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RESEARCH ARTICLE

Continental Drivers of Population-Level Intraspecific Trait Variability in Salamanders, Birds, and Small Mammals

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ABSTRACT

Aim: Intraspecific trait variability (ITV) is a key component of biodiversity because it informs how organisms respond to abiotic and biotic conditions. Understanding how the variability among individuals within a population (population-level ITV) changes along environmental gradients offers insight into how local processes contribute to broad-scale biodiversity patterns. Here, we examine how climate and species-richness interact to drive population-level ITV across taxa with distinct life-histories.

Location: United States and Canada.

Time Period: Present.

Major Taxa Studied: *Plethodon* salamanders, birds, and small mammals.

Methods: Individual body-size measurements were compiled from multiple large-scale biodiversity data sources, and population-level ITV across populations of the focal taxa was quantified as the coefficient of variation (CV). Using Bayesian phylogenetic generalized linear mixed models (PGLMMs), we tested the effects of mean annual temperature, precipitation, and relative humidity, as well as their interactions with species richness, while accounting for species identity, phylogeny, and site.

Results: The influence of environmental predictors on population-level ITV differed across taxonomic groups. Salamander ITV declined with humidity and increased with temperature in species-rich sites, bird ITV increased with temperature, and small-mammal ITV decreased with precipitation but increased with humidity and temperature in species-rich sites.

Main Conclusions: We found that abiotic and biotic conditions shape trait diversity within populations, and that these factors differ across taxonomic groups according to their life-histories. Groups with relatively low mobility and that are closely tied to their microhabitats showed increased population-level ITV in warm, species-rich environments. These findings challenge the classic niche-packing expectations by suggesting that responses to climatic stress and interspecific competition can increase individual variation within populations, potentially reflecting differences in the strategies individuals adopt to cope

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with environmental challenges. Together, these insights underscore the importance of studying intraspecific trait variation for understanding macroecological patterns in biodiversity.

1 | Introduction

Phenotypic variability within natural populations arises from a combination of evolutionary and ecological processes that cause individuals to differ from one another. Individuals carry distinct genetic material that underlies heritable differences in phenotype (e.g., morphology, physiology, and behaviour; Bolnick et al. 2003). This genetic variation can be shaped by processes such as adaptation and frequency-dependent selection, which may act to reduce, maintain, or increase variability within populations (Svensson and Connallon 2019). Ontogeny and sexual dimorphism also contribute to population-level variability, as individuals express different traits or trait values across life stages and/or between sexes (Nosil and Reimchen 2005; Warne et al. 2013). Individuals in a population may also differ from one another due to phenotypic plasticity, which enables individuals to adjust trait expression in response to local environmental conditions, without necessarily reflecting underlying genetic differences (Bonnet et al. 2021). Such environmental conditions include climate (Heldstab 2021), resource availability, and mutualistic or antagonistic interactions with other species (Van Valen 1965; Roughgarden 1972, 1974; Violle et al. 2012). In addition, novel genotypes or plastic responses shaped in different environments can be introduced to a population via immigration and dispersal (Bolnick and Nosil 2007). Together, these interacting ecological and evolutionary mechanisms shape trait variability within populations.

Among the many ways individuals can differ from one another, morphological traits stand out as particularly integrative, reflecting the combined influences of evolutionary and ecological factors (Grant et al. 1976). Regardless of whether morphological variation originates from genetics or plasticity, it has important implications for relationships among organisms and between organisms and their environment (Violle et al. 2012). Body size has long been a fundamental trait for testing key ecological and evolutionary hypotheses due to its close association with both physiological responses to the environment (e.g., thermoregulation, metabolic processes) and interactions involving resource use and competition (e.g., diet, intra- and interspecific competition; Anderson-Teixeira et al. 2009; Gardner et al. 2011). For example, leveraging information on body size of multiple individuals within the same population (or species) has been used as an approximation of niche width (Read, Baiser, et al. 2018; Read, Grady, et al. 2018). In addition, since body size is a measurable trait across taxa, it allows for direct comparisons across groups with different life histories (e.g., ectotherms and endotherms; Gillooly et al. 2001). Taken together, these features make body size a powerful trait for assessing the drivers of trait diversity across multiple levels of ecological organization (Anderson-Teixeira et al. 2009), including variability within populations.

Trait variability among individuals within a population (i.e., population-level intraspecific trait variability; ITV) can be evaluated across spatial scales to provide insights into the scale-dependent processes driving trait variation and associated patterns of biodiversity. For example, the site scale captures multiple individuals of the same population, whereas broader regional scales capture multiple populations at different sites across environmental gradients (Fluck et al. 2024). Just as environmental filtering can shape community assemblages by favouring species with suitable traits, similar processes may occur within populations, filtering out individuals whose traits are less suited to local conditions (Violle et al. 2012). Further, exploring whether abiotic and biotic conditions constrain or promote population-level ITV can provide insight into broad biodiversity patterns based on the fine-scale individual responses to their environments.

At the population level, abiotic conditions (e.g., climate) may shape trait variability within populations, but their effects are not unidirectional (Kuppler et al. 2020). On one hand, harsh or selective environments may reduce variation within populations by favouring a narrower range of phenotypes through stabilizing selection, limiting dispersal into unfavourable environments, or reducing the genetic and demographic variation available locally (Braz et al. 2023). On the other hand, stressful environments may also favour greater variation within populations when phenotypic variability increases resilience to environmental change (Kim et al. 2013) or allows individuals to persist under fluctuating conditions (Clark 2010; Kuppler et al. 2020). Thus, abiotic gradients can either decrease or increase population-level ITV, depending on whether they primarily constrain viable phenotypes or promote variability within populations, underscoring population-level ITV as a crucial dimension by which environmental factors influence how populations respond to broad-scale ecological gradients.

