

Fish from the sky: Airborne eDNA tracks aquatic life

Yin Cheong Aden Ip^{1*} Gledis Guri^{1*} Elizabeth Andruszkiewicz Allan¹
Ryan P. Kelly¹

August 20, 2025

¹ School of Marine and Environmental Affairs, University of Washington, Seattle, Washington, USA
* shared first authorship

corresponding author adenip@uw.edu

Teaser

Aquatic life leaves traces in the air, opening a new frontier in passive biodiversity monitoring.

Abstract

Water and air are generally treated as separate reservoirs of environmental DNA (eDNA) derived from the species resident in those respective environments. However, it is likely that eDNA routinely crosses the air-water boundary in both directions as a result of deposition, evaporation, or other processes. Here, we systematically tested methods of sampling eDNA at the air-water interface, showing for the first time that aquatic life can be reliably detected from passive air samples collected nearby. We deployed four simple air samplers — three different kinds of filters and one open tray of deionized water — alongside paired water samples and visual counts over a six-week peak run of Coho salmon (*Oncorhynchus kisutch*) at a local spawning stream. We then quantified eDNA concentrations in both air and water (air: copies/day/cm²; water: copies/L) using quantitative PCR, to estimate (1) the concentration of target eDNA in air vs. water, and (2) the capture performance of each filter type. Despite an approximate 25,000-times dilution versus water, passive air collectors captured quantitative airborne eDNA signals that closely paralleled salmon counts, although recovery varied with sampler design and orientation. We show the air-water interface is a quantifiable source of aquatic genetic information using simple, passive samplers that do not require electricity, making them appealing for biomonitoring in remote or resource-limited settings. This work points the way to using airborne eDNA as a robust pathway for biological information critical to conservation, resource management, and public-health protection.

Keywords: environmental DNA, Air eDNA, Passive Air Filtration, Aquatic Biomonitoring, Aerosolization, Evaporation, Non-invasive Sampling, Quantitative eDNA Analysis, Salmon, Environmental Genomics

1 Introduction

Monitoring aquatic life is fundamental to understanding ecosystem health, guiding conservation efforts, and managing valuable natural resources [1, 2]. Over the past decade, environmental DNA (eDNA) has upended our paradigm for biodiversity assessment by detecting and quantifying organisms through the genetic material they shed into their surroundings. Water-based eDNA surveys have proven particularly effective for monitoring endangered species ([3]), early detection of invasive species incursions ([4]), characterizing community composition ([5]), and even providing quantitative assessments for complementing traditional surveys ([6, 7, 8]).

Meanwhile, airborne eDNA research has emerged as a promising frontier, though to date it has focused almost exclusively on terrestrial organisms. Both active and passive air filtration methods have been shown to recover DNA from mammals, birds, insects, and plants under field and enclosed conditions ([9, 10, 11, 12, 13, 14, 15]). Intriguingly, these same air-sampling techniques sometimes detect strictly aquatic taxa. Yet in almost every case, these signals were never the focus of the study and are often treated as suspected contamination or attributed to zoo feed or piscivores fecal bioaerosols [16, 17, 18, 15], rather than recognized as a genuine ecological signal [19].

Aquatic species signals detected in airborne eDNA surveys are often discarded [20, 17, 21, 18]. Yet, these overlooked detections hint at a genuinely unexplored, rich, untapped source of data for a complementary biodiversity monitoring approach. Environmental systems are inherently interconnected [22], and basic physics points to why aquatic DNA should appear in air [23, 24]. Natural physical processes at the air-water interface, such as evaporation, bubble-burst aerosolization from ripples and splashes, and leaping fish, churning substrates, create splash-driven aerosols; all of these provide plausible mechanisms for transferring eDNA into the atmosphere [25, 26, 27, 28]. These potential mechanisms would suggest that air could act as a diluted, but still informative, extension of the aquatic environment, representing biological signals that are real, quantifiable, and ecologically meaningful.

To test this hypothesis, we conducted the first targeted investigation of cross-medium water-to-air eDNA transfer, specifically examining whether genetic material from aquatic organisms can be detected in air samples collected above water surfaces. Leveraging the behavior of Coho salmon (*Oncorhynchus kisutch*) during their spawning season [26], we collected and measured eDNA concentrations in paired water and passive air samples over a six-week peak migration period, with visual fish counts from hatchery staff. To evaluate the mechanisms of airborne DNA capture and settlement, we deployed four passive air collection methods: vertically orientated gelatin air filters (commonly used in low-flow air filtration systems), polytetrafluoroethylene filters (PTFE; standard in high-flow air applications), and mixed cellulose ester filters (MCE; traditionally employed for water filtration), as well as an open, horizontal tray of deionized water exposed to ambient conditions [17]. These were chosen for their distinct physical properties, contrasting orientations, and different particle capture efficiencies targeting different aerosol types. By comparing detection sensitivity, temporal patterns, and quantitative performance of these four collectors against water eDNA concentrations and visual counts, we show that—even at roughly 25,000-times dilution—airborne eDNA can reliably track real-world aquatic population dynamics.

Our findings provide the first evidence that aquatic genetic material can indeed transfer from water to air under natural conditions, and extends further with quantitative demonstrations that reflect actual population dynamics with just passive air samplers. Far from weighing air against water sampling, this cross-medium detection and quantification represents not merely a technical advancement, but a conceptual leap in ecological monitoring: the previously ignored air–water interface now emerges as a measurable reservoir of aquatic genetic information. While this study centers on salmon, its implications extend broadly, proving that aquatic eDNA in the air is quantifiable and potentially species rich. This advancement re-imagines ecological monitoring as one that bridges water and air to build more resilient, comprehensive surveillance networks in a rapidly changing world. Such integrated approach can become particularly valuable during extreme environmental conditions—when droughts parch rivers, floods render wading unsafe, or public-health concerns close off contaminated waters [29, 30, 31]—indicating that airborne eDNA can offer a complementary pathway for capturing aquatic genetic signals.

2 Methods

2.1 Field Sampling

We conducted this study in Issaquah Creek, a salmon spawning stream, outside of the Issaquah Salmon Hatchery (47.529501° N, 122.039133° W) from 26 August 2024 to 18 November 2024, with nine sampling events. We chose nine field trips that spanned the entire coho salmon (*Oncorhynchus kisutch*) run, from the first arrivals in early fall of August, through peak abundance around 17 October 2024 and into the tail end of the migration in November. This schedule ensured that our eDNA sampling captured both the lowest and highest levels of fish activity. Within the same sampling period, visual fish counts were performed by the hatchery staff, and salmon escapement data were obtained from the Washington Department of Fish

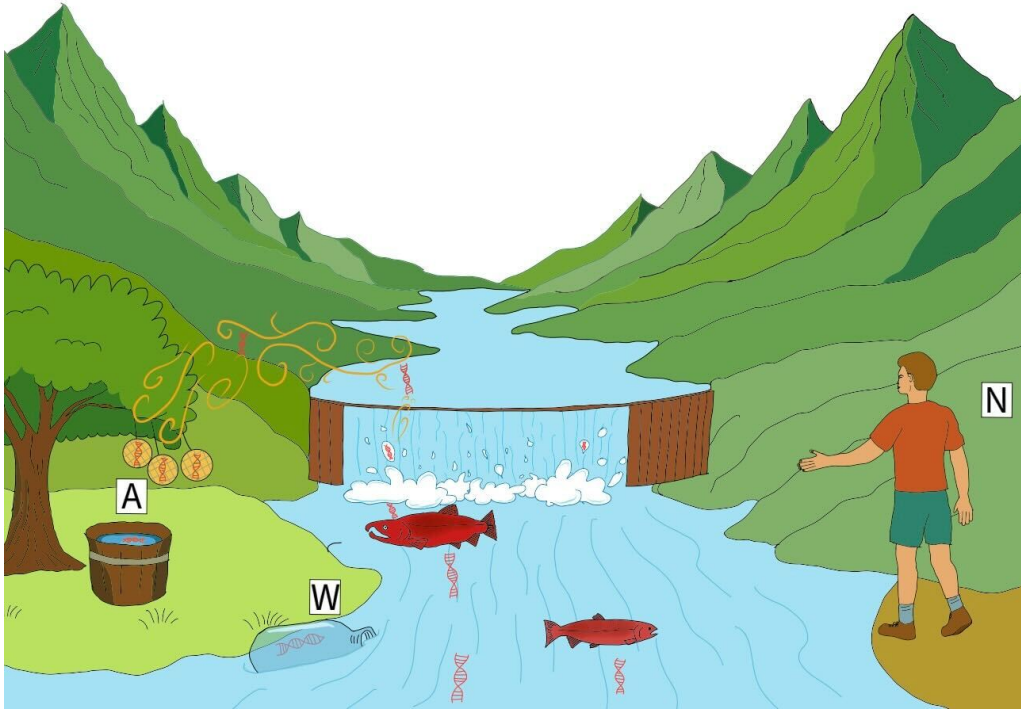


Figure 1: Conceptual illustration of cross-medium eDNA sampling above a salmon-spawning stream. Natural processes, including evaporation, bubble-burst aerosolization at riffles and splashes, and the vigorous movement of spawning Coho salmon, launch trace amounts of DNA from the river surface into the atmosphere. Passive airborne samplers, shown here as three vertically hung filters and an open tray of deionized water (A), intercept settling airborne eDNA, while paired water-grab sampling (W) and visual counts by hatchery staff (N) provide concurrent reference measurements.

and Wildlife escapement reports (<https://wdfw.wa.gov/fishing/management/hatcheries/escapement#2024-weekly>). Throughout our nine sampling events, weather conditions ranged from clear, calm days to periods of rainfall; detailed records of air temperature, wind speed, relative humidity, and precipitation are provided in Supplementary Material 1.

