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STUDENT AWARDEE PAPER

Weak Coupling Between Gas Exchange and Water Loss in Lungless Salamanders

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Synopsis Gas exchange requires a permeable respiratory surface, yet the same permeability also creates a pathway for water loss, posing a particular challenge for organisms whose respiratory surfaces are directly exposed to the terrestrial environment. Woodland salamanders (*Plethodon*) are a diverse radiation of lungless, terrestrial amphibians that rely entirely on cutaneous respiration, coupling gas exchange and water loss through a shared surface. Whether this shared surface produces a consistent relationship between water loss and metabolic rate across species, or whether the two traits can diverge despite their functional link, remains unresolved. Here, we quantified metabolic rate, water loss rate, and the ratio between these traits across 30 *Plethodon* species and related these traits to elevational distributions, geographic range size, and climatic conditions across species' ranges. We also compared the relationship between gas exchange and water loss in *Plethodon* to that observed across a broader set of amphibian taxa. Metabolic rate and water loss were not tightly correlated across *Plethodon*, despite a positive association across amphibians more broadly. Instead, physiological traits correlated with different aspects of species' elevational limits, range sizes, and climatic niches. Metabolic rate was most consistently associated with elevation and climate, with lower values observed in species occupying higher, cooler environments. Water loss alone showed weaker and less consistent environmental associations, but the transpiration ratio varied with elevational limits such that species extending into lower-elevation environments exhibited greater hydric efficiency. These patterns were also reflected in phylogenetic path analyses, which supported lower elevational limit as a mediator linking physiology to geographic range size. These results suggest that although cutaneous respiration imposes broad hydric costs across amphibians, *Plethodon* species do not show a single, shared pattern of physiological coupling between gas exchange and water loss.

Introduction

Life on land imposes a fundamental physiological challenge: organisms must exchange respiratory gases with the environment while limiting evaporative water loss (Woods and Smith 2010). This trade-off arises because respiratory exchange occurs most effectively across moist, thin, highly vascularized tissues, but these same features also increase the potential for evaporative water loss. As a result, gas exchange and water loss are often linked in terrestrial organisms, and the amount of water lost per unit gas exchanged can be quantified as the transpiration ratio (TR), a metric of the hydric cost of respiration (Welch and Tracy 1977; Maina 2002; Woods and Smith 2010; Burger et al. 2024). In many terrestrial lineages, this physiological tension is reduced by shifting gas exchange away from the external body surface through the improved use of respiratory systems and by evolving integumentary barriers that limit evaporative loss (Maina 2002; Lillywhite 2006). However, some lineages, such as amphibians, continue to rely predominantly on cutaneous respiration, which maintains a fundamental trade-off between gas exchange and water loss and may strongly shape physiological diversity among species.

Amphibians are unique among terrestrial vertebrates in retaining thin, highly permeable skin that plays a ma-

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jor role in gas exchange but also increases susceptibility to dehydration (Feder and Burggren 1985; Toledo and Jared 1993). Most amphibians rely extensively on cutaneous respiration at rest (Senzano and Andrade 2018), and comparative work suggests that they lose large amounts of water per unit oxygen consumed, resulting in unusually high TRs (Riddell et al. 2024). Relative to other terrestrial taxa, these values are extreme: average amphibian TRs are approximately 145-fold higher than in plants and about 66,000-fold higher than in birds (Riddell et al. 2024). Even among amphibians, the hydric cost of respiration may further vary depending on respiratory mode. Nearly two-thirds of extant salamander species belong to Plethodontidae, a wholly lungless family (AmphibiaWeb 2026). In these salamanders, and in a single caecilian species, the skin is the primary site of gas exchange and water loss (Wilkinson and Nussbaum 1997; Lewis et al. 2022). The consequences of this shared surface should be especially pronounced when cutaneous respiration occurs on land, where maintaining a moist, permeable respiratory surface also exposes animals to evaporative water loss. In terrestrial lungless salamanders, any reduction in skin permeability that limits water loss could also impede oxygen uptake, creating a potential constraint on the independent evolution of hydric and metabolic traits. Therefore, these salamanders provide a powerful system for testing whether reliance on cutaneous respiration is associated with tighter relationships between water loss and metabolism, particularly relative to other amphibians with lungs, which compartmentalize gas exchange within a more saturated internal environment (Riddell et al. 2024).

Among lungless salamanders, woodland salamanders (genus *Plethodon*) are a particularly compelling group for examining how this trade-off shapes physiological variation. This diverse North American radiation comprises direct-developing species that are fully terrestrial throughout their life cycle, yet vary widely in elevational and latitudinal distributions, climatic associations, and geographic range size (DeGross and Bury 2007; Markle and Kozak 2018; Nottingham and Pelletier 2021; Graham et al. 2023; Alomar et al. 2026). This combination of shared respiratory mode and substantial geographic variation makes *Plethodon* well suited for testing whether a hydric-respiratory trade-off contributes to interspecific differences in physiology, distribution, and range size. Woodland salamanders may already operate near an important constraint boundary, as plethodontids have exceptionally low metabolic rates relative to most vertebrates and rely entirely on diffusion across the skin, an inherently limited pathway for oxygen uptake (Feder 1983). Further, evidence from *Plethodon metcalfi* indicates that a hydric-respiratory trade-off can occur within *Plethodon*, with reduced water loss accompanied by reduced oxygen uptake (Riddell et al. 2018). More recent work suggests that the strength of this relationship can vary across seasonal and experimental contexts, pointing to an important role for plasticity (Assis et al. 2025). Whether this within-species trade-off scales up to explain interspecific variation across *Plethodon* remains an open question.

Whether water loss and metabolism remain coupled across species determines whether the underlying trade-off constrains physiological diversification in *Plethodon*. Under tight coupling, species with higher metabolic rates should also exhibit higher rates of water loss, causing hydric and metabolic traits to respond similarly to environmental gradients. Such a shared constraint could limit the conditions under which species maintain both hydration and oxygen uptake, shaping elevational distributions and geographic range sizes. Alternatively, weaker coupling would allow each trait to track different environmental components, with metabolic traits primarily responding to thermal conditions (Muñoz et al. 2022) and hydric traits to humidity and water availability (Winters and Gifford 2013; Riddell and Sears 2015). Because temperature generally declines with elevation while moisture conditions vary across mountain gradients (Körner 2007), physiological responses may together determine where species can persist (Peterman and Semlitsch 2014) and how broadly they are distributed (Slatyer et al. 2013). Determining whether hydric and metabolic traits covary is therefore central to understanding the diversification of this clade.