In addition to abiotic gradients, biotic factors may likewise influence population-level ITV in opposite directions. Biotic interactions can strongly influence population-level ITV since traits related to resource use can be shaped by interspecific competition and predation (Van Valen 1965; Roughgarden 1972, 1974; Violle et al. 2012). In assemblages where niche space is strongly partitioned among coexisting species, biotic filtering or niche packing may reduce the range of phenotypes expressed within a population, limiting the extent of overlap or variation maintained among individuals of the same species (MacArthur and Levins 1967). For example, populations of passerines inhabiting islands can exhibit character or ecological release due to the absence of biotic pressure experienced on the mainland (Ebenman and Nilsson 1982). In contrast, greater competition or ecological opportunity can increase population-level ITV when individuals specialize in different resources or microhabitats, thereby expanding trait variation within populations (Araújo et al. 2011; Araújo and Costa-Pereira 2013). Thus, biotic interactions can either constrain or expand within-population trait distributions, depending on whether trait differentiation occurs primarily among species or among individuals within species. Frameworks that integrate ITV into species and community-level trait distributions have been foundational for advancing the study of functional diversity patterns across levels of biological organization (Carmona et al. 2016). Nevertheless, while trait differentiation *among* species has been widely explored in ecological studies, approaches that directly link patterns of

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TABLE 1 | Datasets used in the main analyses for *Plethodon* salamanders, birds, and small mammals.

Group	*Plethodon* salamanders	Birds	Small mammals
Species	43	180	49
Sites	1472	822	42
Populations	1600	5053	158
Years	1950–2000	1989–2017	2012–2022
Source	Adams 2007	MAPS, IBP	NEON 2024
Body size measure	SVL (mm)	Grams (g)	Grams (g)

population-level ITV to variation in abiotic and biotic conditions are fundamental for a finer understanding of macroecological relationships.

How population-level ITV scales up to macroecological patterns is likely to differ across taxonomic groups, as the balance among mechanisms that promote or constrain variation within populations depends on their distinct life histories and ecological strategies (Aragón et al. 2010). Taxa with greater physiological dependence on external conditions, such as ectotherms, can exhibit strong plastic responses or local adaptations to site-specific conditions (Lind and Johansson 2007; Caruso et al. 2014). In contrast, the thermal independence of endotherms may reduce their direct sensitivity to climate gradients. However, there is still potential for the influence of abiotic conditions through indirect mechanisms when broad-scale climate affects resource availability via biotic interactions (Read, Grady, et al. 2018). Comparing population-level ITV-environment relationships across organisms with different life history strategies has the potential to reveal both general patterns and taxon-specific responses of ITV to environmental gradients.

In this study, we take a macroecological approach to examine how population-level intraspecific trait variation (ITV) in body size relates to broad abiotic and biotic gradients, with the goal of improving our understanding of how local ecological processes scale up to shape broad spatial patterns of biodiversity. Using data from *Plethodon* salamanders, birds, and small mammals across the United States and Canada (hereafter, 'North America'), we ask whether macroecological gradients are associated with population-level ITV, and whether the direction of these relationships is consistent across taxonomic groups with contrasting life histories. Our hypothesis is that population-level ITV is shaped jointly by abiotic (climate) and biotic (species richness) conditions, and that these relationships differ depending on each group's life history.

Specifically, (i) we expect population-level ITV to decrease under restrictive abiotic conditions, where strong physiological constraints and environmental filtering are expected to reduce the range of viable phenotypes within populations; and (ii) we predict population-level ITV will tend to decrease with species richness when stronger competition limits variation within populations (Read, Baiser, et al. 2018; Read, Grady, et al. 2018). Because the effects of climate may depend on local biotic context, we further predict that (iii) abiotic and biotic factors will interact (Mod et al. 2014), such that the relationships between climate and population-level ITV will vary across richness gradients.

Finally, given the differences in life history, physiology, and ecological strategies among the groups under study, we also expect (iv) these relationships to differ among taxa, including the interactive effects of climate and species richness on population-level ITV. Of the three groups, salamanders are expected to show the strongest relationships between population-level ITV and environmental conditions due to their ectothermic physiology and dependence on fine-scale microhabitat conditions. Among the endothermic groups, small mammals are likely to exhibit more pronounced responses, given their limited mobility compared to that of birds, whose greater movement range allows them easier access to limiting resources. Because many mechanisms may operate simultaneously and differ across taxonomic groups, our study is intended not only to test general theoretical expectations but also to characterize how broad macroecological gradients in environmental and biotic conditions are associated with population-level ITV across taxa with different life histories.

2 | Methods

To elucidate the drivers of population-level ITV across taxa, we compiled individual morphological measurements related to body size from multiple populations across three taxonomic groups: *Plethodon* salamanders, birds, and small mammals across North America (Table 1, Figure 1). Although population-level ITV may involve a range of traits, the term refers specifically to population-level variation in body size when considered within this study. We quantified body size using snout-vent length (SVL; mm) in salamanders and body mass (g) in birds and small mammals, as these are standard body size measures for each group. For each population, we also obtained data on abiotic and biotic factors at the given location.