Sampling for eDNA was conducted in 24-hour blocks with deployment and recovery around 9 a.m. (river water was collected only on the first day/timepoint). Four passive collection methods were evaluated: three filter types—gelatin (Sartorius, 47 mm diameter), PTFE (Whatman, 47 mm diameter), and MCE (Sterlitech, 5.0 μm pore size, 45mm diameter)—and an open container of deionized water. The rationale for selecting these materials is as follows: gelatin filters are effective at capturing airborne particles and are particularly suited for applications where maintaining viability (e.g., for subsequent bacterial culturing; [32]) is desired; PTFE filters are noted for their high durability and are widely used in active air sampling experiments [33]; whereas MCE filters, typically employed for water filtration, were included to assess their performance in an airborne context [6]. All three passive filters were deployed via custom 3D-printed “honeycomb” puck filter holders, based on open-source Thingiverse designs (IDs 4306478 and 979318; Zachary Gold, pers. comms.), and were suspended from a hatchery railing approximately 3 m above the river water level (Figure 1), with their collection surfaces oriented horizontally. All three passive filters were deployed via 3D-printed “honeycomb” puck holders, based on open-source Thingiverse designs (IDs 4306478 and 979318)¹ and generously shared by Mautz et al. (2025).

This configuration minimizes splash contamination and captures airborne DNA particles driven by gravitational settling. The positioning relative to flowing water demonstrates how these passive collectors operate at a vantage point above the stream, facilitating non-invasive DNA capture in real-world field conditions. Two biological replicates were deployed for both gelatin and PTFE, while only one replicate was used for MCE. After the overnight deployment, filters were carefully recovered using sterile, disposable forceps and immediately immersed in 1.5 mL of DNA/RNA Shield.

The fourth passive collection method was an open container (25 cm width, 30 cm length, 10 cm depth) filled with 2 L of deionized water [17] also positioned about 3 m above the river and about 30 cm above the suspended passive filters. The open container was also deployed for about 24 hours at the same times as the passive filters. The container had an open surface (i.e., oriented horizontally) to capture airborne particles settling by gravity. The surface area of the container was approximately 750 cm^2 , in contrast to the roughly 16 cm^2 surface area offered by the 47-mm circular filter disks. Only one replicate was used for the open water container method. Note that although 2 L of deionized water was placed in the container, heavy rainfall during overnight deployments sometimes increased the water level. Any debris (e.g., bugs, leaves) was removed from the container before on-site filtration using the same system as for river water samples (see below for details).

Concurrent with airborne sampling, water samples were collected by hand from the river directly adjacent to the coho salmon aggregation school, just downstream of the fish ladder entrance. The ladder is operated continuously by hatchery staff throughout the salmon run, ensuring fish passage and visual counts. A total of 3 L of water was filtered on site using a Smith-Root Citizen Science Sampler equipped with 5.0 μm mixed cellulose ester (MCE) filters [6]. Three 1 L replicates were processed and immediately preserved in 1.5 mL of DNA/RNA Shield (Zymo Research) using clean disposable plastic forceps. Field-negative filtration blanks (1 L of Milli-Q water each) were also processed using the same system. All equipment was decontaminated with 10% bleach, thoroughly rinsed with deionized water, and handled with gloves to minimize contamination. All filters (passive air, passive open container, water) were stored at -20°C until processing, typically within one week.

2.2 Wet-Laboratory Procedures

DNA extraction from both river water samples and airborne filter samples was performed using the Qiagen Blood and Tissue Kit according to the manufacturer’s protocols. During extraction, it was noted that the gelatin filters dissolved completely in the DNA/RNA Shield. Samples were vortexed for 1 minute, and 500 μL of the shield was used for DNA extraction.

qPCR assays targeted a 114-bp fragment of the cytochrome b gene of coho salmon, using primers derived from [34]—COCytb.980-1093 Forward: CCTTGGTGGCGGATATACTTATCTTA and COCytb.980-1093

¹<https://www.thingiverse.com/thing:4306478>; <https://www.thingiverse.com/thing:979318>

Reverse: GAACTAGGAAGATGGCGAAGTAGATC. SYBR Green chemistry was employed using SYBR Select Master Mix (Fisher Scientific) on an Applied Biosystems QuantStudio 5 real-time PCR system with a 384-well block. Each 10 μL reaction consisted of 5 μL of SYBR Select Master Mix, 0.4 μL of 10 mM forward primer, 0.4 μL of 10 mM reverse primer, 2.2 μL of molecular grade water, and 2 μL of DNA template. Melt curve analysis was performed to confirm the amplification of the target fragment, with an accepted melting temperature of $81^\circ\text{C} \pm 1^\circ\text{C}$.

Standard curves were constructed using a coho tissue DNA extract quantified with a Qubit fluorometer. The stock solution was diluted to 1.0 ng/ μL and designated as 10^6 copies/ μL . Serial dilutions were then prepared, with 10^5 , 10^4 , and 10^3 copies/ μL run in triplicate, 10^2 copies/ μL in quadruplicate, and 10^1 / μL copies in triplicate.

2.3 Joint statistical model

2.3.1 Visual observation model

In summary, we synthesize three methods of observations (visual counting of fish, water eDNA measurements, and air eDNA measurements) which derive from a single unknown true fish accumulation rate (denoted here as X). Through this joint approach, we can estimate: the aerosolization factor (η ; the magnitude of water eDNA transferred to air), the effectiveness and reliability of different passive air filtering techniques (τ), and the replicability of various filters (ρ) throughout the 6-week peak coho salmon spawning period.

We model the upstream migration of coho salmon (*Oncorhynchus kisutch*) as arising from the inferred unknown true density of fish. As individuals move upriver, fish accumulate in a holding area immediately downstream of the hatchery river dam. At discrete times t , the hatchery staff opens the ladder gate to allow passage into holding tanks. Between successive gate-opening events (Δt), additional coho salmon arrive and join the backlog in the holding area, increasing the number of individuals awaiting passage. Let X represent the true daily accumulation rate (also fish density at the river dam) in units of fish/day at time t , and E denote the number of days elapsed between consecutive gate openings ($E_t = \Delta t$; hence $E_{t=1} = 0$). Prior to each gate opening (at time t), the crew conducts a visual count N_t of accumulated fish. Assuming X_t remains relatively constant between successive gate-opening events (Δt), we model the observed fish counts as a Negative Binomial process:

$$\lambda_t = X_t \cdot E_t \quad (1)$$

$$N_t \sim \text{Negative Binomial}(\lambda_t, \phi) \quad (2)$$

where, N is the visually observed number of fish at time t , λ_t is the expected number of fish accumulated over the E_t -day interval with a fixed overdispersion parameter shared across time points ($\phi = 20$; hence variance $\lambda + \frac{\lambda}{\phi}$) [35, 7]

2.3.2 Molecular process model

Let W be the unobserved eDNA concentration (copies/L) in the water at time t and let ω be the “integrated eDNA factor” – the conversion factor between X and W (see [7] for further interpretation of this parameter). We can express the relation between the fish density and water eDNA concentration as:

$$W_t = X_t \cdot \omega \quad (3)$$

Let A be the unobserved eDNA concentration (copies/day/ cm^2) in the air at time t that is filtered using passive collection method j . We model the air eDNA concentration as a log-linear function of the water eDNA with intercept η , slope = 1, and error term ε (unexplained variability; time and filter specific):

$$\ln(A_{tj}) = \eta_j + \ln(W_t) + \varepsilon_{tj} \quad (4)$$

Here the intercept η can be interpreted as the water-to-air transferability (or dilution) factor and ε as the error term parameter (similar to the sum of squares error) from a linear regression where $\varepsilon_{tj} \sim \mathcal{N}(0, \tau_j)$.

