

RESEARCH ARTICLE

Phenotypic outcomes of predator–prey coevolution are predicted by landscape variation in climate and community composition

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Funding information

National Science Foundation, Grant/Award Number: 065391526

Handling Editor: Timothy Higham

Abstract

1. Landscape patterns of phenotypic coevolution are determined by variation in the outcome of predator–prey interactions. These outcomes may depend not only on the functional phenotypes that mediate species interactions, but also on aspects of the environment that enable encounters between coevolutionary partners.
2. Exploring the relationship between coevolutionary traits and the environment requires extensive sampling across the range of the interaction to determine the relationship between local ecological variation and coevolution.
3. In this study, we synthesized >30 years of data on predator–prey interactions between toxic newts (*Taricha granulosa*) and their snake predators (*Thamnophis sirtalis*) to explore the environmental predictors of arms race escalation.
4. We found that geographic variation in phenotypes at the interface of coevolution was best predicted by a combination of community and climatic variation. Coevolutionary phenotypes were greatest in environments with climate favourable for newt–snake overlap. We found prey toxicity was elevated in regions with more predator species, and predator resistance was higher in regions with more prey species.
5. Our results suggest specific environmental conditions reinforce the process of coevolution, signifying the phenotypic outcomes of coevolutionary arms races are sensitive to local ecological contexts that vary across the landscape.

KEYWORDS

bioclimate, coevolution, community ecology, sodium channel, tetrodotoxin

1 | INTRODUCTION

One of the major goals of evolutionary ecology is to describe the ecological factors that influence species interactions and coevolution (Thompson, 1994). Spatiotemporal variation in climate and

community diversity can have dramatic impacts on community structure by directly facilitating the conditions that determine where and when species can interact (Barton & Ives, 2014; Jamieson et al., 2012). These ecological factors can also strengthen the evolutionary mechanisms that translate species interactions into broader

patterns of coevolutionary mosaics (Brockhurst et al., 2003; Lopez-Pascua & Buckling, 2008). Species interactions that generate coevolutionary mosaics play out differently across space and time, where variation in the frequency or intensity of the interaction generates complex patterns of phenotypic and genetic evolution (Thompson, 2005). Geographic variation in reciprocal selection that species exert on one another during coevolutionary interactions is often used to explain heterogeneous patterns of trait evolution across populations (Thompson, 2005). Often, these explanations are made without any specific investigation or understanding of how ecological gradients covary with patterns of reciprocal selection. Linking the biotic and abiotic factors that impact individual ecology to the phenotypes critical to the coevolutionary interface is a critical step in understanding why coevolutionary mosaics vary geographically and foster phenotypic and genetic diversity (Duncan et al., 2017; Thrall et al., 2007; Wolinska & King, 2009).

The geographic mosaic theory of coevolution (Thompson, 2005) suggests the strength of coevolution varies geographically, and is determined by variation in the frequency and intensity of species interactions. Regions throughout the interaction with stronger or weaker reciprocal selection between coevolutionary partners (Brockhurst et al., 2003) often explain landscape variation in traits that mediate coevolution (i.e. the phenotypic interface of coevolution). Describing the ecological factors which covary with geographic differences in the outcomes of coevolution allows us to quantify how the environment facilitates predator–prey encounters, and how this facilitation is related to coevolutionary outcomes in nature. For instance, local variation in temperature might allow for greater amounts of activity and overlap between interacting partners (Hunsicker et al., 2013), so that coevolutionary outcomes might track variation in climate. When coevolutionary interactions take place over climatic or community gradients, however, reciprocal selection might be reinforced by other types of selection that contribute to evolutionary changes in traits at the interface of coevolution.

Phenotypic matches between interacting partners—such as prey defences and predator exploitation—are often used as evidence for coevolution, and phenotypic differences across populations are attributed to variation in reciprocal selection (Anderson & Johnson, 2008; Brodie III et al., 2005; Mezquida & Benkman, 2005; Reimche et al., 2020; Thompson, 1999; Zangerl & Berenbaum, 2003). For example, the coevolutionary arms race between toxic newts (genus: *Taricha*) and their snake predators (genus: *Thamnophis*) has become a classic system used to study the geographic mosaic of coevolution (Brodie et al., 2002; Brodie III & Brodie, 1990). *Taricha* newts possess a potent neurotoxin, tetrodotoxin (hereafter TTX), which binds to the outer pore of voltage-gated sodium channels in nerve and muscle tissue when ingested (Fozzard & Lipkind, 2010). TTX binding inhibits the movement of sodium ions across cellular membranes and blocks the initiation and propagation of action potentials, which leads to immobilization, respiratory distress and paralysis (Abal et al., 2017; Brodie, 1968). However, *Thamnophis* snakes have repeatedly evolved mutations in the III and IV domains of muscle sodium channels that confer increased resistance to TTX (Feldman