2.1 | Data

The first taxonomic group for which we assessed ITV was salamanders in the genus *Plethodon*. *Plethodon* salamanders are endemic to North America and underwent a rapid radiation resulting in high diversity in the Appalachian Mountains in the eastern United States (Highton 1995). We procured *Plethodon* salamander data from Adams and Church (2008), who measured snout-vent length (SVL; mm) of individual salamanders

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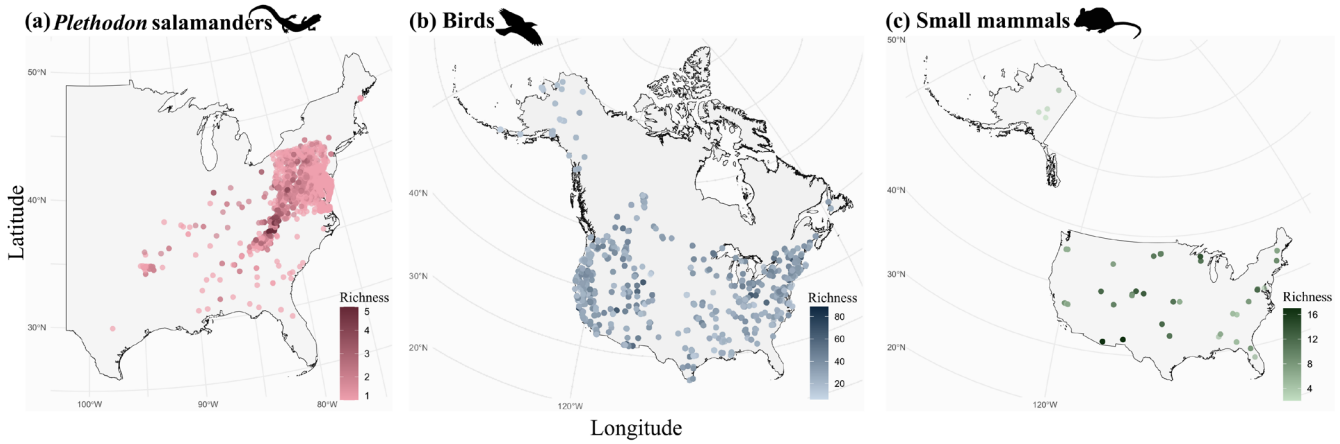


FIGURE 1 | Sampling sites for (a) *Plethodon* salamanders, (b) birds, and (c) small mammal populations. Each dot represents a unique site (latitude, longitude combination) where > 20 individuals were sampled for at least one species. Colour gradients indicate the species richness of each site before filtering for > 20 individuals.

housed in the collections at the National Museum of Natural History in Washington, D.C., USA. Specimens were originally collected across the eastern United States from the early 1950s to the early 2000s. At the time of original sampling, specimens were identified to species and latitude, longitude, and elevation were recorded for each geographic location (Adams 2007). Adams and Church (2008) removed juveniles, individuals from hybrid populations, and individuals of uncertain species designation or geographic location, resulting in a data set that included 4057 sites, 44 species, and 99,025 individual salamander measurements.

We obtained data on birds from the Monitoring Avian Productivity and Survivorship (MAPS) programme, a continent-wide collaborative bird banding project led by The Institute for Bird Populations (IBP) (Desante et al. 2004). MAPS captures birds through a standardized, constant-effort mist netting and banding methodology applied at hundreds of stations (i.e., locations where sampling is conducted, hereafter 'sites') distributed across North America during the breeding season each year (Desante et al. 2004). We used MAPS capture data collected from 1989 through 2017. Each captured bird was identified to species, aged, weighed (g), and had its wing measured (mm) (DeSante et al. 2024). To avoid confounding population-level variation in body weight attributed to age, we only retained data for adult individuals (i.e., after hatch year), resulting in a dataset containing 941 sites and 281 species with 401,024 individuals.

Finally, we obtained small mammal data from the National Ecological Observatory Network (NEON; DP1.10072.001 released in September 2024). NEON collects ecological data at sites distributed across ecoclimate domains in the United States using standardized sampling designs specific to each taxonomic group (Li et al. 2022). Captured small mammals were identified to species, sexed, aged, checked for reproductive status, and weighed to the nearest gram (Paull et al. 2022). Due to the sampling design, this dataset consisted of small, non-volant mammals including mice, voles, chipmunks, and shrews, primarily from the families *Cricetidae*, *Heteromyidae*, *Sciuridae*, and *Soricidae*, which are typically nocturnal or crepuscular, ground-dwelling taxa. We used data from 2012 to 2022 and included only adults, non-pregnant females, and first-time captures, resulting in data from 44 sites and 100 species totaling 18,402 individuals of small mammals.

In addition to the taxa-specific data criteria mentioned above, we applied the following filtering across taxonomic groups. First, we removed body size outliers for each population (i.e., site-species combination) based on a z-score > |3|. Second, populations with < 20 individuals were removed from the final dataset to avoid type I and type II errors (Yang et al. 2020; Fluck et al. 2024). See Table 1 for information on the resulting dataset. We recognize that our datasets include observations collected across multiple years and may capture temporal variation in population-level ITV. However, this study focuses on spatial variation, with temporal variation treated as background variability. If spatial patterns persist despite potential temporal variability, it suggests that spatial drivers are particularly influential.

2.2 | Explanatory Variables

For each georeferenced population (i.e., site-species combination), we obtained monthly high-resolution (30 s) data on bioclimatic variables including mean temperature, mean precipitation, and mean relative humidity from CHELSA (Karger et al. 2017; Brun et al. 2022) using the R package *raster* (Hijmans 2018). To determine the annual mean of each climatic variable, we averaged the monthly values for each year. For each taxonomic group, we used environmental data over the time period of the species sampling (Table 1).

The species richness of each site was quantified as the number of species captured at each site before removing populations with < 20 individuals. We used capture-based species richness to maintain consistency across groups, even though additional species were likely present and observed in bird and small mammal datasets. We obtained phylogenetic trees for each taxon to control for phylogenetic relatedness in our analyses. Time-calibrated phylogenies were procured for salamanders (Bonett and Blair 2017), birds (Hackett et al. 2008; Jetz et al. 2012) and small mammals (Upham et al. 2019). The salamander phylogeny

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included all species except *Plethodon sherando*, which was excluded from the analyses since only one location in the dataset included this species. Birds and mammals each had 10 k species-level phylogenies available, from which we randomly sampled 200 per group.