Here, we test whether water loss rate and metabolic rate covary across species of *Plethodon*, and whether hydric and metabolic physiology are associated with species distributions. We also test whether water loss rate and metabolic rate covary across a broader set of amphibians and compare these patterns to those observed in *Plethodon*. Specifically, we ask whether physiological traits, including the TR, relate to geographic range size, elevational distributions, and climatic conditions across species' ranges, and whether associations between physiology and range size are better explained as direct or mediated through elevation. By integrating water loss, metabolism, hydric efficiency, and multiple components of species distributions, we evaluate whether cutaneous respiration constrains these traits to covary across species or whether they can diverge despite their functional link. We then show how the hydric cost of respiration in lungless salamanders compares to that observed across lunged amphibians.

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Methods

Data collection

We measured water loss and metabolic rate in 277 salamanders across 30 Plethodon species (n = 5–15 individuals per species) collected across the southeastern United States between 2021 and 2024 (Alomar et al. 2026; Table S1). Animals were housed at Yale University at 15°C and 75% relative humidity, acclimated for at least three weeks, and fasted for 10 days prior to trials to standardize physiological state across measurements.

Water loss rate was measured at 13°C, 17°C, and 23°C under two vapor pressure deficit (VPD) treatments (0.50 and 0.70 kPa), whereas metabolic rate was measured at the same temperatures under 0.50 kPa VPD only. The higher VPD treatment was used to characterize water loss under greater evaporative demand, whereas metabolic rate was measured only at 0.50 kPa because our primary focus was on the effects of temperature on metabolism and additional VPD treatments were not feasible within the experimental schedule. Accordingly, all analyses in this study used water loss and metabolic rate measured under the shared 0.50 kPa treatment. Trials were conducted using a Sable Systems flow-through respirometry system (Sable Systems International, Las Vegas, NV, USA) that regulated airflow, humidity, and chamber temperature. Air was drawn by an SS-4 sub-sampler pump, humidified with a DG-4 dew point generator, split among chambers using an MF-8 manifold, and sampled sequentially with a MUX-8 multiplexer. For water-loss measurements, air was routed through eight acrylic cylindrical chambers (17.78 cm long, 1.60 cm radius) at 175 mL/min. For metabolic measurements, lower flow rates were used to improve detection of salamanders' low CO_2 output, with most individuals measured at 45 mL/min and individuals under 1 g measured in smaller chambers (17.78 cm long, 1.28 cm radius) at 30 mL/min. Chambers were maintained at the target temperature in an insulated chamber controlled by a PELT-5 temperature controller. Excurrent air then passed through an RH-300 Water Vapor Analyzer and a CA-10 Carbon Dioxide Analyzer, and traces were recorded and processed in Expedata during trials lasting approximately 3–3.5 h. These procedures are consistent with established flow-through respirometry approaches used to measure water loss and metabolic rate in salamanders (Riddell et al. 2018; Alomar et al. 2026).

Each salamander was measured repeatedly across treatment combinations in randomized order. Individuals were allowed to acclimate to chamber conditions before sampling, and physiological rates were estimated from stable resting portions of the trace (Riddell et al. 2017). Measurements affected by unstable traces, CO_2 spikes, or waste excretion were rerun when possible or otherwise excluded, representing 3.13% of measurements. Water loss rate and metabolic rate were calculated using standard flow-through respirometry equations that account for water vapor dilution, flow-rate correction, and chamber-based gas analysis (Lighton 2008; Riddell et al. 2017).

Transpiration ratio

We calculated TR as the ratio of molar water loss to molar O_2 consumption (mol H_2O/mol O_2), which has been interpreted as an index of hydric efficiency (lower TR = greater hydric efficiency) (Riddell et al. 2024). CO_2 exchange rates were recorded as μL CO_2 h^{-1} and converted to mol CO_2 day^{-1} using the ideal gas law with assay temperature (K) and standard atmospheric pressure (101.325 kPa). We then converted mol CO_2 day^{-1} to mol O_2 day^{-1} using an assumed respiratory quotient (RQ), where $RQ = VCO_2/VO_2$ and thus $VO_2 = VCO_2/RQ$. We used RQ = 0.7, consistent with predominantly lipid-based metabolism expected in fasting terrestrial vertebrates (Price and Mager 2020). Water loss rates were recorded as g H_2O s^{-1} and converted to mol H_2O day^{-1} by converting to g day^{-1} and dividing by the molar mass of water (18.015 g mol^{-1}). For phylogenetic analyses using the species-level tree, we calculated species means for each trait within each assay temperature and then computed TR as the ratio of species-mean molar water loss to species-mean molar O_2 consumption under matched conditions.

Environmental data

Species range polygons were obtained from the U.S. Geological Survey Gap Analysis Project (USGS GAP) and processed as ESRI shapefiles. We used these polygons to summarize climate in two complementary ways: standard bioclimatic variables and multiyear daily climate data summarized across the active season. This allowed us to test whether physiological associations were consistent across bioclimatic and daily active-season climate summaries. For bioclimatic summaries, we extracted BIOCLIM variables (~1 km resolution) across each species' range polygon. Rasters were cropped and masked to each polygon, and we summarized values for each BIOCLIM layer across the polygon (mean, median, SD, minimum, maximum, and range). For daily climate, we summarized Daymet conditions across each species' range by sampling 75 random points within the USGS GAP polygon. For each point, we downloaded daily Daymet data (2012–2022) and summarized conditions across the active season (April 1–October 21), including temperature, precipitation, and VPD (kPa), calculated from Daymet vapor pressure (Pa) and saturation

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vapor pressure estimated from mean daily temperature. These summaries were then averaged to obtain species-level Daymet estimates. Elevational limits (lower, midpoint, and upper) were compiled from Raffaëlli (2022), and geographic range size (km^2) was calculated from the range polygons.