et al., 2010; Geffeney et al., 2005; Hague et al., 2017). Toxin levels and toxin resistance are at the phenotypic interface of coevolution between *Taricha* and *Thamnophis*, and evolved differences in these traits should follow ecological clines because climate determines where, how and when these two coevolving species interact. Both snakes and newts are ectothermic (Huey & Berrigan, 2001), and are dependent on environmental sources of water and heat to facilitate activity, reproduction and locomotion. If favourable conditions for newt or snake life history are more available in space and time, then encounter rates between these coevolving taxa may increase, leading to stronger reciprocal selection and facilitating a hotspot in the geographic mosaic (Lopez-Pascua & Buckling, 2008). Climate facilitates movement within and among microhabitats for newts and snakes, where the interactions that result in reciprocal selection between predators and prey play out. Because of the strong link between the environment and ectotherm physiology (Huey, 1982), hotspots reciprocal selection between newts and snakes should occur in environments favourable for either player. Some work suggests the strength of coevolution increases in high-resource environments (Lopez-Pascua & Buckling, 2008; Poisot et al., 2011), but these ideas have not been extended to describing coevolutionary interactions across a landscape.

Moreover, more diverse communities of interacting predators and prey might enable more interactions that produce the same evolutionary outcome—either selection for increased prey toxicity or increased predator resistance. The *Taricha*–*Thamnophis* system is comprised of a multi-species assemblage, where multiple *Taricha* species that possess TTX (including *Ta. granulosa*, *Ta. torosa*, *Ta. sierrae* and *Ta. rivularis*) interact with multiple garter snake predators (including *Th. sirtalis*, *Th. atratus*, *Th. elegans*, *Th. gigas*, *Th. hammondi* and *Th. couchii*; Brodie III et al., 2005; Feldman et al., 2009; Reimche et al., 2020), all of whom overlap with and have been known to consume toxic newts. Unlike many diffuse coevolution scenarios, each of the predators and prey in these assemblages share the same phenotypic interface of TTX and sodium channel structure, with interspecific variation existing primarily along a quantitative axis. Snake populations that co-occur with a greater diversity of toxic newts may experience stronger selection from this biotic interaction, thus exaggerating the evolution of resistance to TTX (Feldman et al., 2009, 2010; Hanifin et al., 2008). More predation on newts by multiple co-occurring snake species could also exaggerate toxicity evolution. Spatial coevolutionary hot spots may have a greater likelihood to evolve in habitats favourable to the activity and reproduction of either player (Vogwill et al., 2009), spaces with the greatest diversity of interacting taxa, or where the environment reinforces the evolutionary response of predators or prey. In this case, reciprocal selection may be a product of how the environment facilitates the coevolutionary interaction, suggesting these factors may shape coevolutionary dynamics across large spatial scales.

In this study, we synthesize over 30 years of data detailing the geographic mosaic of the coevolutionary arms race between *Thamnophis* and *Taricha*. Our goal was to quantify how functional phenotypic variation was predicted by variation in the environment,

and to identify if the spatial structure of this coevolutionary mosaic parallels underlying biotic and abiotic factors. We focus on the two most well-studied players in the *Taricha-Thamnophis* system, *Ta. granulosa* and *Th. sirtalis* because these two have the most extensive repository of phenotypic and spatial data. We synthesized data from 79 unique populations of *Th. sirtalis* and 47 of *Ta. granulosa* to address the following questions: (1) is geographic variation in predator resistance to TTX correlated with geographic variation in bioclimate? (2) does prey TTX toxicity vary across the same geographic cline? and (3) do predator and prey diversity covary with the phenotypes of natural enemies?