For some filter types j (PTFE filters ($j = P$); gelatin filters ($j = G$)) we sampled two biological replicates and we used the mean of those biological replicates to determine the average concentration in the air A at time t as following:

$$\ln(A_{tjb}) = \ln(A_{tj}) + \delta_{tjb} \quad \text{for } j \in \{P, G\} \quad (5)$$

where δ_b indicates the deviation of individual biological replicate from the average concentration (A_{tj}), following a normal distribution with mean 0, $\delta_{tjb} \sim \mathcal{N}(0, \rho_j)$, with ρ_j indicating the magnitude of the replicates deviation from the mean sample. Because we have only two replicates at each sampled time, we impose a sum to zero constraint on the replicates (b) collected from a single sampling time ($\sum_b \delta_{tjb} = 0$).

To estimate the levels of eDNA concentration in water (W) and air (A), we make use of the qPCR observation models (as described in [36, 37], with slight modifications). The model compartment uses the standard curve samples to estimate the intercept (ϕ, β_0, γ_0) and slope (β_1, γ_1) parameters between the known concentration (K) and the observed data (Z and Y) from qPCR machine as follows:

$$Z_{kr} \sim \text{Bernoulli}(\psi_k) \quad (6)$$

$$\psi_k = 1 - \exp(-K_k \cdot \theta) \quad (7)$$

$$Y_{kr} \sim \text{Normal}(\mu_k, \sigma_k) \quad \text{if } Z_{kr} = 1 \quad (8)$$

$$\mu_k = \beta_0 + \beta_{1p} \cdot \ln(K_k) \quad (9)$$

$$\sigma_k = \exp(\gamma_0 + \gamma_1 \cdot \ln(K_k)) \quad (10)$$

where Z is the binary outcome of target amplification for sample (k) and technical replicate (r) being present (1) or absent (0) following a Bernoulli distribution given the probability of detection ψ for each sample (k). The parameter ϕ is the intercept of the function between probability of detection ψ and the known DNA concentration (K ; copies/ μL reaction) as the predictor variable. Additionally, for equations 8-10, Y is the observed cycle threshold (Ct) for sample (k) and technical replicate (r) which follows a normal distribution with mean μ (mean Ct) and standard deviation σ for each sample (k). We model μ as a linear function of known eDNA concentration (K) with intercept β_0 and plate specific (p) slope β_1 and the standard deviation σ of the observed Y as an exponential function of known eDNA concentration with intercept γ_0 and slope γ_1 .

Subsequently, we build the same model compartment for estimating eDNA concentration in water and air by substituting U_t and Q_{tj} (and Q_{tjb} for $j \in \{P, G\}$) respectively, with K_k through equation 6-10 (see SI Appendix, Fig. S1), where U and Q are concentration normalized per reaction volume ($V = 10\mu\text{L}$) and surface area ($S = 16 \text{ cm}^2$ for gelatin, PTFE, and MCE, and 750 cm^2 for the open containers of deionized water) of W and A respectively as follows:

$$U_t = W_t/V_{itp} \quad (11)$$

$$Q_{tjb} = A_{tjb} \cdot S_{tj}/V_{tjbrp} \quad (12)$$

The intercept and slope parameters (from equation 7, 9, and 10) between qPCR observations and eDNA concentration of water, air and the standard samples are shared between model compartments.

2.4 Model conditions

The joint model (SI Appendix, Fig. S1) was implemented using the Stan language as implemented in R (package: Rstan) running four independent MCMC chains using 5000 warm-up and 5000 sampling iterations (for parameters and their prior distribution see SI Appendix, Table S1). The posterior predictions were diagnosed using statistics (Gelman and Rubin 1992) and considered convergence for values less than 1.05 and effective sample size (ESS) greater than 1000 for all parameters.

3 Results

Airborne eDNA passively detected Coho salmon and closely mirrored their abundance in the river during the upstream migration period. Detection efficiency and signal strength varied considerably among the different passive airborne eDNA capture methods.

3.1 Fish accumulation based on visual counts and eDNA in river water

Coho salmon migration occurs not as a single continuous event, but rather as a series of distinct burst peaks from mid-October through late November, where the peaks are highly likely to be connected with environmental factors such as water temperature and discharge. The average daily accumulation rate (X ; black line in Figure 2) was estimated at 160.4 fish/day with peaks exceeding up to 286 fish/day and low activity of ca. 78 fish/day (Figure 2).

Because both observation methods (river water eDNA and visual observation) are jointly used to estimate the daily accumulation rate (X), their concordance was best evaluated through the parameter ω . A converged and narrowly distributed ω parameter indicates strong agreement between the two methods and simultaneously a reliable conversion parameter from fish/day to eDNA copies/L. In this case, $\omega = 9.578$ (95% quantile range of 9.352 to 9.804; (SI Appendix, Fig. S4)), suggesting consistent concordance between observed fish counts and eDNA concentrations hence, biologically, this implies that an accumulation rate of 1 fish/day corresponds to approximately 15000 (± 3000) copies/L.

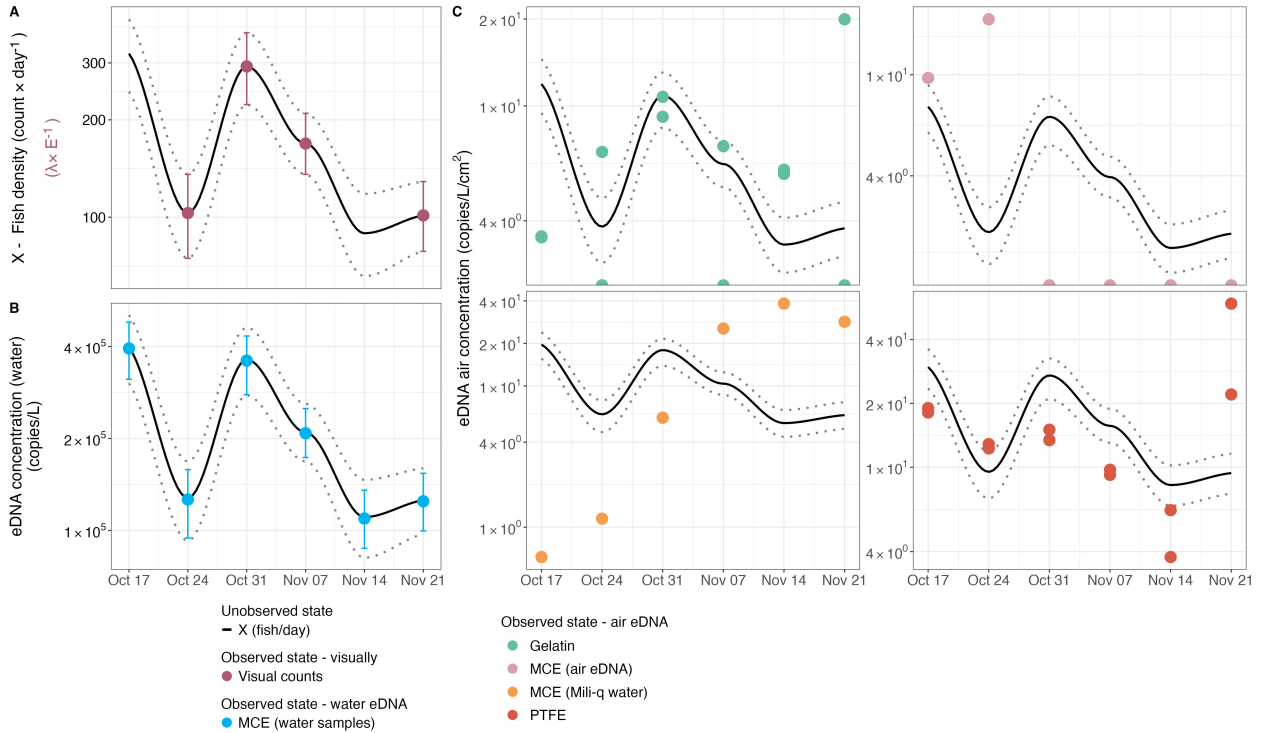


Figure 2: The temporal dynamics of estimated fish density in units of fish/day (X ; black line with 95 confidence intervals - dotted lines) from October 17th to November 21st compared to the posterior distributions of visual observations (A), eDNA concentrations (copies/L) in water (B), and eDNA concentrations (copies/day/cm²) in air using various filter types (C).

3.2 Air eDNA signals

Airborne eDNA originating from coho salmon was successfully detected across all passive air collection methods deployed (gelatin, PTFE, MCE filters suspended in air, and open containers of deionized water - MCE DI water). These results provide compelling proof-of-concept evidence that genetic material from aquatic organisms can be recovered from the atmosphere without requiring active airflow systems, thereby demonstrating the viability of fully passive sampling approaches for detecting airborne aquatic eDNA under field conditions.