Phylogenetic generalized least squares

All comparative analyses were conducted in R (R Core Team 2025). Species-level phylogenetic generalized least squares (PGLS) models were fitted using the package caper (Orme et al. 2013). We used the time-calibrated *Plethodon* phylogeny of Waldron et al. (2025), inferred from anchored hybrid enrichment loci, and pruned to the species included in each analysis. Phylogenetic covariance was modeled under Brownian motion and models included log-transformed body mass.

To assess the relationship between water loss and metabolism among species, we fitted PGLS models relating water loss rate to metabolic rate, with body mass included as a covariate. These models were run separately at 13°C, 17°C, and 23°C and repeated using species mean metabolic rate and water loss averaged across experimental temperatures. We evaluated the direction and magnitude of the O_2 effect to assess the strength of the trade-off. We also used recently collected data from a broader set of amphibians (Riddell et al. 2024) to test whether the trade-off observed across amphibians at a higher taxonomic level also extended across *Plethodon*.

We next tested whether physiological traits covaried with geographic range size and elevational limits. For range size (km^2), we fitted PGLS models of the form:

$$\text{trait} \sim \log 10\left(\text{rangearea}\right) + \log 10\left(\text{bodymass}\right),$$

Elevational models related each trait to lower elevational limit, elevational midpoint, and upper elevational limit, each with body mass included:

$$\text{trait} \sim \text{elevationmetric} + \log 10\left(\text{bodymass}\right).$$

Traits were log-transformed prior to analysis (log10 TR, log10 water loss rate, log10 metabolic rate).

To examine whether climatic conditions across species' ranges were associated with physiological variation, we fitted PGLS models relating each physiological trait to individual climatic variables extracted across species' ranges. We ran separate models for BIOCLIM and Daymet variables to test whether physiological traits were associated with climate summarized from bioclimatic variables as well as from daily data across the active season. For each trait and temperature, we fitted models of the form:

$$\text{trait} \sim \text{climate variable} + \log 10\left(\text{bodymass}\right),$$

where climate variables included mean and variability of temperature, precipitation, and (for Daymet) VPD metrics summarized across each species' range. Due to the multiple climate predictors for each trait, we controlled for multiple comparisons within each trait by applying a false discovery rate (FDR) correction to *P*-values.

As a complementary approach, we repeated key analyses using phylogenetically informed mass-corrected residuals calculated with phyl.resid in the R package phytools (Revell 2012). This allowed us to assess whether the results depended on accounting for body mass directly in the regression model or through mass-corrected residuals.

Individual-level mixed-effects analysis

To test whether averaging measurements to the species level obscured relationships at finer biological scales, we analyzed matched evaporative-water-loss and metabolic-rate measurements collected from the same individuals at the same assay temperatures under 0.50 kPa VPD. The dataset included 542 observations from 200 individuals across all 30 species. We fitted Bayesian mixed-effects models using the R package brms (Bürkner 2017). Models related log-transformed metabolic rate to the within-individual, among-individual within-species, and among-species components of log-transformed evaporative water loss, with experiment temperature and log-transformed body mass included as covariates. Individual identity was included as a random effect to account for repeated measurements, and species was included as a phylogenetically structured random effect using a covariance matrix. We separated evaporative water loss into within-individual, among-individual within-species, and among-species components to test whether covariation with metabolic rate differed across levels of biological organization. Models were run using four chains with 5000 iterations per chain, including 2500 warmup iterations. All models showed satisfactory convergence based on R-hat values and effective sample sizes (Vehtari et al. 2021).

Phylogenetic path analysis

The analyses described above can reveal associations among physiology, elevation, and range size, but do not resolve how these variables are linked, or whether relationships with range size arise directly or through elevational limits. To evaluate alternative causal structures linking physiology, elevational distributions, and geographic range size, we conducted phylogenetic path analysis using the R package phylopath (van der Bijl 2018). Phylogenetic path analysis compares support for

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alternative causal models and tests the direct and indirect relationships among variables while accounting for shared ancestry among species. We focused on lower elevational limit as the elevational metric in these analyses because it was the only elevational variable significantly associated with range size in comparative models, making it the most appropriate candidate for testing whether physiology relates to range size indirectly through elevation. We compared three biologically motivated candidate models: (1) a direct model in which physiology predicts both lower elevational limit and range size, (2) a mediated model in which physiology predicts lower elevational limit, which then predicts range size, and (3) a combined model including both direct and mediated pathways. These path analyses tested whether physiological traits were associated with lower elevational limit after accounting for body size, and whether associations between physiology and range size were better explained as direct or mediated through lower elevational limit.

We fitted these candidate model sets using physiology measured at 13°C, 17°C, and 23°C to test whether support for alternative path structures and the strength of each path differed across temperatures. We did not include TR in the path analysis because it is a ratio derived from water loss and metabolic rate, and we instead modeled the component traits directly to keep path interpretation clearer. In all models, body mass was included as an upstream predictor of both physiological traits to account for body-size scaling. Prior to analysis, variables used in the path models were z-scored to place coefficients on a comparable scale. Models were fitted with a phylogenetic error structure by estimating Pagel's λ (Pagel 1999) (bounded between 0 and 1) for each component regression. Candidate models were compared using CICc, the small-sample-corrected information criterion implemented in the R package phylopath (van der Bijl 2018), and support was summarized using model weights and ΔCICc.