2 | MATERIALS AND METHODS

2.1 | Data collection and synthesis

We synthesized phenotypic data from garter snakes ($n=3754$) and newts ($n=476$) from 126 different populations throughout the entire geographic range of the interaction collected between 1985 and 2017. To meet inclusion in our analysis, snake populations must have had a minimum of five measurements of resistance to TTX measured across at least two individual snakes. These thresholds were used because of very low intrapopulation variability in arms race phenotypes (Brodie et al., 2002; Hanifin et al., 2008). The newt populations included in our analysis all had a minimum of two individuals assayed for toxin levels for inclusion in our analysis (for a detailed list of locality information, see [Supporting Information](#)). No new data were collected for the purposes of this manuscript and did not require fieldwork or ethical approval. However, we briefly outline previous methods for measuring newt and snake phenotypes below.

2.2 | Measuring newt toxicity

Our methods for quantifying whole animal toxin levels in newts followed one of two approaches (Gall et al., 2011; Hanifin et al., 2002, 2004; Lehman, 2007; Stokes et al., 2012). Prior to 2005, we used high-performance liquid chromatography with fluorescence detection (HPLC-FLD), and after 2005 we used a competitive inhibition enzymatic immunoassay (CIEIA). CIEIA can quantify concentrations within the expected range of TTX for individuals that had previously been assayed using HPLC-FLD (Stokes et al., 2012) and is a more accessible and faster assay to quantify skin TTX than HPLC-FLD. We extracted TTX from 3 or 5 mm skin biopsies taken from the dorsum of wild newts using a human skin-biopsy punch (Hanifin et al., 2002, 2004; Stokes et al., 2012). Skin TTX is uniformly distributed over the dorsum of the newt and is tightly correlated with toxin levels in other anatomical regions (Hanifin et al., 2004). We used the calculation in Hanifin et al. (2004) to extrapolate TTX present in our skin biopsies to whole-organism levels of TTX. Population means of newt toxicity were log-transformed prior to our analyses to meet assumptions of normality.

2.3 | Measuring snake resistance to tetrodotoxin

We used a locomotor performance bioassay to describe phenotypic resistance to TTX (Brodie III & Brodie, 1990; Brodie et al., 2002; Ridenhour et al., 2004). Wild snakes were captured and housed individually in tanks, that were provided with natural diel light, water ad libitum, a basking spot and shaded refuge. To measure TTX resistance, first we raced snakes down a 4 m racetrack lined with infrared photosensors every 0.5 m to measure baseline speed. Once we established baseline speed for all individuals, snakes were given a 48 h resting period and then given an intraperitoneal injection of TTX that we diluted with Ringer's solution. Resistance to TTX was scored as the change in performance relative to baseline values. We varied TTX injection concentrations across populations because of substantial genetic and phenotypic variation in resistance to TTX throughout the range of *Th. sirtalis*. Because TTX resistance is body-size dependent in garter snakes (Brodie et al., 2002), we report estimates of mean population resistance using a mass-adjusted mouse unit (MAMU) scale. One MAMU represents the dosage of TTX required to kill a 20 g mouse in 10 min ($0.01429 \mu\text{g}$ of TTX per snake adjusted by snake mass, Brodie III & Brodie, 1990; Ridenhour et al., 2004). We conducted comparisons across populations using the 50% MAMU dose, the dose of TTX that reduces locomotor performance to 50% of baseline speed. Snakes given multiple injections of TTX at varying concentrations were allowed 48 h of rest prior to additional races.

For each population, we estimated the 50% MAMU dose with a dose-response curve using a curvilinear regression with the transformation: $y' = \ln(1/y - 1)$; Brodie et al., 2002), where $y=0.5$ (i.e. 50% dose), $y'=0$ and we can estimate the 50% dose as $\hat{x} = -\alpha/\beta$, where α is the intercept and β is the slope from the regression. Because \hat{x} is a ratio, we estimated the standard error of the 50% dose using standard methods for the variance of a ratio (Brodie et al., 2002; Lynch et al., 1998). Snake ID was used as random effect to account for individuals that received multiple injections of TTX. In our regression analysis, any values of resistance = 1 we replaced with 0.999 and any values of resistance = 0 we replaced with 0.001 for curve-fitting procedures. Population estimates of 50% doses were log-transformed prior to our analyses to meet assumptions of normality.