All filter types demonstrated that airborne eDNA concentrations were approximately $e^{-10.21}$ ($\bar{\eta} = 10.21$) lower than corresponding waterborne eDNA concentrations, establishing a quantifiable dilution factor be-

tween water and air matrices. On average 1 copies/day/cm² captured in air is equivalent to ca. 25,000 copies/L in water. Despite the general consistency in estimating the water-to-air dilution coefficient, method-specific variations in collection efficiency were observed (Table 1; SI Appendix, Fig. S2A). PTFE filters exhibited higher capture efficiencies, collecting 2 times more eDNA than the mean across all air sampling methods (Table 1). Deionized water tray (MCE DI water) demonstrated the second highest efficiency (1.3 times the average; Table 1), while gelatin filters and air suspended MCE filters showed comparatively lower capture efficacy (0.8 and 0.5 times the average, respectively; Table 1).

In terms of alignment with the biological activity, PTFE and gelatin filters best mirrored the daily fish accumulation patterns, exhibiting the lowest residual error magnitude (expressed as the standard deviation of ε) with $\tau = 0.473$ and 0.570 , respectively (Table 1; SI Appendix, Fig. S2B). Conversely, MCE DI water, despite having the largest surface area, showed less agreement with the fish migration dynamics ($\tau = 1.780$; Table 1; SI Appendix, Fig. S2B). The MCE air suspended filters performed least effectively in tracking temporal migration patterns, failing to amplify coho salmon DNA beyond the first two weeks of the sampling campaign Figure 2C.

Subsequently, biological replicates for gelatin and PTFE filters revealed additional insights regarding methodological robustness and reproducibility. PTFE filters produced the most consistent quantifications, with lower variance (expressed as the standard deviation of δ) between replicates ($\rho = 0.154$; Table 1; SI Appendix, Fig. S2C), whereas gelatin filters showed a higher degree of variability ($\rho = 0.386$; Table 1; SI Appendix, Fig. S2C), indicating reduced reproducibility of quantitative outcomes.

In sum, these performance differences across sampling methods likely reflect inherent physical and operational characteristics of each filter type and collection method, which in turn influence their ability to capture either discrete or cumulative biological signals from the source species.

Table 1: Estimated posterior means of dilution parameter (η), standard deviation of the residuals (τ), biological replicability (ρ), and capturing efficiency ($e^{(\eta-\bar{\eta})}$)

Filter type	Dilution (in \log_e) (η)	Standard deviation (τ)	Biological rep. error magnitude (ρ)	Capturing efficiency $e^{(\eta-\bar{\eta})}$
Gelatin	-10.45	0.473	0.386	0.785
PTFE	-9.53	0.570	0.154	1.979
MCE Air	-10.91	0.949	-	0.496
MCE DI water	-9.95	1.780	-	1.295

3.3 Model diagnostics

Convergence and reliability of the Bayesian model were assessed through comprehensive diagnostics. All parameters (SI Appendix, Table S1) exhibited reliable Gelman-Rubin convergence statistics ($\hat{R} < 1.01$) and effective sample sizes (ESS) exceeding 1000 per parameter, indicating successful convergence and efficient mixing of the six independent chains (SI Appendix, Fig. S3A).

No divergent transitions were detected during sampling, and the maximum tree depth was not exceeded, indicating no issues with divergence or exploration limits (SI Appendix, Fig. S3B). The posterior likelihood demonstrated convergence before the sampling phase began, with all chains exhibiting high mixing, confirming robust exploration of the parameter space (SI Appendix, Fig. S3B).

Prior sensitivity analyses revealed that posterior estimates differed from priors, demonstrating that the posteriors were appropriately updated based on the observed data rather than being heavily influenced by prior assumptions (SI Appendix, Fig. S4). Additionally, the posterior predictive checks (PPC) demonstrated that the model reliably reproduced the observed data, supporting the validity of parameter estimates (SI Appendix, Fig. S5).

Collectively, these diagnostics confirm the reliability and validity of the Bayesian model used here.

4 Discussion

4.1 A New Dimension of Biodiversity Monitoring

Our study establishes, for the first time, that passive airborne eDNA sampling can reliably capture and track molecular signals from aquatic organisms. This represents a paradigm shift in how we access aquatic biodiversity—through the air, without ever touching the water. In salmon-spawning streams, genetic material from the river is transported into the air likely by evaporation, bubble-burst aerosolization at riffles and splashes, and the rigorous churning of spawning fish [38, 39]. Collections from multiple passive samplers, when compared with conventional water-based eDNA assays and daily visual counts, reveal a clear and quantitative relationship between airborne eDNA concentration and salmon density.

Until now, airborne eDNA surveys have reported fish or other strictly aquatic taxa as likely to be laboratory contamination, zoo-feed artifacts, or piscivore fecal bioaerosols [17, 18, 16, 15]. Our data suggest otherwise: this is a real ecological signal rather than an experimental artifact. It is likely that wind speed, relative humidity, and temperature will determine how far and how long aerosolized aquatic eDNA will travel before being redeposited [40, 41]. For example, high humidity and rainfall force rapid settling and very localized deposition while dry, windy conditions might carry genetic plumes further distances downwind [42, 43]. These environmental controls, combined with air currents above riffles and splashes, should be considered when determining how passive samplers capture transient pulses of biological activity.

4.2 Sampler Design Shapes Signal Detection

Over 24-hour deployments, vertically oriented gelatin and PTFE filters acted as higher-resolution “fish-activity” samplers [44]. Ambient air currents likely swept fine, splash-generated aerosols rich in salmon DNA onto their membranes, producing yields that rose and fell in sync with live fish counts and water-eDNA levels [45]. In contrast, the large horizontal tray of deionized water seemed to function more like a hydraulic-driven deposition trap. The tray saw a steady accumulation of eDNA over the six weeks and thus could have been collecting more coarse spray, foam, and decay-derived particulates from river turbulence and from decomposing carcasses [46, 39]. Because salmon carcasses often remain in shallow banks and backwaters as the spawning season progresses, it is plausible that river turbulence and discharge could generate larger droplets over decomposing tissue, potentially facilitating eDNA dispersal [38, 47]. These coarse droplets settle rapidly and dominate deposition on horizontal collectors while the fine fraction produced by active fish movement is under-represented. Gelatin and PTFE filters thus seem to provide snapshots of biologically driven eDNA flux whereas the water tray seemed to integrate both flow-driven and decay-driven inputs into a steadily rising accumulation curve.

The filter materials and operational context also shaped the air sampling performance. PTFE filters, known for their durability, delivered the most consistent results of all the passive filtration methods; gelatin filters yielded the highest sensitivity but showed greater variability; mixed cellulose ester filters captured negligible airborne DNA; and the open tray, with roughly 50 times more surface area than the vertical filters, recovered the highest total DNA yield. These samplers respond differently to weather. PTFE filters are generally unaffected by rain, whereas gelatin filters perform best in dry conditions because they dissolve when wet. Rainfall also introduces a trade-off for the tray: heavy rain can dilute the accumulated eDNA but may also scour additional airborne or splash-borne DNA into the water. Real-world debris, such as leaves, insects, sediment, can also wash into the tray, increasing the risk of clogging or necessitating pre-filtration before DNA extraction. Although our sample size is too small to quantify these opposing effects, future work should explicitly test how precipitation intensity influences both concentration and total yield [12].

4.3 Air is Dilute Water: Balancing Capture and Decay

On average, our data showed that eDNA in the air was roughly 25,000 times less concentrated than in the water, at a level that approaches the lower limits of qPCR detection. Despite this extreme dilution, our rigorous sampling, laboratory methods, and statistical models reliably picked up those sparse molecules, obtaining consistent, quantitative signals across the entire spawning season. To put this in perspective, dissolving a teaspoon of salt into a large aquarium yields a similar dilution magnitude: only a tiny fraction of shed DNA ever makes it into the overlying air, yet those few copies suffice to track real-time salmon

activity. In particular, vertically oriented filters intercepted transient eDNA peaks that rose and fell in concert with visual counts, demonstrating that even at extreme dilution, airborne eDNA can still capture fine scale changes in fish presence that reflects real-world population dynamics.