2.3 | Analyses

Closely related species often exhibit similar trait values due to their shared evolutionary history. Accounting for this relationship is essential to separate the effects of evolutionary relatedness from those of environmental and biotic factors on population-level trait variation (Rezende and Diniz-Filho 2012). To account for variability and non-independence due to phylogenetic relationships, we fit a Bayesian phylogenetic generalized linear mixed model (PGLMM) using the *pglmm* function in the R package *phyr*, which implements approximate Bayesian inference through Integrated Nested Laplace Approximation (INLA) (Li et al. 2020). Our response variable was the coefficient of variation (CV) of body size for each population at each site, calculated using Bao's CV estimator (Yang et al. 2020). We used this metric because it quantifies trait variability relative to the population mean, allowing comparisons of within-population variation across populations and species that differ in average body size while reducing bias associated with sample size, skewness, and kurtosis (Yang et al. 2020).

To investigate the drivers of population-level ITV, we used a full model for each group. Fixed effects included abiotic predictors (mean annual temperature, mean annual precipitation, and relative humidity), biotic predictors (species richness), and interactions between abiotic and biotic variables. The model structure included random intercepts for species, phylogeny, and sites, as well as random slopes for each predictor to capture species-specific responses, instead of assuming that all species respond in the same way or at the same magnitude. This was important given the macroecological scope of the study and expected heterogeneity in physiology, life history, and local context across species. We transformed the response variable (CV) using natural log and standardized the predictor variables (mean = 0, SD = 1) to facilitate the comparison of coefficients.

We opted for a Bayesian approach because it provides full posterior distributions for both fixed effects and random effects, including estimates for each level of the random effects (i.e., species-specific responses). This modelling approach allowed us to directly quantify the variation among species in their responses to environmental predictors. Additionally, we applied the 'pc.prior.auto' setting, which automatically assigns weakly informative penalized complexity (PC) priors to random effect variances, helping to prevent overfitting while maintaining flexibility in the model structure (Simpson et al. 2017). We assessed the uncertainty of the estimated effects using 95% Bayesian credible intervals. Intervals that did not include zero were interpreted as providing strong evidence for an effect, while those that included zero were considered to indicate weak or uncertain evidence. Model fit was assessed using residual diagnostics.

For birds and mammals, we ran a PGLMM for each of the 200 (randomly chosen) phylogenetic trees and compared the resulting mean posterior estimates by evaluating their standard errors (SE). For both groups, models with different phylogenies yielded similar results (i.e., low SE; Table S1a,b). Therefore, we randomly chose one phylogeny for each group to fit the PGLMM model with the specifications described above.

After fitting the model for each group, we assessed multicollinearity among predictors by calculating Variance Inflation Factors (VIF; O'Brien 2007). These VIF values were obtained by fitting standard linear models using the same predictor variables as in the Bayesian models, which allowed us to evaluate the level of collinearity between predictors. In addition, we checked for high correlation values among predictors by examining the posterior covariance matrix of the fixed effects. We found low VIF values (<3) and low correlations between posterior samples (<0.7), indicating that multicollinearity was not a concern in our models (Table S2a,b).

Finally, we calculated marginal and conditional R^2 values for each model to quantify the variance explained by the different components of the PGLMM. Marginal R^2, which reflects the proportion of total variance explained by the fixed effects, was calculated as the variance of predicted values from the fixed effects divided by the total variance. Representing the proportion of variance explained by both fixed and random effects, the conditional R^2 was calculated as the sum of the variance of predicted values from the fixed effects and the model-estimated random effects variances divided by the total variance (Nakagawa et al. 2017; Gelman et al. 2019).

As supplementary analyses, we evaluated three potential sources of bias in the main results. To assess broad spatial structure, we refit the models for each group including standardized latitude and longitude. To assess temporal heterogeneity, we fit models of population-level ITV as a function of sampling year where year information was available. Because birds showed a temporal trend, we then refit the full bird model including year, with all predictors recalculated at the site-species-year level. To assess whether pooling individuals across years inflated CV estimates, we used permutation analyses to identify populations with frequent evidence of pooled-year inflation and repeated the original full models after excluding those populations. These temporal and permutation analyses were not possible for salamanders because year-of-collection information was unavailable for individual records. Details are provided in the Supporting Information S1.

3 | Results

Posterior estimates from the PGLMMs indicated that the effects of climate (hypothesis i) and its interaction with richness (hypothesis iii) on population-level intraspecific trait variation (ITV) were taxon-specific (hypothesis iv). Among the fixed effects, mean annual temperature was supported for all groups, either as a main effect or as part of an interaction with richness (Table S3). While temperature was the main driver of bird population ITV, salamanders and small mammals showed consistent responses to the temperature-richness