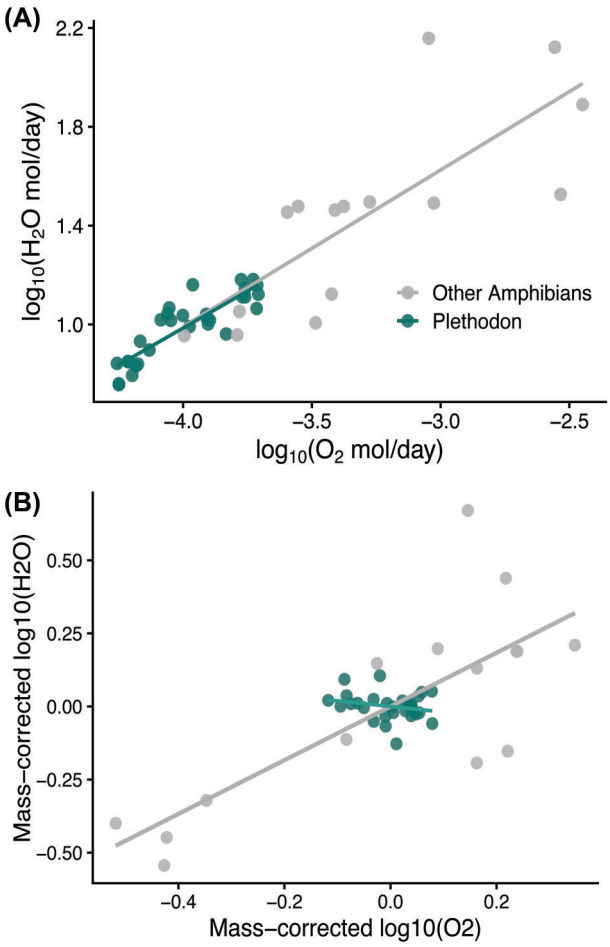

Fig. 1 Relationship between oxygen uptake and water loss in amphibians. (A) Raw species-level relationship between log10 oxygen uptake (O_2 mol day − 1) and log10 water loss (H_2O mol day − 1). (B) Mass-corrected relationship, shown as residual log10 oxygen uptake and residual log10 water loss after accounting for body mass within each dataset. Points represent species means; lines show fitted linear relationships for visualization. *Plethodon* species and species from the broader amphibian comparative dataset are identified in the figure legend.

Results

Correlation of water loss and metabolism

Across species-level phylogenetic models, we did not find evidence for a simple, general trade-off between water loss and metabolism across *Plethodon* species. In models relating water loss to metabolism (while accounting for body mass), the metabolic term was not significant in the overall model (Fig. 1B; slope = −0.1345 ± 0.1466 SE, $P = 0.367$) or in any temperature-specific model (13°C: slope = 0.0012 ± 0.1305, $P = 0.993$; 17°C: slope = −0.0394 ± 0.1373, $P = 0.776$; 23°C: slope = −0.1856 ± 0.3115, $P = 0.556$). The same result held in a residual-based check using mass-corrected residuals (slope = −0.1345 ± 0.1439, $P = 0.358$). The slopes were small and inconsistent in direction across experimental temperatures, so species with higher metabolism did not consistently show either higher or lower rates of water loss. The individual-level analysis yielded a similar overall pattern. After accounting for assay temperature, body mass, repeated measurements, and phylogenetic covariance, evaporative water loss was not detectably associated with metabolic rate within the same individuals across temperatures (posterior mean = 0.010, 95% credible interval = −0.087 to 0.103; Table S3). The among-species effect was likewise centered near zero (posterior mean = −0.009, 95% credible interval = −0.333 to 0.317; Table S3). However, the relationship among individuals within species leaned positive,

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Table 1 Phylogenetic generalized least squares (PGLS) models relating physiology to geographic range size and elevational distributions across *Plethodon* species.

Env. trait	Phys. Trait	Elevation metric	Slope env	*P*-env	Slope mass	*P*-mass	R^2
Range size	Transpiration ratio	–	−0.0315	0.045	−0.268	0.001	0.465
Range size	Water loss	–	−0.0182	0.070	0.425	<0.001	0.739
Range size	Metabolic rate	–	0.0136	0.213	0.689	<0.001	0.878
Elevation	Transpiration ratio	Lower limit	0.1045	0.047	−0.247	0.004	0.463
Elevation	Transpiration ratio	Midpoint	0.0887	0.072	−0.255	0.003	0.449
Elevation	Transpiration ratio	Upper limit	0.0334	0.282	−0.290	0.001	0.404
Elevation	Water loss	Lower limit	0.0467	0.174	0.427	<0.001	0.729
Elevation	Water loss	Midpoint	0.0004	0.989	0.398	<0.001	0.709
Elevation	Water loss	Upper limit	−0.0157	0.388	0.388	<0.001	0.716
Elevation	Metabolic rate	Lower limit	−0.0581	0.110	0.670	<0.001	0.882
Elevation	Metabolic rate	Midpoint	−0.088	0.006	0.650	<0.001	0.902
Elevation	Metabolic rate	Upper limit	−0.0484	0.018	0.674	<0.001	0.895

Notes: Range models included log10(range area, km^2) and log10(body mass). Elevation models included log10(body mass) and one elevation metric (lower limit, midpoint, or upper limit); elevation slopes are reported per 1000 m. TR is transpiration ratio (mol H_2O/mol O_2).

with individuals that generally lost more water tending to have higher metabolic rates than other individuals of the same species, although the estimate remained uncertain (posterior mean = 0.148, 95% credible interval = −0.155 to 0.444; Table S3). Thus, the relationship was not consistently expressed across levels of biological organization, although it may be more evident among individuals within species than within individuals or among species (Fig. S2).

By contrast, across amphibians, water loss increased significantly with metabolic rate after accounting for body mass (slope = 0.7210, $P < 0.001$), indicating a positive association consistent with a hydric cost of gas exchange. When all species were analyzed together, this positive relationship remained significant (slope = 0.5878, $P < 0.001$, Fig. 1A), suggesting that the overall cross-amphibian pattern was driven more by the broader dataset than by *Plethodon* alone.

Correlation with environmental data

In PGLS models including body mass, direct relationships between physiology and geographic range size were modest (Table 1; Fig. 2A–C). Water loss showed a weak negative trend with range size (slope = −0.0182, $P = 0.070$; Fig. 2C), whereas metabolic rate was not associated with range size (slope = 0.0136, $P = 0.213$; Fig. 2B). TR (mol H_2O/mol O_2) showed a similar weak negative association with range size (slope = −0.0315, $P = 0.045$; Fig. 2A), consistent with greater hydric efficiency (lower water loss per unit O_2) in more widespread species.

In contrast, hydric and metabolic traits showed clearer structure across elevational limits. Metabolic rate declined with elevational midpoint (slope = −0.0880 per 1000 m, $P = 0.006$; Fig. 2E) and upper elevational limit (slope = −0.0484 per 1000 m, $P = 0.018$; Fig. 2D), consistent with lower metabolic rates in species centered higher on mountains or reaching higher elevations. Water loss showed no detectable association with elevational limits (Table 1). By contrast, TR increased with lower elevational limit (slope = 0.1045 per 1000 m, $P = 0.047$; Fig. 2F), with a similar but weaker trend for midpoint elevation (slope = 0.0887 per 1000 m, $P = 0.072$); these results indicate that species extending into lower-elevation environments tend to have lower TR and thus greater hydric efficiency.

