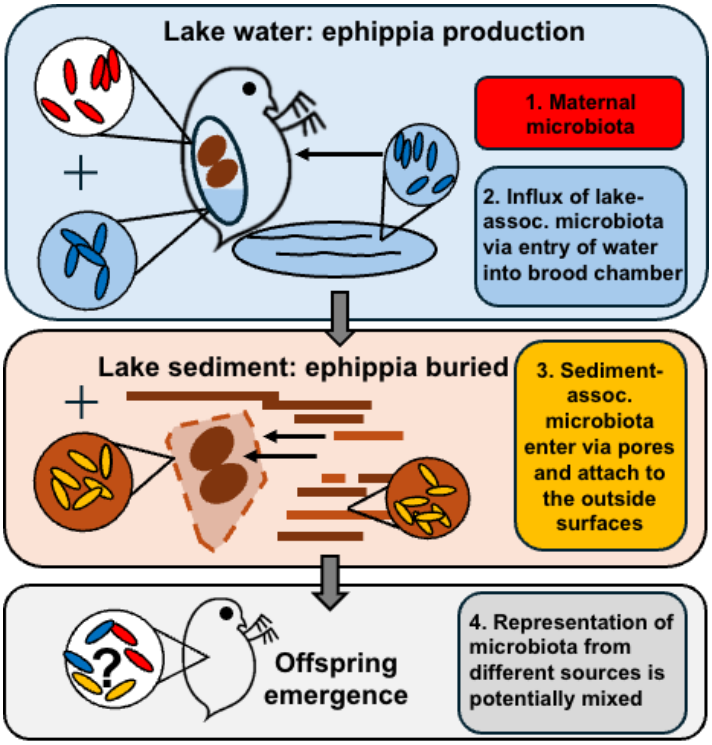


Figure 2. Potential sources of microbiota associated with dormant *Daphnia* ephippia. (1) The ancestral host may pass on some of its microbiota (red) during diapause. (2) Environmental microbiota from the lake (blue) may enter the brood chamber (Schultz, 1977). (3) Following burial in lake sediment, environmental microbiota from the surrounding sediment (orange) may attach to the outside of the egg case (dashed brown line), potentially penetrating its pores (Schultz, 1977). (4) The relative contributions of environmental (lake- and sediment-derived) and ancestral host-associated microbiota to the communities of emerging offspring remain unknown, as do the relative roles of direct vertical and environmentally mediated transmission in sustaining long-term host–microbiota associations.

Mushegian et al. (2018) showed that bacteria associated with field-collected ephippia could support normal *Daphnia magna* growth and reproduction after hatching. However, they did not characterise surrounding sediment microbiota, so the origins of these bacteria could not be established. Ephippia were collected from bulk sediment in 2009 and stored moist, in darkness, at 4°C for several years; individual ages were unknown. Although beneficial bacteria remained associated with the stored ephippia, the study did not test whether storage altered microbial composition or viability. These

limitations caution against treating ephippia-associated communities as verified historical host microbiomes.

Two complementary approaches could address these uncertainties. First, controlled laboratory experiments could manipulate maternal microbiota, lake-water exposure, and sediment-associated microorganisms independently, characterising communities in maternal hosts, water, newly formed ephippia, and emerging offspring. Second, field studies could compare freshly collected ephippia with matched sediment and water samples, standardising and documenting storage. Controlled storage experiments could assess effects on community composition and microbial viability, since storage can alter inferred microbiome composition in other sample types (Lauber et al., 2010; Poulsen et al., 2021). Such effects should be tested rather than assumed.

Compartment-specific analyses could further distinguish candidate sources (Figure 3). The ephippial casing, internal matrix, and dormant eggs could be analysed separately and compared with environmental samples. Sequencing would identify candidate taxa, while cultivation, where feasible, would establish whether viable isolates can be recovered for subsequent tests of colonisation and host fitness.