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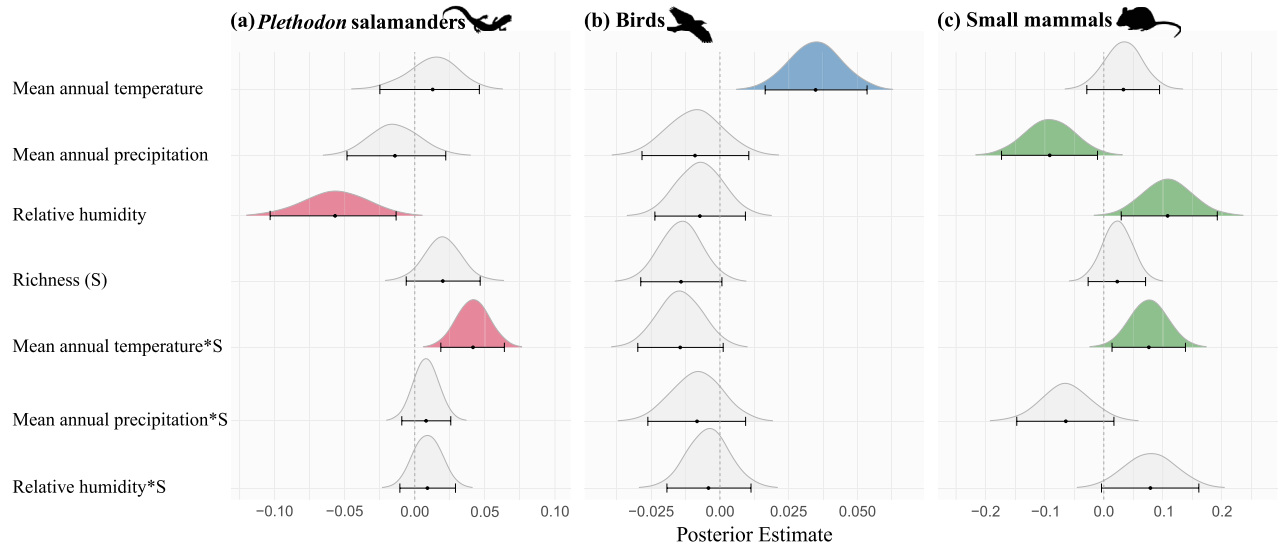


FIGURE 2 | Results of PGLMMs with posterior estimates of fixed effects for (a) *Plethodon* salamanders, (b) birds, and (c) small mammals. Credible intervals that exclude zero (strong support) are highlighted in colour, whereas those that include zero (weak support) are shown in grey.

interaction as well as divergent responses to other climate variables. Richness alone did not influence ITV in any group, providing no support for our second hypothesis. However, fixed effects explained only a small portion of the variance in population-level ITV, with random effects accounting for a substantially greater share. Among the random effects, species-specific slopes captured variation in environmental responses but accounted for a relatively small portion of the variance compared to random intercepts of species, site, and phylogenetic covariance. In particular, the phylogenetic intercept stood out as an important source of variance across all groups, supporting the influence of evolutionary history on population-level ITV trends (Table S4, Figure S1). Estimates of species-specific intercepts and slopes are shown in Supporting Information S2.

Model diagnostics showed no strong systematic patterns in residuals, no clear evidence of pronounced heteroscedasticity, and residual distributions that were broadly consistent with normality, supporting the adequacy of the models (Figure S2). Supplementary spatial analyses showed that including latitude and longitude did not qualitatively alter the main fixed-effect patterns in any group (Table S5), suggesting limited influence of broad spatial structure on the main results. In addition, supplementary temporal analyses showed a decrease in bird ITV through time, whereas no effect was detected in small mammals (Table S6). Subsequent analyses for birds further indicated that accounting for year weakened support for the effect of temperature in this group (Table S7). Permutation analyses suggested that pooling across years could inflate CV estimates in some cases (16% of bird and 23% of small mammal site-species-year populations were significantly less variable than their respective site-species populations), but refitting the models after excluding the most affected site-species populations did not change the overall interpretation of the main model results (Table S8).

3.1 | *Plethodon* Salamanders

Among all *Plethodon* species included in the analyses, *Plethodon cinereus* was the most widespread species, occurring in 80.5% of the sites, followed by *P. glutinosus* and *P. montanus*, which occurred in 4.28% and 2.72% of the sites respectively. The overall population-level ITV of *Plethodon* salamanders ranged from 0.043 to 0.28, with a mean of 0.1 and SD of 0.028 (Table S9a). The PGLMM for this group revealed that population-level ITV decreased with relative humidity (Estimate = −0.058; 95% CI = −0.106 to −0.014; Figure 2a) and showed an interaction between temperature and species richness, with a stronger positive effect of temperature across richer sites (Estimate = 0.042; 95% CI = 0.019 to 0.064; Figure 3a). Fixed effects alone explained a smaller portion of the variance in population-level ITV (marginal $R^2 = 0.06$), compared to the variance explained when accounting for random effects (conditional $R^2 = 0.71$).

3.2 | Birds

The dataset for birds was composed mostly of Passeriformes with *Melospiza melodia*, *Turdus migratorius*, and *Dendroica petechia* being the most widespread across North America, occurring in 25.8%, 22.9%, and 22.6% of the sites respectively. The population-level ITV for birds ranged from 0.029 to 0.286, with a mean of 0.084 and SD of 0.029 (Table S9b). The PGLMM for birds showed that population-level ITV increased with mean annual temperature, the only fixed effect with a credible interval that excluded zero (Estimate = 0.035, 95% CI = 0.017 to 0.053; Figure 2b). The interaction between temperature and richness, although weak, showed a negative trend, with a negative effect of temperature in richer sites (Estimate = −0.015, 95% CI = −0.030 to 0.001; Figure 3b). Among the random effects, site-level intercepts accounted for the largest portion of variance, indicating that site-specific