Longer passive-sampler deployments naturally accumulate more settled eDNA, but they also expose collected material to ultraviolet radiation, microbial degradation and fluctuating humidity, all of which erode DNA integrity over time [48]. [49] showed that waterborne eDNA degrades with a half-life of hours to days under natural sunlight and microbial loads, suggesting that once deposited, airborne fragments may decay on comparable or even faster timescales. By contrast, [17] found that passive air particle collections continued to accrue new species detections for up to 96 hours, without specifying when deposition begins to be outpaced by degradation. In practical terms, this means that in a week-long deployment much of the DNA captured from early days may have degraded long before retrieval, so that the majority of signal reflects material deposited in the final one or two days of sampling. We therefore selected a 24-hour deployment to capture transient eDNA plumes while limiting post-deposition loss[12]. Future work should vary deployment lengths from a few hours to several days, and pair them with controlled decay assays, for example by spiking synthetic DNA onto filters and tracking its persistence, to determine the point at which accumulation and degradation balance.

Our findings also agree with the recent work by [44] who showed that passive air samplers outperform active pumps by sampling intermittent, DNA-rich plumes over long intervals and detecting greater species richness. In our streams, vertical filters captured transient bursts of salmon eDNA in near real-time, while the open tray, and likely longer deployments, would tend to smooth those peaks into an integrated signal. Contrastingly, active-pump systems operating for only hours would average across plumes and risk overlooking fine-scale temporal changes.

By systematically mapping this interplay between deposition and degradation, and by benchmarking passive against active approaches, we can establish best-practice guidelines for airborne eDNA sampling durations. This effort would mirror how water-based eDNA workflows define optimal filtration volumes and storage times [50, 20] and would enable robust, context-specific deployments that maximize genuine signal recovery for real-time biodiversity monitoring.

4.4 Minimal Tools, Maximum Reach and Navigating Limitations

Perhaps most striking result from our work is the simplicity and versatility of passive airborne sampling. No pumps or power are needed, and equipment is extremely low cost and easy to deploy. This minimal-infrastructure approach makes it viable for remote headwaters, steep mountain channels, urban stormwater networks, and contaminated waters where sampling is unsafe [51, 52]. By integrating visual surveys, water-based eDNA and airborne eDNA, we establish a biomonitoring framework that is non-invasive, scalable and low-impact. In an era of intensifying droughts, floods and public-health risks such as bacterial outbreaks in stagnant waters, airborne eDNA offers resilient pathways for rapid invasive-species alerts, real-time disease surveillance in flood-prone wetlands and non-invasive population censuses in protected spawning grounds.

Naturally, challenges remain. Passive deployments rely on surface-area-by-time metrics rather than standardized air-volume units, complicating direct comparisons across studies. Optimal exposure times must balance accumulation against DNA degradation from UV, microbes and moisture [48]. Weather variability in wind, humidity and rain can alter deposition rates and sampler efficiency [12, 21]. Future work should refine sampler design, systematically compare vertical and horizontal orientations, explore automated or drone-based retrieval and integrate river discharge and meteorological data into quantitative models [42, 53, 54, 38].

Our study begins to chart a portion of airborne eDNA ecology’s in five key dimensions [21]. We confirm origin by matching airborne DNA trends to co-occurring water eDNA and fish counts. We elucidate transport mechanisms such as evaporation, bubble bursts and fish activity. We quantify dispersal and dilution by measuring a 25,000-times concentration difference between water and air samples. We demonstrate fate through differential deposition on vertical filters and horizontal trays. Finally, we show that airborne DNA fragments remain amplifiable, offering an initial glimpse into their molecular state after transport. These insights lay the groundwork for future studies on persistence, degradation and particle-size distributions from airborne eDNA [55].

Overall, our work overturns the assumption that aquatic eDNA belongs solely underwater. By demonstrating that genetic signals from fish and other aquatic life routinely escape into and can be captured

from the air, we open a new paradigm for ecological monitoring. The atmosphere above water emerges as a reliable, quantifiable reservoir of biodiversity data. This advance promises transformative applications from invasive species alerts in drought-stricken reservoirs to pathogen surveillance in flood-prone wetlands and non-invasive censuses in protected streams, equipping managers with a resilient, real-time window into aquatic ecosystems.

Acknowledgments

We thank Natasha Kacoroski, Larry Franks, and the dedicated volunteers at Friends of the Issaquah Salmon Hatchery for their generous support in the field. We are also grateful to Travis A. Burnett and Darin Combs at the Washington Department of Fish and Wildlife for facilitating access and permitting field experimental work at the Issaquah Hatchery. Additional thanks to Pedro F.P. Brandão-Dias for assistance with air filter deployments, and to Kevan Yamanaka at the Monterey Bay Aquarium Research Institute for fabricating the 3D-printed passive filter holders. We are especially grateful to Chris Sergeant for valuable insights on salmon biology that shaped the interpretation of our findings, and to Ole Shelton for statistical advice that improved our analytical approach. We acknowledge funding support from the Packard Foundation [Grant No. GR016745].

Author contributions

Y.C.A.I. conceived the study. Y.C.A.I. G.G and E.A.A. designed the field and laboratory protocols. Y.C.A.I. and G.G. jointly designed the downstream statistical analyses and Bayesian modeling framework. G.G. conducted all statistical analyses, with inputs from R.P.K. The fieldwork was performed by Y.C.A.I. and E.A.A., while Y.C.A.I. and G.G. co-wrote the manuscript. R.P.K. supervised the project, contributed to conceptual guidance, and provided critical revisions. All authors contributed to the study design and approved the final manuscript.

Data availability

The authors declare that they have no competing interests. All data needed to evaluate the conclusions in this paper are available in the main text and/or the Supplementary Materials. Codes are available on <https://github.com/gledguri/Air-eDNA-quant>. Additional data, code, and materials will be made available upon reasonable request. No materials were subject to material transfer agreements (MTAs).

References

- [1] David Dudgeon, Angela H. Arthington, Mark O. Gessner, Zen-Ichiro Kawabata, Duncan J. Knowler, Christian L  v  que, Robert J. Naiman, Anne-H  l  ne Prieur-Richard, Doris Soto, Melanie L. J. Stiassny, and Caroline A. Sullivan. Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81(2):163–182, 2006. ISSN 1464-7931, 1469-185X. doi: 10.1017/S1464793105006950. URL <https://onlinelibrary.wiley.com/doi/10.1017/S1464793105006950>.
- [2] Andrea J. Reid, Andrew K. Carlson, Irena F. Creed, Erika J. Eliason, Peter A. Gell, Pieter T. J. Johnson, Karen A. Kidd, Tyson J. MacCormack, Julian D. Olden, Steve J. Ormerod, John P. Smol, William W. Taylor, Klement Tockner, Jesse C. Vermaire, David Dudgeon, and Steven J. Cooke. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3):849–873, 2019. ISSN 1464-7931, 1469-185X. doi: 10.1111/brv.12480. URL <https://onlinelibrary.wiley.com/doi/10.1111/brv.12480>.
- [3] Jeremy Biggs, Naomi Ewald, Alice Valentini, Coline Gaboriaud, Tony Dejean, Richard A. Griffiths, Jim Foster, John W. Wilkinson, Andy Arnell, Peter Brotherton, Penny Williams, and Francesca Dunn. Using eDNA to develop a national citizen science-based monitoring programme for the great crested newt (*Triturus cristatus*). *Biological Conservation*, 183:19–28, 2015. ISSN 00063207. doi: 10.1016/j.biocon.2014.11.029. URL <https://linkinghub.elsevier.com/retrieve/pii/S0006320714004546>.
- [4] Austen C. Thomas, Samantha Tank, Phong L. Nguyen, Jake Ponce, Mieke Sinnesael, and Caren S. Goldberg. A system for rapid eDNA detection of aquatic invasive species. *Environmental DNA*, 2(3):261–270, 2020. ISSN 2637-4943, 2637-4943. doi: 10.1002/edn3.25. URL <https://onlinelibrary.wiley.com/doi/10.1002/edn3.25>.
- [5] Shaun P. Wilkinson, Amy A. Gault, Susan A. Welsh, Joshua P. Smith, Bruno O. David, Andy S. Hicks, Daniel R. Fake, Alastair M. Suren, Megan R. Shaffer, Simon N. Jarman, and Michael Bunce. TICI: A taxon-independent community index for eDNA-based ecological health assessment. *PeerJ*, 12:e16963, 2024. ISSN 2167-8359. doi: 10.7717/peerj.16963. URL <https://peerj.com/articles/16963>.
- [6] Elizabeth Andruszkiewicz Allan, Ryan P. Kelly, Erin R. D’Agnese, Maya N. Garber-Yonts, Megan R. Shaffer, Zachary J. Gold, and Andrew O. Shelton. Quantifying impacts of an environmental intervention using environmental DNA. *Ecological Applications*, 33(8):e2914, 2023. ISSN 1051-0761, 1939-5582. doi: 10.1002/eap.2914. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2914>.
- [7] Gledis Guri, Andrew Olaf Shelton, Ryan P. Kelly, Nigel Yoccoz, Torild Johansen, Kim Pr  bel, Tanja Hanebrekke, Jessica Louise Ray, Johanna Fall, and Jon-Ivar Westgaard. Predicting trawl catches using environmental DNA. *ICES Journal of Marine Science*, 81(8):1536–1548, 2024. doi: 10.1093/icesjms/fsae097. URL <https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsae097/7728836>.
- [8] Michael D. Tillotson, Ryan P. Kelly, Jeffrey J. Duda, Marshal Hoy, James Kralj, and Thomas P. Quinn. Concentrations of environmental DNA (eDNA) reflect spawning salmon abundance at fine spatial and temporal scales. *Biological Conservation*, 220:1–11, 2018. ISSN 00063207. doi: 10.1016/j.biocon.2018.01.030. URL <https://linkinghub.elsevier.com/retrieve/pii/S0006320717313277>.
- [9] Elizabeth L. Clare, Chloe K. Economou, Chris G. Faulkes, James D. Gilbert, Frances Bennett, Rosie Drinkwater, and Joanne E. Littlefair. eDNAir: Proof of concept that animal DNA can be collected from air sampling. *PeerJ*, 9:e11030, 2021. ISSN 2167-8359. doi: 10.7717/peerj.11030. URL <https://peerj.com/articles/11030>.
- [10] Nina R. Garrett, Jonathan Watkins, Nancy B. Simmons, Brock Fenton, Alejandro Maeda-Obregon, Daniel E. Sanchez, Emma M. Froehlich, Faith M. Walker, Joanne E. Littlefair, and Elizabeth L. Clare. Airborne eDNA documents a diverse and ecologically complex tropical bat and other mammal community. *Environmental DNA*, 5(2):350–362, 2023. ISSN 2637-4943, 2637-4943. doi: 10.1002/edn3.385. URL <https://onlinelibrary.wiley.com/doi/10.1002/edn3.385>.