To place these elevational patterns in climatic context, we related species traits to climate summaries across their ranges using both bioclimatic variables and daily active-season climate summaries. We analyzed both mean metabolic rate across experimental temperatures and metabolic rate measured separately at 13°C, 17°C, and 23°C. The mean metabolic rate increased with temperature-related BIOCLIM variables (BIO8, BIO10) and decreased with precipitation-related variables (BIO12–BIO14), with an additional positive association with precipitation seasonality (BIO15; Table S4). This climatic pattern mirrors the elevational results, with higher metabolic rates in lineages associated with warmer, lower-elevation conditions and lower metabolic rates in cooler, higher-elevation lineages. Temperature-specific analyses at 13°C and 23°C showed the same pattern (Table 2),

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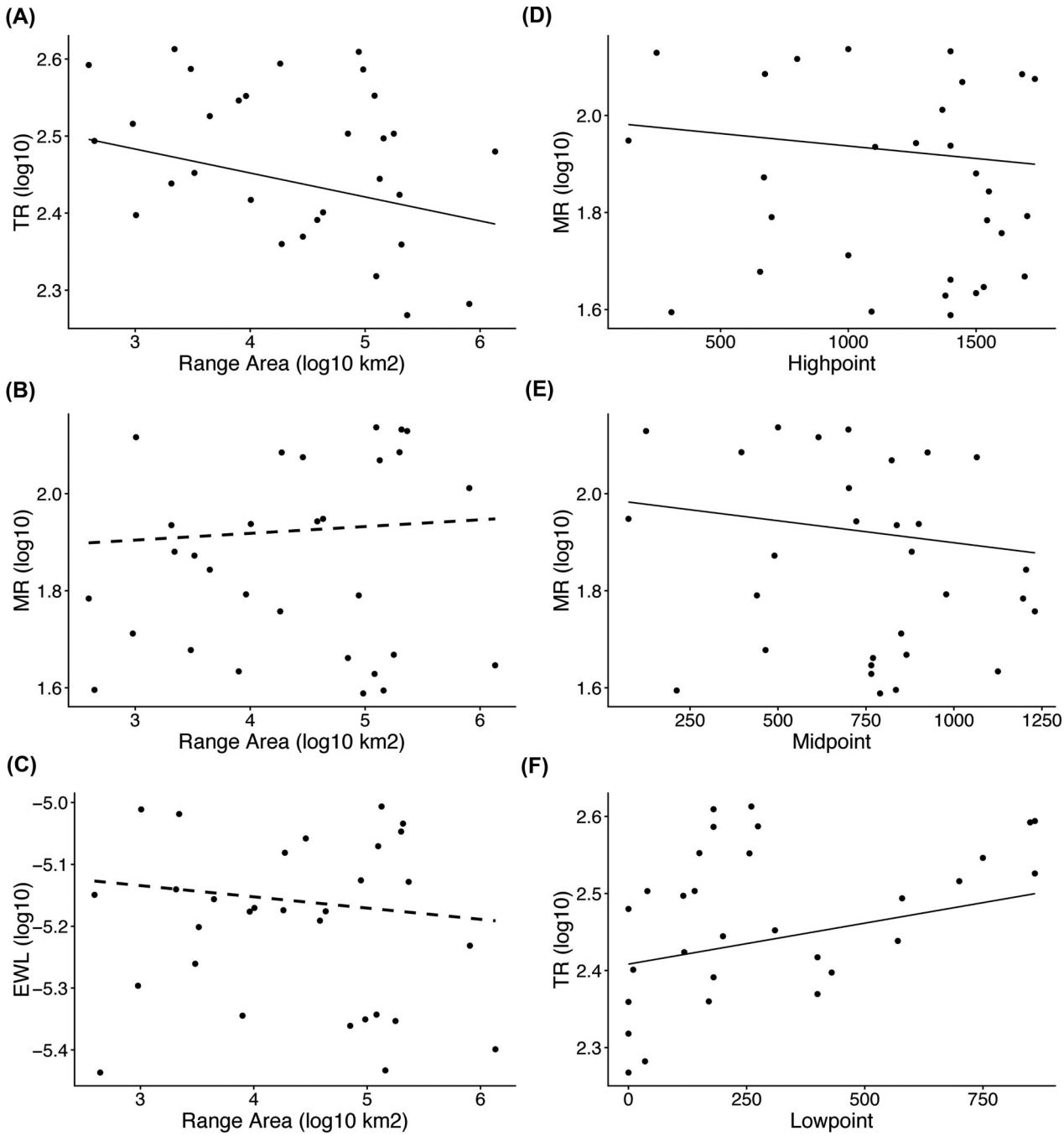

Fig. 2 Relationships between physiology, geographic range size, and elevational distributions across *Plethodon*. Panels (A–C) show PGLS relationships between physiological traits and geographic range size (log10 range area, km^2): TR decreased with range size (A), metabolic rate (MR) showed little association with range size (B), and water loss rate (WLR) showed a weak negative trend (C). Panels D–F show the key elevational relationships: MR decreased with upper elevational limit (m) (D) and elevational midpoint (E), whereas TR increased with lower elevational limit (F). Lines show fitted relationships from PGLS models that included body mass as a covariate (dotted indicates insignificant relationship, solid line indicates significant).

whereas at 17°C the BIO10 association remained positive but fell just below the FDR threshold (q = 0.052; Table S5).

Climate summaries derived from daily active-season data showed the same general pattern for metabolic rate. Mean metabolic rate across experimental temperatures increased with mean daily temperature (slope = 4.44, FDR q = 0.0001) and with VPD (the drying demand of the air) (slope = 58.06, q = 0.0001), while the association with mean daily precipitation was weaker and not FDR-supported (slope = −11.23, q = 0.0791; Table S4). Across experimental temperatures, metabolic rate con-

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Table 2 PGLS results for significant metabolic rate–climate associations across *Plethodon*.