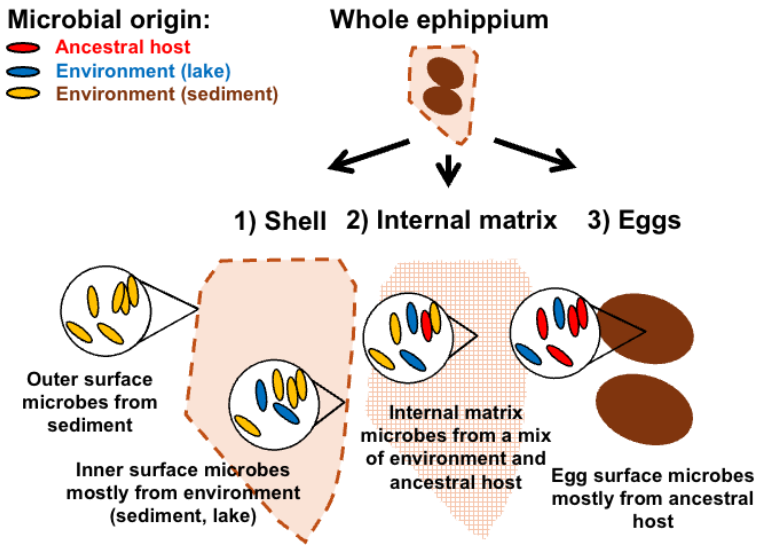


Figure 3. Compartment-specific characterisation of ephippium-associated microbiota. Putative microbial sources across different structural components of ephippia. Whole ephippia can be divided into three components with presumed differences in where their localised microbes originate from (explained in Fig. 2). 1)

The protective cover (a chitinous shell) with microbes on its outer and inner surfaces that presumably originate from the sediment (orange) and ancestral lake (blue) environments (sediment entry via pores and mixing of ancestral lake water with brood chamber during ephippial development; Schultz, 1977). 2) The internal matrix covering the resting eggs (Hiruta and Tochinai, 2014) with a mixture of microbes that presumably originate from both the environment and ancestral host genotype (red). 3) The pair of dormant eggs (each containing a single embryo in the blastula stage; von Baldass 1941) with microbes that presumably originate mainly from the ancestral lake environment (entry of water into the brood chamber during resting egg development; Schultz, 1977; Mushegian et al., 2018) and ancestral host genotype via maternal investment into dormant eggs (limited sediment originating microbes expected due to non-exposure).

Neither compartmentalisation nor taxonomic similarity alone demonstrates vertical transmission: microorganisms may move between compartments, and shared taxa may reflect environmental acquisition. DNA detection also does not establish viability, while failure to cultivate a taxon does not demonstrate its absence (Emerson et al., 2017). Robust inference therefore requires environmental reference samples, negative controls, standardised sampling and storage, and complementary molecular and cultivation-based methods.

5. A reciprocal transplantation framework

If historical hosts and viable candidate microbial inocula can be recovered, reciprocal transplantation could test whether temporal matching affects host fitness (Figure 1 – Step 4). Historical and contemporary hosts would receive microbial communities from both periods under common conditions. Survival, growth and reproduction would be measured alongside microbial persistence and community composition (Rawls et al., 2006; Greyson-Gaito et al., 2020).

The primary test is the host-origin × microbiome-origin interaction: temporal matching would be supported if each host group performs better with microbiota from its own period. Multiple host genotypes per period and common-garden conditions would help distinguish temporal effects from genotype-specific responses and environmental carry-over. Standardised inocula, handling controls and negative controls are also

important, particularly when working with low-biomass samples (Knight et al., 2018). Microbiome-reduction treatments require validation because antibiotics can alter both microbial communities and host fitness (Cooper et al., 2021; Villegas et al., 2026).

Finally, microbial composition alone cannot establish adaptive benefit. Tracking community persistence alongside host fitness would help distinguish microbial effects from failed colonisation or community convergence (Rawls et al., 2006; Greyson-Gaito et al., 2020). Where viable isolates can be recovered, experiments using individual strains or defined consortia could further distinguish community-level effects from those of particular microbial taxa.