- [11] Mark D. Johnson, Robert D. Cox, and Matthew A. Barnes. Analyzing airborne environmental DNA: A comparison of extraction methods, primer type, and trap type on the ability to detect airborne eDNA from terrestrial plant communities. *Environmental DNA*, 1(2):176–185, 2019. ISSN 2637-4943, 2637-4943. doi: 10.1002/edn3.19. URL <https://onlinelibrary.wiley.com/doi/10.1002/edn3.19>.
- [12] Mark D. Johnson, Matthew A. Barnes, Nina R. Garrett, and Elizabeth L. Clare. Answers blowing in the wind: Detection of birds, mammals, and amphibians with airborne environmental DNA in a natural environment over a yearlong survey. *Environmental DNA*, 5(2):375–387, 2023. ISSN 2637-4943, 2637-4943. doi: 10.1002/edn3.388. URL <https://onlinelibrary.wiley.com/doi/10.1002/edn3.388>.
- [13] Christina Lynggaard, Tobias Guldberg Frøslev, Matthew S. Johnson, Morten Tange Olsen, and Kristine Bohmann. Airborne environmental DNA captures terrestrial vertebrate diversity in nature. *Molecular Ecology Resources*, 24(1):e13840, 2024. ISSN 1755-098X, 1755-0998. doi: 10.1111/1755-0998.13840. URL <https://onlinelibrary.wiley.com/doi/10.1111/1755-0998.13840>.
- [14] Fabian Roger, Hamid R. Ghanavi, Natalie Danielsson, Niklas Wahlberg, Jakob Löndahl, Lars B. Pettersson, Georg K. S. Andersson, Niklas Boke Olén, and Yann Clough. Airborne environmental DNA metabarcoding for the monitoring of terrestrial insects—A proof of concept from the field. *Environmental DNA*, 4(4):790–807, 2022. ISSN 2637-4943, 2637-4943. doi: 10.1002/edn3.290. URL <https://onlinelibrary.wiley.com/doi/10.1002/edn3.290>.
- [15] Christina Lynggaard, Mads Frost Bertelsen, Casper V. Jensen, Matthew S. Johnson, Tobias Guldberg Frøslev, Morten Tange Olsen, and Kristine Bohmann. Airborne environmental DNA for terrestrial vertebrate community monitoring. *Current Biology*, 32(3):701–707.e5, 2022. ISSN 09609822. doi: 10.1016/j.cub.2021.12.014. URL <https://linkinghub.elsevier.com/retrieve/pii/S0960982221016900>.
- [16] Alexis R. Sullivan, Edvin Karlsson, Daniel Svensson, Björn Brindefalk, Jose Antonio Villegas, Amanda Mikko, Daniel Bellieny, Abu Bakar Siddique, Anna-Mia Johansson, Håkan Grahm, David Sundell, Anita Norman, Per-Anders Esseen, Andreas Sjödin, Navinder J Singh, Tomas Brodin, Mats Forsman, and Per Stenberg. Airborne eDNA captures three decades of ecosystem biodiversity, 2023. URL <http://biorxiv.org/lookup/doi/10.1101/2023.12.06.569882>.
- [17] Martin Johannesen Klepke, Eva Egelyng Sigsgaard, Mads Reinholdt Jensen, Kent Olsen, and Philip Francis Thomsen. Accumulation and diversity of airborne, eukaryotic environmental DNA. *Environmental DNA*, 4(6):1323–1339, 2022. ISSN 2637-4943, 2637-4943. doi: 10.1002/edn3.340. URL <https://onlinelibrary.wiley.com/doi/10.1002/edn3.340>.
- [18] Christina Lynggaard, Sébastien Calvignac-Spencer, Colin A. Chapman, Urs Kalbitzer, Fabian H. Leendertz, Patrick A. Omeja, Emmanuel A. Opito, Dipto Sarkar, Kristine Bohmann, and Jan F. Gogarten. Vertebrate environmental DNA from leaf swabs. *Current Biology*, 33(16):R853–R854, 2023. ISSN 09609822. doi: 10.1016/j.cub.2023.06.031. URL <https://linkinghub.elsevier.com/retrieve/pii/S0960982223008138>.
- [19] Orianne Tournayre, Joanne E. Littlefair, Nina R. Garrett, James J. Allerton, Andrew S. Brown, Melania E. Cristescu, and Elizabeth L. Clare. First national survey of terrestrial biodiversity using airborne eDNA, 2025. URL <http://biorxiv.org/lookup/doi/10.1101/2025.04.07.647580>.
- [20] Florian Altermatt, Marjorie Couton, Luca Carraro, François Keck, Lori Lawson-Handley, Florian Leese, Xiaowei Zhang, Yan Zhang, and Rosetta C. Blackman. Utilizing aquatic environmental DNA to address global biodiversity targets. *Nature Reviews Biodiversity*, 2025. ISSN 3005-0677. doi: 10.1038/s44358-025-00044-x. URL <https://www.nature.com/articles/s44358-025-00044-x>.
- [21] Mark Johnson and Matthew A. Barnes. Macroalgal airborne environmental DNA analysis: A review of progress, challenges, and recommendations for an emerging application. *Molecular Ecology Resources*, 24(7):e13998, 2024. ISSN 1755-098X, 1755-0998. doi: 10.1111/1755-0998.13998. URL <https://onlinelibrary.wiley.com/doi/10.1111/1755-0998.13998>.