2.4 | Extraction of climate and community data

For each population, we used the geographic means of our sampling coordinates to extract bioclimatic variables to examine the association between resistance and toxicity phenotypes and environmental variation. We used bioclim variables (www.worldclim.org) sampled at a resolution of 30 s (0.86 km^2) to ensure the scale of measurement used in these bioclim variables maintain ecological relevance for our focal species. Garter snakes exhibit large home ranges (Tinkle, 1957), and newts facultatively migrate to reproduce (Pimentel, 1960), therefore the scale of these

bioclim variables is representative of the climates experienced by both species during activity. Because these variables can exhibit multicollinearity, we used a principal components analysis (PCA) to reduce the dimensionality of these variables. We conducted this analysis separately for bioclimate variables extracted for newt and snake populations. We retained the first three axes from both PCAs for our subsequent analysis (see Section 3 for more details). We assembled geographic distribution layers for each *Thamnophis* and *Taricha* species using geographic occurrence records obtained from VertNet (Constable et al., 2010). We subsetted these occurrences to only focus on wild-caught adult individuals for each species, and created minimum convex polygons from these occurrence points in ArcGIS. For each of our focal *Ta. granulosa* and *Th. sirtalis* populations, we scored the number of overlapping enemy species as an index of predator or prey richness.

2.5 | Data analysis

2.5.1 | Spatial interpolation

Our synthesis of over 30 years of phenotypic data from across the range of *Th. sirtalis* and *Ta. granulosa* revealed that sampling localities of newts and snakes were not precisely overlapping. Because snake and newt data often came from nearby but not identical locales, we cannot directly regress estimates of phenotypes on each other on a per locality basis. To accommodate this sampling pattern, we spatially interpolated our population estimates of the 50% dose and mean newt toxicity in ArcGIS (ESRI, 2011). Spatial interpolation techniques are useful to describe spatial variability in phenotypes across uneven sampling distributions (Li & Heap, 2008). We investigated two distinct interpolation methods: inverse distance weighting (IDW) and ordinary kriging (OK). These methods have been widely applied to ecological data in a variety of taxa (Knudby et al., 2013; Li & Heap, 2011, 2014; Rufino et al., 2005; Surette et al., 2007). Both techniques are based on the idea that samples are spatially autocorrelated by distance, and as distance increases between populations, the more dissimilar their phenotypes would become. Using this principle, we can interpolate values in an unsampled point in space by giving more weight to samples closer to that point. IDW uses arbitrary exponential weighting of the influence of each sample according to distance to a point, whereas OK directly models spatial autocorrelation using a semivariogram. We defined the searching window of our interpolation analysis by the geographic extremes of our population estimates for either resistance or toxicity. We transformed our interpolated maps to raster surfaces in ArcGIS for visual inspection. Our visual inspection of interpolated raster surfaces generated by IDW and OK demonstrated that the IDW surface matched observed patterns better than the OK surface. We applied all semivariogram models to our OK surfaces, and all had a common issue in that the presence of super-resistant snake

populations (where snakes had escaped arms race escalation, see Hanifin et al., 2008) led to the swamping of real resistance values adjacent to those populations. For example, a population with a 50% dose of seven MAMUs adjacent to a population with a 50% dose of 800 MAMUs would have its real value swamped by the extreme phenotypes present in a neighbouring population. Our IDW surfaces did not exhibit this effect, and we therefore retained the IDW raster surfaces and extracted resistance and toxicity values accordingly for our subsequent regression analyses. This interpolation approach is sensitive to the genetic nonindependence of populations, and previous work has revealed that population genetic structure does covary with arms race phenotypes in a small subset of our sampling populations (Hague et al., 2020). Presently, we do not have sequence data for all populations that have historically been studied in this system that would allow us to incorporate a genetic distance axis with our environmental data, but acknowledge this as a critical forward direction into describing the environmental covariates of coevolutionary outcomes.

2.5.2 | Data analysis

We first investigated whether our phenotypic data were spatially autocorrelated by calculating Moran's I in the R package *ape* v5.4-1 (Paradis & Schliep, 2019). We first determined the relationship between resistance and toxicity using a general linear model (GLM). Because multiple previous studies have shown matched phenotypic variation in resistance and toxicity over the landscape of the interaction (Hague et al., 2020; Hanifin et al., 2008), a positive relationship between real phenotypes and interpolated values for the opposing phenotype provides evidence that spatial interpolation is a useful technique to capture reciprocal selection.