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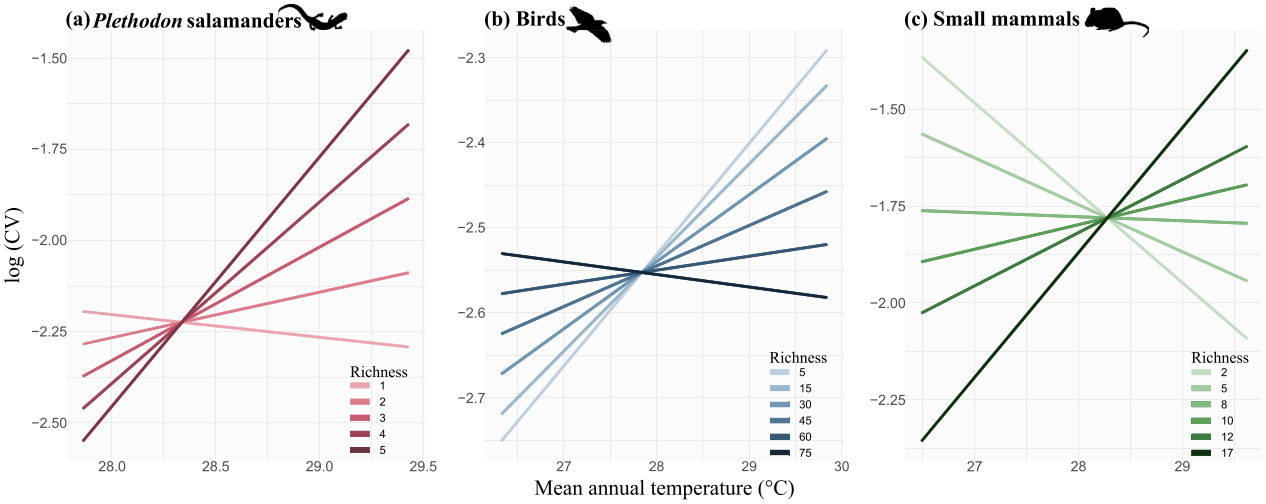


FIGURE 3 | Model predictions for the interaction between mean annual temperature and richness on population-level ITV of (a) *Plethodon* salamanders, (b) birds, and (c) small mammals, with all other predictors held at their means. For birds, the support for the interaction was weak (95% CI overlapped 0) compared to the other taxonomic groups.

factors not captured by our environmental predictors contributed to variation in population-level ITV (Table S4b). Fixed effects alone explained a small proportion of the variance (marginal $R^2 = 0.03$), compared to that explained by both fixed and random effects (conditional $R^2 = 0.45$).

3.3 | Small Mammals

Among the small mammal species in this study, *Peromyscus maniculatus* and *P. leucopus* were by far the most widespread taxa, occurring in 61.9% and 40.5% of the NEON sites, respectively. Across all populations, small mammal ITV ranged from 0.081 to 0.364, with a mean of 0.185 and SD of 0.048 (Table S9c). The PGLMM revealed that population-level ITV increased with relative humidity (Estimate = 0.107, 95% CI = 0.024 to 0.193) and decreased with precipitation (Estimate = −0.091, 95% CI = −0.172 to −0.011; Figure 2c). The interaction between mean annual temperature and richness (Estimate = 0.077, 95% CI = 0.015 to 0.139) indicated greater increases in ITV with temperature in species-rich communities (Figure 3c). Similar to the other taxonomic groups, fixed effects explained less variability (marginal $R^2 = 0.11$) compared to random effects (conditional $R^2 = 0.65$).

4 | Discussion

Our results reveal that the continental-scale drivers of population-level ITV differ among *Plethodon* salamanders, birds, and small mammals, supporting expectations based on their distinct life histories. In salamanders and mammals, body size ITV was greater where warmer conditions aligned with higher species richness. Relative humidity tended to reduce ITV in salamanders and increase ITV in small mammals. Additionally, temperature alone was positively associated with ITV only in birds, while precipitation showed a negative effect only in mammals. Therefore, our results contrast the expectations that stress (hypothesis i) and greater species richness (hypothesis ii) should constrain ITV and promote species specialization (MacArthur and Levins 1967; Read, Grady, et al. 2018), and show that biotic factors interact with climate to drive population-level ITV (hypothesis iii). Ultimately, our results suggest that both climate and community context drive population-level ITV, with their influences varying among vertebrate groups according to their life history characteristics (hypothesis iv).

While we did not directly test the specific mechanisms underlying the broad relationships observed here, our findings contribute to discussions of ecological processes and life history attributes that may influence population-level ITV across different taxa. Below, we interpret the results for each group by examining how their characteristics (e.g., physiology and behaviour) may influence their responses to environmental gradients. Taken together, these group-specific patterns form a broader macroecological comparison, illustrating how abiotic and biotic factors contribute to widespread variation in population-level ITV.

4.1 | *Plethodon* Salamanders

Among the vertebrate groups studied, *Plethodon* salamanders, the only ectotherms, exhibited greater population-level ITV in drier conditions and warm environments with high species richness. These trends are likely related to *Plethodon* ectothermic physiology and reliance on behavioural thermoregulation under stressful conditions (Feder 1983). In dry environments, greater heterogeneity in microhabitat moisture exposes individuals to varying physiological conditions, contributing to developmental differences within populations (Lind and Johansson 2007). *Plethodon* salamanders rely on cutaneous respiration and thus restrict their activity to moist microhabitats when conditions are dry, which may increase individual differences in microclimatic exposure and hydration conditions (Heatwole 1962). Given the close link between body size and metabolism in salamanders (Feder 1983; Caruso et al. 2014), such environmental differences can drive divergence in growth, reproduction, and overall fitness (Warne et al. 2013; Charbonnier et al. 2018), leading to

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greater population-level ITV under drier conditions. Conversely, under humid conditions, individuals likely experience more homogenous moisture conditions across microhabitats, potentially reducing variation in physiological stress and allowing individual growth to converge on a body size that confers the best balance for resource intake, metabolic demands, and reproductive success (Brown et al. 1993). As a result, the similarity of growth opportunities may promote consistent developmental outcomes within populations, reducing population-level ITV (Warne et al. 2013).

