

## Spatial dependence of phenotype-environment associations for tadpoles in natural ponds

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**Abstract** Within natural habitats, phenotypes are shaped by many environmental factors. Consequently, heterogeneity of these factors can promote phenotypic divergence. However, because environments exhibit heterogeneity at different spatial scales, phenotypic divergence should also exhibit such scale-dependence. Using hierarchical linear models, I determined how multiple environmental factors at two spatial scales affected the morphology of wood frog (*Rana (Lithobates) sylvatica*) tadpoles collected from natural ponds. Among ponds, predation risk intensity and tadpole density were strong predictors of tadpole morphology, while within ponds, other environmental variables such as water depth and leaf litter were more important. Spatial analyses revealed that water depth and leaf litter, but not predation risk intensity or tadpole density, exhibited heterogeneous spatial distributions within ponds, suggesting that spatial properties of environmental variables influenced the scale at which they shaped phenotypes. Furthermore, patterns of phenotypic variation with respect to predation risk intensity and tadpole density among ponds largely matched observations from previous laboratory studies. These results emphasize the importance of considering phenotype-environment associations across multiple spatial scales.

**Keywords** Adaptive divergence · Environmental heterogeneity · GIS · Hierarchical linear model · Phenotypic plasticity · Spatial autocorrelation

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