To determine how traits at the interface of coevolution track ecological variation, we used a model selection framework using *glmulti* v1.0.8 (Calcagno, 2020) with a GLM approach. We used automated model selection and discriminated among models using a corrected Akaike information criterion (AICc) where the difference in AICc scores between competing models ($\Delta AICc$) >2 denoted improved model fit, and the lowest AICc score indicated the best-fit model (Burnham & Anderson, 2002). We searched for all possible models and did not include any interaction terms to avoid over-fitting during our model selection analysis (Tables 1 and 2). Our candidate model for snakes included resistance as our dependent variable, and included the first three snake climate PC axes, newt species richness and interpolated newt toxicity. Our candidate model for newts included toxicity as our dependent variable, and included the first three newt climate PC axes, snake species richness and interpolated snake resistance. We also used model averaging to report the Akaike weights (W_i) of our top three models for newts and for snakes and base our inference of the best-fit model as the one with the lowest AICc and highest W_i . We conducted all analyses in R v4.1.0 (R Core Team, 2020).

TABLE 1 Model selection analysis of ecological factors that influence coevolutionary phenotypes in newts (TTX levels) and snakes (TTX resistance). The top models are presented with their associated corrected Akaike information criterion (AICc) scores and Akaike weight. Δ AICc scores are taken as the difference between a focal model and the best-fit model.

Species (phenotype)	Model	Predictor variables	AICc	Δ AICc	W_i
<i>Ta. granulosa</i> (TTX levels)	Model 1	PC Axis 3, snake richness, resistance	124.8	0	0.25
	Model 2	PC Axis 2, Axis 3, snake richness, resistance	125.2	0.6	0.22
	Model 3	Snake richness, resistance	125.3	0.7	0.19
<i>Th. sirtalis</i> (TTX resistance)	Model 1	PC Axis 3, newt richness, toxicity	210.5	0	0.33
	Model 2	Newt richness, toxicity	211.6	1.1	0.18
	Model 3	PC Axis 1, Axis 3, newt richness, toxicity	211.8	1.2	0.16

Bold indicates the best fit model.

Species (phenotype)	Model term	T value	p-Value	Coefficient
<i>Ta. granulosa</i> (TTX levels)	PC Axis 3	-1.8	0.08	-0.39
	Snake richness	-2.7	0.01	-0.95
	Snake resistance	3.5	<0.001	0.77
<i>Th. sirtalis</i> (TTX resistance)	PC Axis 3	-2.3	0.07	0.21
	Newt richness	5.1	<0.001	0.95
	Newt toxicity	2.6	<0.004	0.35

TABLE 2 Model-averaged parameter estimates from our best-fit model of ecological factors that influence newts (TTX levels) and snakes (TTX resistance).

3 | RESULTS

3.1 | Bioclimatic principal component analyses

For both *Ta. granulosa* and *Th. sirtalis*, we retained the first three axes from each PCA. For newts, PC axis 1 (43% variation explained) described temperature and precipitation variation, with more positive values indicating warmer and drier habitats, and negative values corresponding to cooler and wetter habitats. PC axis 2 for newts (32% variation explained) was like PC axis 2 for snakes: this axis described temperature seasonality with more positive values indicating more seasonality, and negative values indicating less seasonality. PC axis 3 for newts (15% variation explained) described winter (i.e. activity season) precipitation, with more positive values corresponding to drier winters, and negative values corresponding to wetter winters.

For snakes, PC axis 1 (43% variation explained) described temperature and precipitation variation, with more positive values indicating cooler, wetter habitats and more negative values indicating warmer and drier habitats. PC axis 2 for snakes (32% variation explained) described temperature seasonality, with more positive values indicating seasonal and warmer habitats and more negative values indicating nonseasonal and cooler environments. PC axis 3 for snakes (15% variation explained) described summer (i.e. activity season) temperature, with more positive values indicating warmer summers, and more negative values indicating cooler summers. All PC loadings are provided in [Supporting Information](#).

3.2 | Spatial interpolation of phenotypic data

We found that newt toxin concentrations exhibited significant spatial autocorrelation (Moran's $I=0.2$, $p<0.001$), while snake

resistance did not exhibit spatial autocorrelation (Moran's $I=0.01$, $p=0.45$). Maps of IDW interpolated resistance ([Figure 1](#)), and mean toxin concentrations ([Figure 2](#)) show elevated phenotypes in regions corresponding to locations of the independent evolution of different TTX-resistance alleles (Feldman et al., 2009; Hague et al., 2017). We found that interpolated toxin concentrations significantly predicted population variation in snake resistance ($F_{1,6}=5.3$, $p=0.02$), and that interpolated snake resistance significantly predicted population variation in newt toxin concentrations ($F_{1,45}=11.7$, $p=0.001$). Phenotypic resistance to TTX in snakes increased with increasing toxin concentrations in newts ([Figure 3](#)).