The interaction between temperature and richness for *Plethodon* salamanders shows that the effect of temperature depends on species richness. Greater body size ITV at high temperatures in species-rich assemblages may be due to competition for thermal refuges. This pattern could stem from the fact that *Plethodon* salamanders are unable to regulate their body temperatures and rely heavily on microhabitats to maintain physiological processes under critically hot conditions (Heatwole 1962; Scheffers et al. 2014). *Plethodon* salamanders exhibit aggressive territorial behaviour against both conspecifics and heterospecifics (Farallo and Miles 2016; Jaeger 2016), with larger individuals often monopolizing high-quality microhabitats, forcing smaller ones into suboptimal conditions (Mathis 1990). This competitive asymmetry is likely intensified in species-rich communities under thermal stressful conditions, which could promote greater population-level ITV due to trade-offs in resource use (Svanbäck and Bolnick 2005; Araújo et al. 2011), and amplified individual developmental differences in growth and maturation (Warne et al. 2013). Previous observed relationships between head-shape variability and resource use (i.e., trophic polymorphism) within *Plethodon* populations corroborate our results and highlight how fine-scale habitat structure and competition can amplify trait differences among individuals (Maerz et al. 2006). In contrast, competition for refugia under extremely cold conditions and less resourceful environments may reduce population-level ITV since individuals that are outcompeted are unlikely to survive (Feder 1983; Storey and Storey 1986; Mathis 1990; Brown 2014).

4.2 | Birds

Body size variation in birds was more pronounced in warmer breeding environments. Regions with higher mean temperatures are generally more climatically stable and productive, offering abundant food and structurally complex habitats that promote ecological opportunity (Schluter 2016). Species persistence in these environmentally stable and diverse regions may foster higher intraspecific genetic diversity, a contrasting scenario seen in higher latitudes where extinctions and population bottlenecks can be more frequent (Smith et al. 2017). This aligns with the idea that niche availability, traditionally applied to interspecific diversity (MacArthur and Levins 1967), may also drive trait variation within populations. Tropical and southern temperate birds also tend to exhibit slower life-history strategies, characterized by extended parental care, smaller clutch sizes, greater investment per nesting, and longer developmental periods (Russell et al. 2004; Llambías et al. 2015). These factors are particularly important for altricial species, whose thermoregulatory systems are still developing (Price and Dzialowski 2018). Due to their limited ability to buffer against environmental changes, altricial species may experience constrained growth and heightened sensitivity to temperature fluctuations (Furic et al. 2025; Madden et al. 2026). As a result, these life history traits may extend the developmental period in southern-breeding bird populations, potentially allowing greater phenotypic variation to emerge before nestlings fledge and become independent, compared to populations in northern regions.

4.3 | Small Mammals

Compared to birds, small mammals showed a broader set of environmental associations, with population-level ITV increasing under high relative humidity, low precipitation, and warmer temperatures in species-rich assemblages. The increase in body size population-level ITV with humidity may reflect the physiological flexibility that moister environments offer for thermoregulation and water balance. Humid environments can benefit both small individuals prone to dehydration and larger individuals with greater water needs (Fuller et al. 2016; Mitchell et al. 2018). In contrast, small mammals in dry regions must rely on both evaporative and dry heat loss to dissipate body heat, but each strategy comes with a trade-off (Mitchell et al. 2018). Dry heat loss (e.g., conduction or convection) depends on access to suitable microhabitats and cooler surfaces, which may be scarce or require extended sheltering. When such opportunities are limited, evaporative heat loss (e.g., panting) becomes critical. However, this strategy requires frequent rehydration, which is challenging in arid environments where hydration relies primarily on moisture obtained from food, particularly seeds (Walsberg 2000). These combined pressures may create constraints on viable body sizes, reducing population-level ITV in drier sites.

The negative relationship we observed between precipitation and body size variability in small mammal populations may be due to seasonal resource bottlenecks (Maron et al. 2015). In our dataset, sites with high annual rainfall were also highly seasonal (Figure S3), where short periods of resource abundance are followed by extended dry intervals. These sharp productivity pulses tend to synchronize biological activity across individuals since small mammals must forage and invest in breeding-related processes within a short window of favourable conditions (Schulte-Hostedde et al. 2002; Stephens et al. 2024). The constraint of this tight temporal window may force individuals to follow similar developmental schedules, reducing opportunities for divergent strategies, which could in turn be reflected in lower diversity of body sizes and, consequently, lower population-level ITV.

We also found that populations in species-poor assemblages had lower ITV in warm sites, while those in species-rich assemblages showed reduced ITV in cold sites. In cold, species-rich environments, individuals face life-history trade-offs between minimizing energy demands and maintaining body heat (Burger et al. 2019). In freezing winters, sustained heat loss combined with resource scarcity may intensify selection against extreme phenotypes, favouring intermediate body sizes through stabilizing selection (Hansson 1992; Mitchell et al. 2018). Narrow seasonal windows for growth and reproduction can also impose developmental synchrony, further reducing trait divergence

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within populations (Heldstab 2021). Our findings are consistent with previous work showing that high latitude environments restrict viable metabolic niches (Anderson and Jetz 2005), and further suggest that cold-induced constraints may limit trait diversity within populations when competition restricts resource availability. In contrast, the decline in population-level ITV along the temperature gradient in species-poor assemblages may reflect the exceptionally high body size variability seen in Alaska relative to the rest of the United States (Figure S4). In these extreme environments, cold-adapted mammals can bypass energetic constraints through behavioural and thermophysiological adaptations, and reduced competition may lessen pressure for convergence, potentially allowing trait diversity to persist (Humphries et al. 2005; Read, Grady, et al. 2018).