6. Feasibility and limitations

The feasibility of microbial resurrection ecology depends on several linked stages: recovering historical hosts, characterising associated microorganisms, identifying viable microbial candidates, and successfully transplanting them. These should be treated as sequential milestones rather than assumed to be equally achievable.

Historical host resurrection is supported by established methods for isolating dormant *Daphnia* eggs from sediment, hatching viable genotypes, and establishing clonal cultures (O'Grady et al., 2022; Burge et al., 2018). Long-term ecological records can help relate historical comparisons to periods of environmental change.

Microbiome resurrection is less straightforward. Low microbial biomass, contamination from sediment and laboratory sources, and the detection of DNA from dead cells complicate reconstruction (Eisenhofer et al., 2019; Emerson et al., 2017). Whole-genome amplification can increase available DNA but introduce biases in estimates of community composition (Yilmaz et al., 2010). Sequencing should therefore include extraction blanks, environmental reference samples, and independent validation, following established recommendations for low-biomass microbiome studies (Eisenhofer et al., 2019; Fierer et al., 2025).

Cultivation offers a route to viable inocula but introduces its own biases: many microorganisms will not grow under the conditions tested, and readily cultured taxa may not represent the original community. Initial experiments could therefore prioritise a limited set of viable candidate taxa or reproducible consortia rather than attempting to resurrect an entire historical microbiome. The findings of Mushegian et al. (2018)

demonstrate the potential functional importance of ephippium-associated bacteria, but do not establish that these communities represent the original microbiota of historical hosts.

A further interpretative limitation is that a reciprocal transplant cannot establish coevolution solely from a temporal matching interaction. Host genotypes may have evolved independently of their microbiomes, while microbial communities may have changed through environmental selection or ecological turnover. Additional evidence, including microbial genomic variation, host-genotype effects, and functional assays, would help distinguish these mechanisms (Koskella & Bergelson, 2020).

These limitations define the evidence needed to progress from historical reconstruction to experimental inference. A staged strategy—establishing microbial provenance and viability, testing effects on resurrected hosts, and then investigating mechanisms—offers a realistic route towards understanding temporal host–microbiome dynamics.

7. Conclusions and future directions

Combining resurrection ecology with microbiome transplantation offers a framework for testing whether host–microbiome interactions change adaptively over ecological timescales. Pairing historical and contemporary hosts with microbial communities from different periods would allow researchers to test whether temporal changes in microbiome composition have functional consequences for host fitness.

Freshwater *Daphnia* provide a promising starting point because dormant eggs preserve historical host genotypes in sediment archives (Burge et al., 2018; O'Grady et al., 2022). However, the provenance and viability of egg-associated microorganisms must be established before they can be interpreted as historically associated host microbiota. Distinguishing host-associated, lake-derived, and sediment-associated microorganisms is therefore central to the framework (Mushegian et al., 2018).

The immediate priority is to determine whether viable, historically relevant microbial inocula can be recovered reproducibly and whether they colonise resurrected hosts under controlled conditions. Reciprocal transplantation could then test for temporal matching, while genomic and functional analyses help distinguish host adaptation, microbial adaptation, and coadaptation (Koskella & Bergelson, 2020).

More broadly, microbial resurrection ecology could connect historical environmental change with experimental tests of microbial contributions to host evolution. Its value lies not in assuming that ancestral host–microbiome partnerships can be reconstructed perfectly, but in making their provenance, viability, and potential adaptive consequences experimentally testable.

Author contributions

Sam Paplauskas: conceptualization (equal), writing – original draft (lead). Dagmar Frisch: conceptualization (equal), supervision (lead), writing – original draft (supporting).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data availability statement

No new data were generated or analysed in this article. Data sharing is therefore not applicable.

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Supporting Information

No supporting information is available for this article.