ENV	Temp	Predictor	Direction	slope_env	q_FDR
BIOCLIM	13°C	Mean temp wettest quarter	+	1.0362	0.0001
BIOCLIM	13°C	Mean temp warmest quarter	+	2.9220	0.0025
BIOCLIM	13°C	Precip wettest month	−	−0.2820	0.0025
BIOCLIM	13°C	Precip driest month	−	−0.3406	0.0082
BIOCLIM	23°C	Mean temp wettest quarter	+	2.0418	0.0001
BIOCLIM	23°C	Mean temp warmest quarter	+	6.6656	0.0001
BIOCLIM	23°C	Precip driest month	−	−0.8280	0.0003
BIOCLIM	23°C	Precip wettest month	−	−0.4740	0.0076
BIOCLIM	23°C	Precip seasonality	+	2.1624	0.0170
Daymet	13°C	High-end VPD (95th percentile)	+	42.8926	0.0041
Daymet	13°C	Mean daily temperature	+	2.9797	0.0041
Daymet	13°C	Mean daily precipitation	−	−10.9556	0.0263
Daymet	17°C	Mean daily temperature	+	3.5840	0.0278
Daymet	23°C	High-end VPD (95th percentile)	+	95.6488	0.0004
Daymet	23°C	Mean daily temperature	+	6.7689	0.0004
Daymet	23°C	Mean daily precipitation	−	−21.7503	0.0217

Notes: For each temperature (13°C, 17°C, 23°C), metabolic rate was modeled as a function of log10(body mass) and a single climate predictor from BIOCLIM (range-wide) or Daymet (range-wide). The table reports the environmental slope (slope_env) and FDR-adjusted q values (q_FDR) for each predictor.

sistently increased with mean daily temperature; precipitation effects were only detectable at 13°C and 23°C (Table 2).

Water loss rates showed limited climatic covariation relative to metabolic rate in both bioclimatic variables and daily active-season climate summaries. Mean water loss rates across experimental temperatures showed no relationships with bioclimatic variables after FDR correction (all $q \geq 0.563$; Table S4) and no associations with daily climatic variables after FDR correction ($q \geq 0.393$; Table S4). Temperature-specific analyses yielded a small number of correlations that did not remain significant after FDR correction. For bioclimatic variables (BIOCLIM), water loss at 13°C showed a negative relationship with annual temperature range (BIO7; $P = 0.022$; FDR $q = 0.177$; Table S6). At 17°C, water loss showed negative relationships with precipitation of the driest month (BIO14; $P = 0.025$; $q = 0.110$) and mean temperature of the driest quarter (BIO9; $P = 0.038$; $q = 0.110$), and a positive relationship with mean temperature of the wettest quarter (BIO8; $P = 0.041$; $q = 0.110$; Table S6). No effects were detected at 23°C (all $P \geq 0.05$). For daily climatic variables, water loss at 17°C showed a positive relationship with VPD ($P = 0.019$), but this result did not remain significant after FDR correction ($q = 0.057$; Table S6). Together, these results suggest that any climate signal for water loss is weak and temperature-dependent, and that water loss is not consistently captured by individual climatic predictors across species.

TR (mol H_2O/mol O_2) likewise showed weak climatic covariation across both bioclimatic variables and daily active-season climate summaries. When considering bioclimatic variables, we found that TR showed a positive relationship with mean diurnal temperature range (BIO2; $P = 0.031$), but this effect did not remain significant after FDR correction ($q = 0.244$), and no other BIOCLIM variables reached $P < 0.05$ (Table S7). When considering daily climate variables, we found that TR showed no relationships with mean daily temperature, precipitation, or VPD (all $P \geq 0.05$; all FDR $q = 0.407$; Table S7). TR did not track individual climate variables consistently across species, despite its clearer association with elevational limits, particularly the lower elevational limit.

Path analysis

Phylogenetic path analysis consistently supported a mediated structure linking physiology, lower elevational limit, and range size across assay temperatures (Table S8; Fig. 3). Among the three candidate models considered (direct, mediated, and combined), the Mediated model was best supported at 13°C, 17°C, and 23°C (model weights = 0.938, 0.924, and 0.930, respectively; Table S8). In this model, metabolic rate and water loss predicted lower elevational limit, and lower elevational limit in turn predicted range size; support was weaker for models in which physiology acted directly on range size (Fig. 3A and B).