4.4 | Synthesis

Plethodon salamanders, birds, and small mammals exhibited distinct relationships between population-level ITV and the abiotic and biotic predictors considered here, highlighting that the macroecological drivers of variation within populations are not uniform across vertebrates. Rather, our results show that population-level ITV reflects not only broad environmental gradients, but also the biological characteristics through which different taxa experience those gradients (e.g., physiology, behaviour). In this sense, the observed patterns did not follow a simple ectotherm versus endotherm division, as we had previously expected. Salamanders and small mammals showed more similar responses to temperature and species richness than either taxon did to birds. This indicates that the mechanisms underlying changes in population-level ITV might rely on ecological and life history characteristics that extend beyond broad physiological categories. While disentangling the mechanisms behind these broad patterns will require finer-scale data on physiology, resource use, and species interactions, our findings already reveal that taxon-specific responses to abiotic and biotic conditions are central to understanding large-scale variation in population-level ITV.

Comparisons among taxa were particularly informative for the interaction between species richness and temperature. For example, despite physiological and ecological differences, *Plethodon* salamanders and small mammals showed increased population-level ITV with temperature in species-rich sites, suggesting that temperature effects on ITV depend on community biotic context, especially for groups closely tied to local microhabitats for reproduction, development, and foraging. The lower dispersal abilities of salamanders and small mammals relative to birds may further increase sensitivity to fine-scale environmental variation and local competition (Freedberg et al. 2021). In such contexts, the greater variability among individuals may release them from the pressure of interspecific competition and allow for broader access to the available resources. This aligns with the idea that intraspecific trait variation facilitates species co-occurrence and promotes local diversity (Hausch et al. 2018; Holdridge and Vasseur 2022). In comparison, the larger home ranges and higher mobility of birds may allow them to more easily access limiting resources, reducing the influence of local richness on population structure (Buchmann et al. 2013). Notably, the isolated effect of species richness on population-level ITV was not supported in any group, suggesting that abiotic factors should be taken into account when studying the influence of biotic interactions on ITV patterns.

Interestingly, while salamanders and small mammals responded similarly to temperature-richness interactions, ITV decreased with humidity in salamanders but increased in small mammals. This contrast likely reflects their different physiological relationships with water balance and the distinct strategies each group employs to cope with dehydration. Together, these results highlight the importance of considering not only temperature but also water availability when comparing trait variability trends of ectothermic and endothermic groups. A relevant consideration in these comparisons is that body size was quantified using different taxon-appropriate measures across groups. SVL (mm) in ectotherms and body mass (g) in endotherms both capture size-dependent links to fitness and key ecological processes underlying intraspecific variation, allowing broad relationships among body size, climate, and species richness to be compared across vertebrates despite differences in physiological mechanisms (Adams and Church 2008; Read, Baiser, et al. 2018; Read, Grady, et al. 2018). At the same time, because different body-size measures have not been widely validated as directly equivalent in macroecological comparisons, our results should be interpreted as comparisons of broad size-related patterns rather than strict equivalence among measures of body size.

Another important result from our models is that broad-scale abiotic and biotic predictors (i.e., fixed effects) explained a small fraction of the variation in population-level ITV when compared with the substantial contribution of random effects, as shown by the difference between marginal and conditional R^2 values. This pattern is common in macroecological studies, where variation in traits within populations differs across local environments and taxa with different evolutionary backgrounds (i.e., phylogeny, species- and site-level random effects). Despite the considerable variation among sites, species, and evolutionary histories, the relationships identified herein suggest that broad-scale predictors retain explanatory value for population-level ITV and highlight the importance of accounting for local ecological contexts when evaluating macroecological patterns.

A further limitation is the temporal mismatch among datasets, which span different sampling periods across groups and could therefore bias or obscure broad-scale spatial relationships. This temporal limitation is also relevant within datasets, as populations were defined as site-species combinations and some population-level ITV estimates include individuals sampled across multiple years, which could introduce temporal heterogeneity within populations. Supplementary permutation analyses suggested that pooling across years led to CV inflation only in a subset of site-species populations and did not change the interpretations of the main effects in either birds or small mammals, although some interaction terms in small mammals gained stronger support after the exclusion of populations with inflated ITV. Additional supplementary analyses including sampling year further indicated that this was not a major concern for small mammals, as no clear temporal trend in ITV was detected for this group. In birds, however, ITV showed a negative temporal trend, and follow-up analyses including year in the main model weakened support for the effect of temperature. Moreover, our

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analyses did not distinguish males and females within bird populations, which may have contributed additional unexplained variation, although available evidence suggests that environmental effects on sexual size dimorphism are often species specific and thus partly absorbed by the species-level structure of the models (Caron and Pie 2025). Together, these observations warrant further investigation, particularly for birds, given the potential influence of long-term changes in breeding phenology or migration dynamics (Hedlund et al. 2015).

5 | Conclusion

Our findings suggest that the processes shaping phenotypic variability within populations do not operate uniformly across taxa or environments. Instead, population-level ITV might not only reflect intrinsic biological differences among taxa, but also the ecological conditions in which populations occur (Van Valen 1965; Roughgarden 1972, 1974; Violle et al. 2012). Based on our results, we suggest that classic niche-packing expectations may not fully capture the processes associated with population-level ITV. Climatic stress and interspecific competition may also be linked to greater trait variability, particularly in taxa that strongly depend on microhabitat conditions, as individuals adopt different ways of coping with environmental challenges (Riddell et al. 2018). By integrating individual trait data across populations and taxa, our study provides a broader view of environmental filtering and advances the understanding of how abiotic and biotic gradients shape macroecological and biogeographic patterns of biodiversity.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code for this study will be made publicly available on Figshare upon publication at https://figshare.com/s/6570f4490d656a0d4850.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Supporting Information S1.** Tables S1–S9 and Figures S1–S4, including detailed results of the main and supplementary analyses and detailed descriptions of the supplementary analyses. **Supporting Information S2.** Figures showing posterior estimates and credible intervals for random intercepts and slopes, including site, species, and phylogenetic effects, for models of *Plethodon* salamanders, birds, and small mammals.

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