3.3 | Ecological drivers of arms race coevolution

Our interpretations below are based on our single best-fit models (highest W_i) for explaining variation in newt toxicity and snake resistance, although multiple models were within Δ AICc <2, suggesting multiple competing hypotheses maintain biological relevance. Nevertheless, our top models all contained at least one climate PC axis, community context and the enemy's phenotype. For both *Ta. granulosa* and *Th. sirtalis*, climate, community and reciprocal selection were factors consistently present in our best-fit models, suggesting interactions between these factors contribute to arms race coevolution. PC axes 2 and 3 for newts were important for predicting variation in toxicity, where toxicity was significantly greater in less-seasonal habitats, and habitats with more winter precipitation. Only PC axis 3 for snakes was found to be important for predicting variation in resistance, where snakes in habitats with warm summers exhibited significantly higher resistance. For snakes, resistance scaled positively with newt richness, where more resistant *Th.*

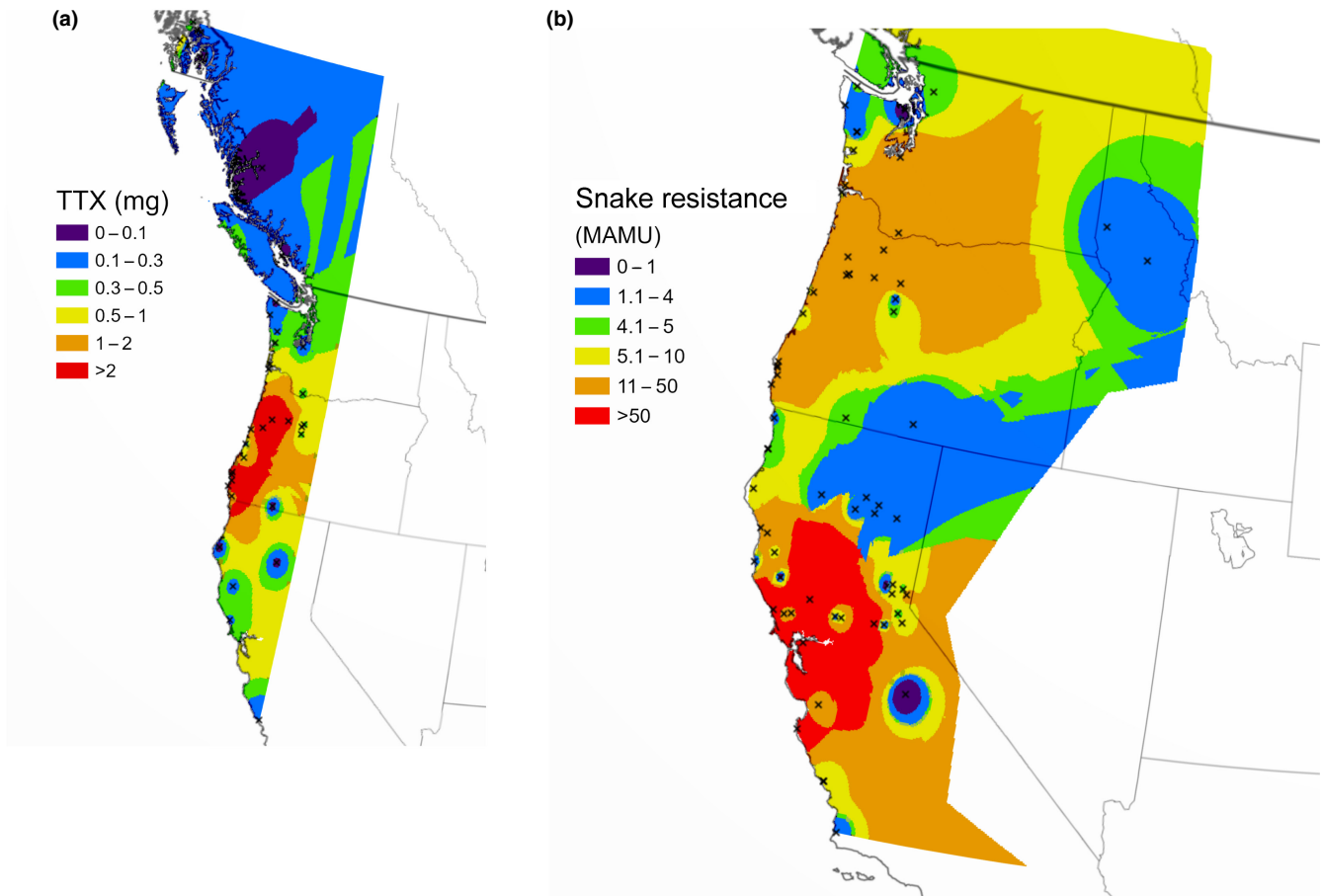


FIGURE 1 Map of coevolutionary phenotypes throughout the range of the interaction for (a) *Taricha granulosa* (newt TTX in mg) and (b) *Thamnophis sirtalis* (snake TTX resistance in 50% MAMU), spatially interpolated using inverse distance weighting. Sampling localities are denoted by crosses. Sample sizes for each locality are provided in [Supporting Information](#). MAMU, mass-adjusted mouse unit.

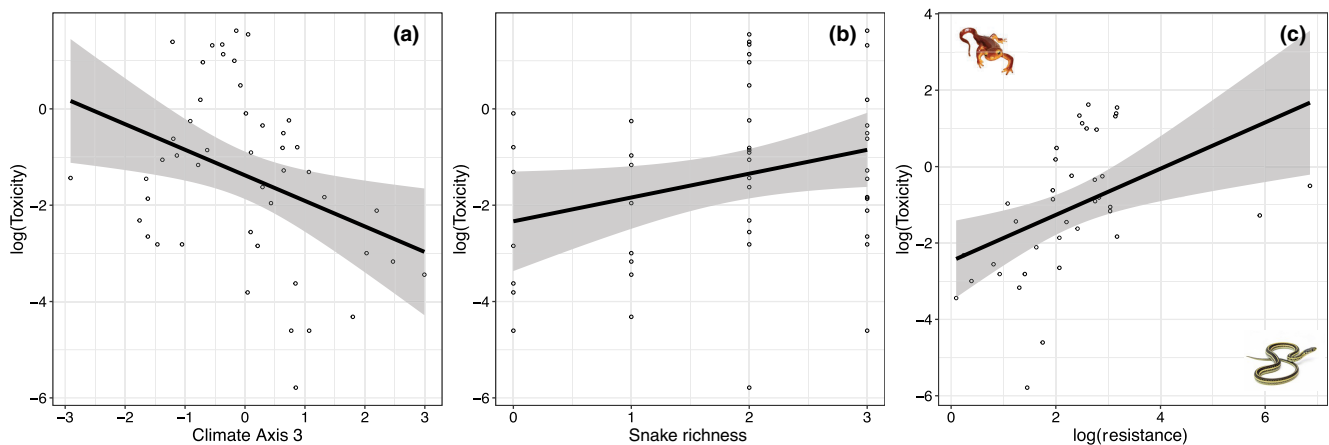


FIGURE 2 Ecological factors that covary with newt toxicity. (a) Toxicity is greater in habitats with wetter winters. (b) Toxicity increases when *Taricha granulosa* co-occurs with more garter snake predators. (c) Toxicity and resistance are positively associated in a pattern consistent with reciprocal selection.

sirtalis co-occurred with multiple *Taricha* species. The same pattern was found for newts: more toxic *Ta. granulosa* co-occurred with more *Thamnophis* snake species. Lastly, the enemy's phenotype

was present in all top models, where resistance and toxicity scaled positively with one another in a pattern consistent with reciprocal selection.