- [22] Carl Folke, Stephen Polasky, Johan Rockström, Victor Galaz, Frances Westley, Michèle Lamont, Marten Scheffer, Henrik Österblom, Stephen R. Carpenter, F. Stuart Chapin, Karen C. Seto, Elke U. Weber, Beatrice I. Crona, Gretchen C. Daily, Partha Dasgupta, Owen Gaffney, Line J. Gordon, Holger Hoff, Simon A. Levin, Jane Lubchenco, Will Steffen, and Brian H. Walker. Our future in the Anthropocene biosphere. *Ambio*, 50(4):834–869, 2021. ISSN 0044-7447, 1654-7209. doi: 10.1007/s13280-021-01544-8. URL <http://link.springer.com/10.1007/s13280-021-01544-8>.
- [23] E.C. Monahan, D.E. Spiel, and K.L. Davidson. A model of marine aerosol generation via whitecaps and wave disruption. In E.C. Monahan and G.M. Niocaill, editors, *Oceanic Whitecaps*, volume 2 of *Oceanographic Sciences Library*. Springer, Dordrecht, 1986. ISBN 978-94-009-4668-2. doi: 10.1007/978-94-009-4668-2.16.
- [24] John H. Seinfeld and Spyros N. Pandis. *Atmospheric Chemistry and Physics: From Air Pollution to Climate Change*. Wiley, 3 edition, 2016. ISBN 978-1-118-94740-1.
- [25] Laurent Duchemin, Stéphane Popinet, Christophe Josserand, and Stéphane Zaleski. Jet formation in bubbles bursting at a free surface. *Physics of Fluids*, 14(9):3000–3008, 2002. ISSN 1070-6631, 1089-7666. doi: 10.1063/1.1494072. URL <https://pubs.aip.org/pof/article/14/9/3000/255789/Jet-formation-in-bubbles-bursting-at-a-free>.
- [26] Robert P. Mueller, Susan S. Southard, Christopher W. May, Walter H. Pearson, and Valerie I. Cullinan. Juvenile Coho Salmon Leaping Ability and Behavior in an Experimental Culvert Test Bed. *Transactions of the American Fisheries Society*, 137(4):941–950, 2008. ISSN 0002-8487, 1548-8659. doi: 10.1577/T06-244.1. URL <https://academic.oup.com/tafs/article/137/4/941/7888500>.
- [27] E. Stell, J. J. Hoover, L. Fuller, and G. R. Parsons. Analyzing Leap Characteristics and Water Escape Velocities of Silver Carp Using In Situ Video Analysis. *North American Journal of Fisheries Management*, 40(1):163–174, 2020. ISSN 0275-5947, 1548-8675. doi: 10.1002/nafm.10388. URL <https://academic.oup.com/naajfm/article/40/1/163/7817142>.
- [28] A. I. J. M. Van Dijk, L. A. Bruijnzeel, and E. H. Eisma. A methodology to study rain splash and wash processes under natural rainfall. *Hydrological Processes*, 17(1):153–167, 2003. ISSN 0885-6087, 1099-1085. doi: 10.1002/hyp.1154. URL <https://onlinelibrary.wiley.com/doi/10.1002/hyp.1154>.
- [29] Wenjian Chen, Junjie Wang, Yuqi Zhao, Yiyong He, Jinlin Chen, Chaoyu Dong, Li Liu, Jun Wang, and Lei Zhou. Contrasting pollution responses of native and non-native fish communities in anthropogenically disturbed estuaries unveiled by eDNA metabarcoding. *Journal of Hazardous Materials*, 480:136323, 2024. ISSN 03043894. doi: 10.1016/j.jhazmat.2024.136323. URL <https://linkinghub.elsevier.com/retrieve/pii/S0304389424029029>.
- [30] Dannise V. Ruiz-Ramos, Rachel S. Meyer, Daniel Toews, Molly Stephens, Monique K. Kolster, and Jason P. Sexton. Environmental DNA (eDNA) detects temporal and habitat effects on community composition and endangered species in ephemeral ecosystems: A case study in vernal pools. *Environmental DNA*, 5(1):85–101, 2023. ISSN 2637-4943, 2637-4943. doi: 10.1002/edn3.360. URL <https://onlinelibrary.wiley.com/doi/10.1002/edn3.360>.
- [31] Jianan Wan, Zhiruo Zhang, Yang Huo, Xianze Wang, Yifan Wang, Jinghui Wu, and Mingxin Huo. Particle Size Matters: Distribution, Source, and Seasonality Characteristics of Airborne and Pathogenic Bacteria in Wastewater Treatment Plants. *Atmosphere*, 14(3):465, 2023. ISSN 2073-4433. doi: 10.3390/atmos14030465. URL <https://www.mdpi.com/2073-4433/14/3/465>.
- [32] Yan Wu, Fangxia Shen, and Maosheng Yao. Use of gelatin filter and BioSampler in detecting airborne H5N1 nucleotides, bacteria and allergens. *Journal of Aerosol Science*, 41(9):869–879, 2010. ISSN 00218502. doi: 10.1016/j.jaerosci.2010.05.006. URL <https://linkinghub.elsevier.com/retrieve/pii/S0021850210001217>.
- [33] Piyanun Harnpicharnchai, Panyapon Pumkao, Paopit Siriarchawatana, Somsak Likhitrattanapisal, Sermsiri Mayteeworakoon, Lily Ingsrisawang, Worawongsin Boonsin, Lily Eurwilaichitr, and Supawadee

- Ingsriswang. AirDNA sampler: An efficient and simple device enabling high-yield, high-quality airborne environment DNA for metagenomic applications. *PLOS ONE*, 18(6):e0287567, 2023. ISSN 1932-6203. doi: 10.1371/journal.pone.0287567. URL <https://dx.plos.org/10.1371/journal.pone.0287567>.
- [34] Jeffrey J. Duda, Marshal S. Hoy, Dorothy M. Chase, George R. Pess, Samuel J. Brenkman, Michael M. McHenry, and Carl O. Ostberg. Environmental DNA is an effective tool to track recolonizing migratory fish following large-scale dam removal. *Environmental DNA*, 3(1):121–141, 2021. ISSN 2637-4943, 2637-4943. doi: 10.1002/edn3.134. URL <https://onlinelibrary.wiley.com/doi/10.1002/edn3.134>.
- [35] David W. Welch and Yukimasa Ishida. On the Statistical Distribution of Salmon in the Sea: Application of the Negative Binomial Distribution, and the Influence of Sampling Effort. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(5):1029–1038, 1993. doi: 10.1139/f93-119. URL <http://www.nrcresearchpress.com/doi/10.1139/f93-119>.
- [36] Gledis Guri, Jessica Louise Ray, Andrew Olaf Shelton, Ryan P. Kelly, Kim Præbel, Elizabeth Andruskiewicz Allan, Nigel Yoccoz, Torild Johansen, Owen S. Wangensteen, Tanja Hanebrekke, and Jon-Ivar Westgaard. Quantifying the Detection Sensitivity and Precision of qPCR and ddPCR Mechanisms for eDNA Samples. *Ecology and Evolution*, 14(12):e70678, 2024. doi: 10.1002/ece3.70678. URL <https://onlinelibrary.wiley.com/doi/10.1002/ece3.70678>.
- [37] Andrew Olaf Shelton, Ana Ramón-Laca, Abigail Wells, Julia Clemons, Dezhong Chu, Blake E. Feist, Ryan P. Kelly, Sandra L. Parker-Stetter, Rebecca Thomas, Krista M. Nichols, and Linda Park. Environmental DNA provides quantitative estimates of Pacific hake abundance and distribution in the open ocean. *Proceedings of the Royal Society B: Biological Sciences*, 289(1971):20212613, 2022. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2021.2613.
- [38] Zachary T. Wood, Anaïs Lacoursière-Roussel, Francis LeBlanc, Marc Trudel, Michael T. Kinnison, Colton Garry McBrine, Scott A. Pavey, and Nellie Gagné. Spatial Heterogeneity of eDNA Transport Improves Stream Assessment of Threatened Salmon Presence, Abundance, and Location. *Frontiers in Ecology and Evolution*, 9:650717, 2021. ISSN 2296-701X. doi: 10.3389/fevo.2021.650717. URL <https://www.frontiersin.org/articles/10.3389/fevo.2021.650717/full>.
- [39] Kimberly A. Prather, Timothy H. Bertram, Vicki H. Grassian, Grant B. Deane, M. Dale Stokes, Paul J. DeMott, Lihini I. Aluwihare, Brian P. Palenik, Farooq Azam, John H. Seinfeld, Ryan C. Moffet, Mario J. Molina, Christopher D. Cappa, Franz M. Geiger, Gregory C. Roberts, Lynn M. Russell, Andrew P. Ault, Jonas Baltrusaitis, Douglas B. Collins, Craig E. Corrigan, Luis A. Cuadra-Rodriguez, Carlena J. Ebben, Sara D. Forestieri, Timothy L. Guasco, Scott P. Hersey, Michelle J. Kim, William F. Lambert, Robin L. Modini, Wilton Mui, Byron E. Pedler, Matthew J. Ruppel, Olivia S. Ryder, Nathan G. Schoepp, Ryan C. Sullivan, and Defeng Zhao. Bringing the ocean into the laboratory to probe the chemical complexity of sea spray aerosol. *Proceedings of the National Academy of Sciences*, 110(19):7550–7555, 2013. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1300262110. URL <https://pnas.org/doi/full/10.1073/pnas.1300262110>.
- [40] Nerea Abrego, Brendan Furneaux, Bess Hardwick, Panu Somervuo, Isabella Palorinne, Carlos A. Aguilar-Trigueros, Nigel R. Andrew, Ulyana V. Babiy, Tan Bao, Gisela Bazzano, Svetlana N. Bondarchuk, Timothy C. Bonebrake, Georgina L. Brennan, Syndonia Bret-Harte, Claus Bässler, Luciano Cagnolo, Erin K. Cameron, Elodie Chapurlat, Simon Creer, Luigi P. D’Acqui, Natasha De Vere, Marie-Laure Desprez-Loustau, Michel A. K. Dongmo, Ida B. Dyrholm Jacobsen, Brian L. Fisher, Miguel Flores De Jesus, Gregory S. Gilbert, Gareth W. Griffith, Anna A. Gritsuk, Andrin Gross, Håkan Grudd, Panu Halme, Rachid Hanna, Jannik Hansen, Lars Holst Hansen, Apollon D. M. T. Hegbe, Sarah Hill, Ian D. Hogg, Jenni Hultman, Kevin D. Hyde, Nicole A. Hynson, Natalia Ivanova, Petteri Karisto, Deirdre Kerdraon, Anastasia Knorre, Irmgard Krisai-Greilhuber, Juri Kurhinen, Masha Kuzmina, Nicolas Lecomte, Erin Lecomte, Viviana Loaiza, Erik Lundin, Alexander Meire, Armin Mešić, Otto Miettinen, Norman Monkhouse, Peter Mortimer, Jörg Müller, R. Henrik Nilsson, Puani Yannick C. Nonti, Jenni Nordén, Björn Nordén, Veera Norros, Claudia Paz, Petri Pellikka, Danilo Pereira, Geoff Petch, Juha-Matti