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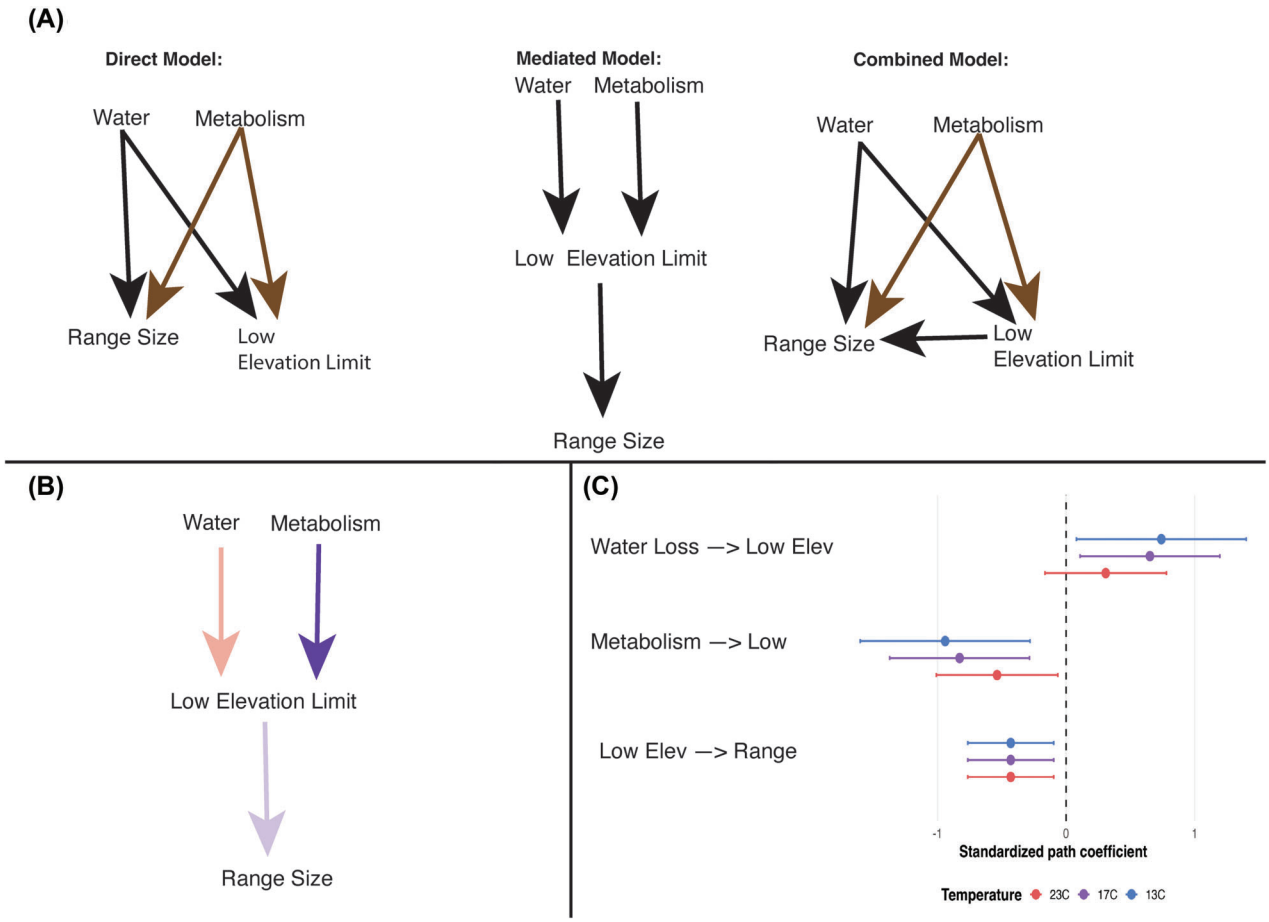

Fig. 3 Candidate and supported phylogenetic path models for physiology, lower elevational limit, and range size. (A) Three alternative hypotheses tested: direct, mediated, and combined. Body mass is omitted from the schematic for clarity, but was included in all fitted path models as an upstream predictor of both physiological traits. (B) Best-supported model structure across temperatures. Arrow colors represent the standardized path coefficients across the best-supported mediated model at 13°C, 17°C, and 23°C. (C) Standardized path coefficients (±95% CI) for the mediated model at each temperature, showing a consistent negative association of metabolism with lower elevational limit, a positive association of water loss with lower elevational limit, and a negative association of lower elevational limit with range size. The lower elevational limit–range size path is shown once for clarity because elevation and range size were not temperature-specific variables.

Specifically, path coefficients from the best-supported model showed a consistent negative association between metabolic rate and lower elevational limit across all temperatures, with stronger effects at cooler assay temperatures (Table S9; 13°C: −0.94; 17°C: −0.83; 23°C: −0.54; Fig. 3C). Water loss rate showed a positive association with lower elevational limit at all temperatures, but this effect was strongest at 13°C and 17°C (Table S9; 0.74 and 0.65, respectively) and weakest at 23°C (Table S9; 0.31; Fig. 3C). The relationship between lower elevational limit and range size was consistently negative across all temperatures (Table S9; −0.43), indicating that species with higher lower elevational limits tended to have smaller ranges (Fig. 3B and C), a pattern that reflects, at least in part, the reduced geographic area available at higher elevations. The path linking lower elevational limit to range size was identical across temperatures because both geographic variables were unchanged across temperature-specific model sets; temperature-specific differences were therefore restricted to the physiology–elevation paths. These results support lower elevational limit as the key mediator linking physiology to range size across temperatures, while indicating that the strength of the physiological paths varies among temperatures.

Discussion

Metabolic rate and water loss are not tightly correlated across *Plethodon*

Physiological processes that depend on the same functional surface are often expected to remain tightly linked. Across amphibians, gas exchange and water loss both occur across the thin, moist, and highly permeable

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skin, resulting in high hydric costs of respiration (Feder and Burggren 1985; Burggren and Vitalis 2005; Woods and Smith 2010; Riddell et al. 2024; Fig. S1). This expectation may be especially strong in terrestrial lungless salamanders, where the skin carries the full respiratory burden while also remaining exposed to evaporative water loss. Within *Plethodon,* however, water loss and metabolic rate did not show the expected significant positive association across either species-level averages or individual-level measurements. The relationship may nevertheless vary across biological scales, as the association among individuals within species trended positive but remained uncertain. Overall, although cutaneous respiration creates a fundamental link between gas exchange and water balance, this link does not produce a uniquely strong relationship within *Plethodon*. Rather, *Plethodon* appear to fall within the broader amphibian relationship, suggesting that lungless salamanders may still be constrained by the same physiological boundary, even as hydric and metabolic traits retain enough flexibility to vary independently across species.

The physiological basis of this weak correspondence is only beginning to emerge. Recent work suggests that the relationship between water loss and oxygen uptake varies across seasonal and experimental contexts and that the two processes can be adjusted through largely trait-specific mechanisms (Assis et al. 2025). For instance, salamanders can regulate water loss independently through changes in skin properties, such as melanin production, while modulating oxygen uptake through variation in oxygen-binding affinity—mechanisms that may not directly influence one another (Assis et al. 2025). Microhabitat use and behavior may further shape the evaporative conditions experienced by salamanders (Farallo et al. 2018, 2020) and therefore more finely shape the selective environment *Plethodon* experience. Together, this physiological and environmental flexibility may allow hydric and metabolic traits to respond differently to environmental pressures despite their shared dependence on the skin.

Physiological traits map onto distinct components of species' environmental niches

Different physiological traits aligned with distinct components of species environment (Fig. 2 and Tables 1–2). Metabolic rate was most consistently associated with broad climatic variables and with midpoint and upper elevational limits. Previous work in plethodontids likewise suggests that metabolic responses vary among species across thermal contexts (Markle and Kozak 2018). Metabolic rate has also been shown to be plastic, with populations from warmer climates reducing metabolic rate under summer acclimation (Riddell et al. 2018; Muñoz et al. 2022), and salamanders showing compensatory increases in colder environments (Catenazzi 2016). However, these within-species responses do not necessarily predict patterns across species. In this context, the negative association between metabolic rate and elevational position in *Plethodon* suggests that species occupying higher elevations tend to have lower standard metabolic rates, potentially reflecting adaptation to cooler, wetter environments. Our climatic results support this interpretation, with metabolic rate higher in species associated with warmer conditions and lower in those associated with cooler, wetter conditions. This negative association between metabolic rate and temperature could reflect differences in long-term energy balance, with high-elevation species experiencing shorter activity windows and reduced energy intake that favor lower maintenance costs, whereas low-elevation species can sustain higher metabolic rates due to longer activity periods and greater energetic throughput. These results highlight metabolic rate as an important trait with significant ecological implications both within and among species.

Water loss alone showed no detectable association with elevational limits (Table 1). By contrast, TR increased with lower elevational limit, with a similar but weaker trend for midpoint elevation, indicating greater hydric efficiency in lineages that extend into low-elevation environments (Table 1 and Fig. 2). TR combines water loss and metabolic rate, meaning that this pattern reflects variation in the balance between the two processes rather than water loss alone. This interpretation is also consistent with work on montane plethodontids showing that lower elevational limits are often climate sensitive: physiological constraints drive the lower elevational boundary of *Plethodon jordani* (Gifford and Kozak 2012), climate is more strongly associated with the lower elevational limit of *P. shenandoah* than competition (Grant et al. 2018), and evaporative water loss varies along elevation within *P. montanus*, with lower-elevation populations losing water more slowly (Winters and Gifford 2013; Riddell and Sears 2015). Across climatic analyses, both water loss and TR showed some environmental associations, but these were weak, inconsistent across variables and temperature treatments, and did not remain significant after correction for multiple tests. This lack of pattern may reflect the fact that humidity is more spatially and temporally variable than temperature, making broad-scale associations more difficult to detect (Riddell et al. 2019). In that context, the clearest elevational signal in our data appears to lie less in evaporative loss alone than in the hydric cost of gas exchange near the warm lower edge of montane salamander ranges. Although our data do not establish that salamanders at these boundaries are op-

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erating near a physiological constraint, the pattern suggests that lower elevational limits may be where this cost becomes most consequential for species persistence.

Elevation mediates the relationship between physiology and range size

Our path analyses suggest that physiology relates to range size primarily through its association with lower elevational limit, consistent with the idea that the warm, dry edge of the climatic niche helps structure species' distributions. In plethodontids, lower elevational boundaries are often where salamanders experience warmer and drier conditions (Riddell and Sears 2015), so the association between physiology and lower elevational limits possibly reflects how physiological constraints interact with environmental gradients to shape persistence across space. That interpretation is consistent with experimental and comparative work in montane salamanders showing that lower elevational limits can be set by physiological constraints and climatic stress, rather than by elevation per se (Gifford and Kozak 2012; Riddell et al. 2017; Grant et al. 2018). In this context, physiology may influence range size indirectly by shaping where and how broadly species can persist along the elevational gradient. Warmer conditions are often expected to impose stronger energetic challenges in plethodontid salamanders, whereas low temperatures can elicit compensatory physiological responses, so the stronger physiology–elevation paths at cooler assay temperatures may reflect the ecological relevance of cooler conditions for among-species divergence in this clade (Catenazzi 2016; Markle and Kozak 2018; Muñoz et al. 2022).

The negative relationship between lower elevational limit and range size might also reflect the spatial structure of mountain systems. Species that extend farther downslope occupy a broader portion of the landscape, whereas species restricted to higher elevations are often confined to smaller, more topographically constrained montane areas. Since the surface area of a mountain does not change monotonically with elevation, variation in area across the elevational gradient can strongly influence the amount of habitat available to montane taxa (Elsen and Tingley 2015). As a result, high-elevation species tend to occupy less geographic space than those occurring at moderate or low elevations. The mediated relationship may therefore reflect both physiological limits on where species can persist and the amount of landscape available at those elevations. Lower elevational limit was the only elevational metric significantly associated with range size, reinforcing its role as a geographic correlate in this system. Consistent support for the same mediated structure across 13°C, 17°C, and 23°C suggests that this relationship is not tied to a single thermal condition. Together, these results identify lower elevational limits as the key link between physiology and range size and suggest that this relationship emerges from the intersection of physiological constraints and mountain geography.

Multidimensional diversification under a shared respiratory mode

Across amphibians, gas exchange and water loss exhibit a trade-off, such that species with higher rates of gas exchange also lose more moisture; this pattern is not observed, however, among species within *Plethodon*. In this genus, the hydric cost of respiration remains high, but it does not translate into a consistent interspecific trade-off across the clade. This interpretation is consistent with recent work in lungless salamanders showing that the relationship between water loss and gas exchange can vary across environments and experimental contexts (Riddell and Sears 2020; Riddell et al. 2024; Assis et al. 2025). In this sense, the shared respiratory surface linking gas exchange and water loss may not have tightly constrained how these traits diverged during *Plethodon* diversification, potentially allowing lineages to differentiate physiologically (Figs. 2–3 and Tables 1–2). This interpretation is consistent with our recent work suggesting that physiological divergence may have contributed to diversification in *Plethodon* in ways not captured by morphology alone (Alomar et al. 2026). More broadly, these results suggest that even strongly linked physiological traits can follow different evolutionary paths, allowing ecologically meaningful variation to arise. Understanding how woodland salamanders navigate the trade-off between gas exchange and water loss may therefore help explain both their diversification and the broader strategies by which amphibians have navigated the hydric challenges of life on land.

Author Contributions

Nathalie Alomar (Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing), Eric Riddell (Conceptualization, Formal Analysis, Funding acquisition, Supervision, Writing—review & editing). Martha Muñoz (Conceptualaization, Funding acquisition, Supervision, Writing—review & editing).

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Supplementary Data

Supplementary Data available at *ICB* online.

Data Availability

The data and code underlying this article will be available in the Yale Dataverse upon publication: Alomar, Nathalie. 2026. "Weak coupling between gas exchange and water loss in lungless salamanders". Yale Dataverse. https://doi.org/10.60600/YU/NFBE2O.

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