- Pitkänen, Flavius Popa, Caitlin Potter, Jenna Purhonen, Sanna Pätsi, Abdullah Rafiq, Dimby Rahar-injanahary, Niklas Rakos, Achala R. Rathnayaka, Katrine Raundrup, Yury A. Rebriev, Jouko Rikkinen, Hanna M. K. Rogers, Andrey Rogovsky, Yuri Rozhkov, Kadri Runnel, Annika Saarto, Anton Savchenko, Markus Schlegel, Niels Martin Schmidt, Sebastian Seibold, Carsten Skjøth, Elisa Stengel, Svetlana V. Sutyryna, Ilkka Syväänperä, Leho Tedersoo, Jebidiah Timm, Laura Tipton, Hirokazu Toju, Maria Uscka-Perzanowska, Michelle Van Der Bank, F. Herman Van Der Bank, Bryan Vandenbrink, Stefano Ventura, Solvi R. Vignisson, Xiaoyang Wang, Wolfgang W. Weisser, Subodini N. Wijesinghe, S. Joseph Wright, Chunyan Yang, Nourou S. Yorou, Amanda Young, Douglas W. Yu, Evgeny V. Zakharov, Paul D. N. Hebert, Tomas Roslin, and Otso Ovaskainen. Airborne DNA reveals predictable spatial and seasonal dynamics of fungi. *Nature*, 631(8022):835–842, 2024. ISSN 0028-0836, 1476-4687. doi: 10.1038/s41586-024-07658-9. URL <https://www.nature.com/articles/s41586-024-07658-9>.
- [41] Michael Giolai, Walter Verweij, Samuel Martin, Neil Pearson, Paul Nicholson, Richard M. Leggett, and Matthew D. Clark. Measuring air metagenomic diversity in an agricultural ecosystem. *Current Biology*, 34(16):3778–3791.e4, 2024. ISSN 09609822. doi: 10.1016/j.cub.2024.07.030. URL <https://linkinghub.elsevier.com/retrieve/pii/S0960982224009333>.
- [42] Sofía Galbán, Ana Justel, Sergi González, and Antonio Quesada. Local meteorological conditions, shape and desiccation influence dispersal capabilities for airborne microorganisms. *Science of The Total Environment*, 780:146653, 2021. ISSN 00489697. doi: 10.1016/j.scitotenv.2021.146653. URL <https://linkinghub.elsevier.com/retrieve/pii/S0048969721017216>.
- [43] Teruya Maki, Kentaro Hosaka, Kevin C. Lee, Yasuhiro Kawabata, Mizuo Kajino, Maoto Uto, Kazuyuki Kita, and Yasuhito Igarashi. Vertical distribution of airborne microorganisms over forest environments: A potential source of ice-nucleating bioaerosols. *Atmospheric Environment*, 302:119726, 2023. ISSN 13522310. doi: 10.1016/j.atmosenv.2023.119726. URL <https://linkinghub.elsevier.com/retrieve/pii/S1352231023001528>.
- [44] Hugo Jager, Krijn B. Trimbos, Jan-Maarten Luursema, Adrianus G.C.L. Speksnijder, and Kathryn A. Stewart. A breath of fresh air: Comparative evaluation of passive versus active airborne eDNA sampling strategies, 2025. URL <http://biorxiv.org/lookup/doi/10.1101/2025.03.26.645491>.
- [45] Duncan C. Blanchard and Alfred H. Woodcock. THE PRODUCTION, CONCENTRATION, AND VERTICAL DISTRIBUTION OF THE SEA-SALT AEROSOL*. *Annals of the New York Academy of Sciences*, 338(1):330–347, 1980. ISSN 0077-8923, 1749-6632. doi: 10.1111/j.1749-6632.1980.tb17130.x. URL <https://nyaspubs.onlinelibrary.wiley.com/doi/10.1111/j.1749-6632.1980.tb17130.x>.
- [46] William C Hinds and Yifang Zhu. *Aerosol technology: properties, behavior, and measurement of airborne particles*. John Wiley & Sons, 2022.
- [47] Braden A. Herman. Use of foreign edna tracers to resolve site- and time-specific edna distributions in natural streams. Master’s thesis, Humboldt State University, spring 2023. Master of Science in Natural Resources, option Fisheries.
- [48] Pedro F. P. Brandão-Dias, Daniel M. C. Hallack, Elise D. Snyder, Jennifer L. Tank, Diogo Bolster, Sabrina Volponi, Ariel J. Shogren, Gary A. Lamberti, Kyle Bibby, and Scott P. Egan. Particle size influences decay rates of environmental DNA in aquatic systems. *Molecular Ecology Resources*, 23(4):756–770, 2023. ISSN 1755-098X, 1755-0998. doi: 10.1111/1755-0998.13751. URL <https://onlinelibrary.wiley.com/doi/10.1111/1755-0998.13751>.
- [49] Katherine M. Strickler, Alexander K. Fremier, and Caren S. Goldberg. Quantifying effects of UV-B, temperature, and pH on eDNA degradation in aquatic microcosms. *Biological Conservation*, 183:85–92, 2015. ISSN 00063207. doi: 10.1016/j.biocon.2014.11.038. URL <https://linkinghub.elsevier.com/retrieve/pii/S0006320714004637>.
- [50] Matthew A. Barnes and Cameron R. Turner. The ecology of environmental DNA and implications for conservation genetics. *Conservation Genetics*, 17(1):1–17, 2016. ISSN 15729737. doi: 10.1007/s10592-015-0775-4.

- [51] Jori B. Harrison, Jennifer M. Sunday, and Sean M. Rogers. Predicting the fate of eDNA in the environment and implications for studying biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, 286(1915):20191409, 2019. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2019.1409. URL <https://royalsocietypublishing.org/doi/10.1098/rspb.2019.1409>.
- [52] Mark Bagley, Erik Pilgrim, Martin Knapp, Chris Yoder, Jorge Santo Domingo, and Aabir Banerji. High-throughput environmental DNA analysis informs a biological assessment of an urban stream. *Ecological Indicators*, 104:378–389, 2019. ISSN 1470160X. doi: 10.1016/j.ecolind.2019.04.088. URL <https://linkinghub.elsevier.com/retrieve/pii/S1470160X19303346>.
- [53] Steffen Kirchgeorg, Jia Jin Marc Chang, Yin Cheong Aden Ip, Meret Jucker, Christian Geckeler, Martina Lüthi, Enrico Van Der Loo, Elvira Mächler, Nicolás D. Franco-Sierra, Mailyn Adriana Gonzalez Herrera, Loïc Pellissier, Kristy Deiner, Andrea Desiderato, and Stefano Mintchev. eProbe: Sampling of Environmental DNA within Tree Canopies with Drones. *Environmental Science & Technology*, 58(37):16410–16420, 2024. ISSN 0013-936X, 1520-5851. doi: 10.1021/acs.est.4c05595. URL <https://pubs.acs.org/doi/10.1021/acs.est.4c05595>.
- [54] Ariel J. Shogren, Jennifer L. Tank, Elizabeth Andruszkiewicz, Brett Olds, Andrew R. Mahon, Christopher L. Jerde, and Diogo Bolster. Controls on eDNA movement in streams: Transport, Retention, and Resuspension. *Scientific Reports*, 7(1):5065, 2017. ISSN 2045-2322. doi: 10.1038/s41598-017-05223-1. URL <https://www.nature.com/articles/s41598-017-05223-1>.
- [55] Pedro Fp Brandao-Dias, Megan Shaffer, Gledis Guri, Kim M Parsons, Ryan P Kelly, and Elizabeth Andruszkiewicz Allan. Differential Decay of Multiple eNA Components from a Cetacean, 2025. URL <http://biorxiv.org/lookup/doi/10.1101/2025.05.09.653189>.