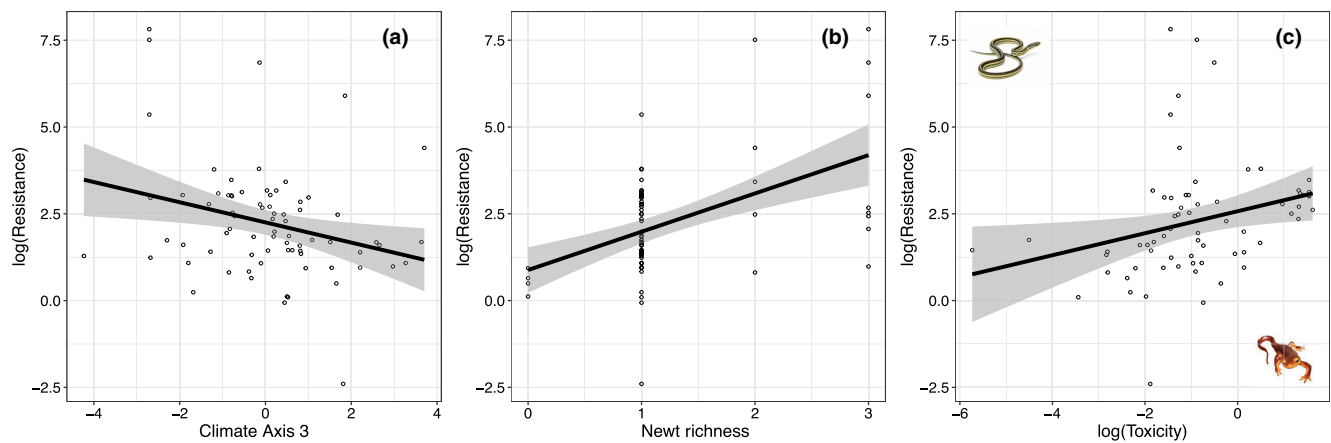


FIGURE 3 Ecological factors that covary with snake resistance to TTX. (a) Snake resistance is greater in habitats with warmer summers. (b) Snake resistance increases when *Thamnophis sirtalis* co-occurs with more toxic newt species. (c) Resistance and toxicity are positively associated in a pattern consistent with reciprocal selection.

4 | DISCUSSION

Coevolutionary interactions can be powerful drivers of community organization and general patterns of biodiversity. When these interactions play out differently across abiotic gradients and ecological contexts, then the environment may be responsible for mediating the magnitude of reciprocal selection where interacting populations each experience favourable conditions. We found newt toxicity and snake resistance both covary with climatic and community variation, suggesting interactions between local climate and community members contribute to geographic patterns of exaggerated arms race escalation. Some previous work on a subset of our sampling populations has identified that arms race phenotypes scale with climatic variation (Hague et al., 2020), but no studies to date have included all sampling populations historically surveyed in this system. Our study expands on previous research by examining every newt and snake population sampled since 1985. As a result, we gain an understanding of the ecological forces that influence the direction and intensity of reciprocal selection across the entire geographic mosaic of coevolution. Our results suggest that coevolutionary mosaics in nature are the result of interactions between reciprocal selection and local ecological contexts, and that this interaction can facilitate the presence or absence of coevolutionary hotspots in nature.

4.1 | Climate predicts arms race escalation

Population demographics are central to antagonistic coevolution. As species abundance, density and population growth increase with local resource availability and productivity, interactions between species may covary similarly (Hochberg, 1996; Hochberg & Van Baalen, 1998; Leibold, 1996). The snake–newt interaction may be most sensitive to population density, as a higher density of individuals may increase encounter rates and the strength of reciprocal selection. However, estimates of population density are challenging to obtain for both newts

and snakes. PC axis 3 for both newts and snakes was an important factor in both of our best-fit models. The positive covariation between PC axis 3 and toxicity and resistance suggest that when activity windows are optimal for newts and snakes, this ecological dynamic contributes to the exaggeration of arms race traits. The mismatch in which climatic factors were most important for newt toxicity or snake resistance suggests that responses to seasonality may be important for enabling predator–prey interactions. In general, seasonality is a ubiquitous property of all environments that exposes organisms to fluctuating temporal selection. The evolutionary effects of seasonality on populations are much less understood (Williams et al., 2017), but for ectothermic vertebrates like newts and snakes, seasonality tends to be most important for dictating activity windows, and (indirectly) population abundance over narrow time-scales (Hjernquist et al., 2012; Kaspari & Valone, 2002). In many places, especially seasonal habitats, newts and snakes possess dissimilar natural histories. Newts emerge in winter and early spring to lay eggs and then migrate back to terrestrial refuges (Stebbins, 1954), while snakes emerge later in spring to reproduce in the summer (Rossman, 1996), well after peak newt activity. Weaker seasonality can lead to a more consistent and greater abundance of newts and snakes, which would provide the ecological setting for more predator–prey interactions to occur. As a result, more newt and snake overlap—impacted by either a less-seasonal environments or more optimal activity conditions—could be a driving factor of arms race escalation in these habitats. Elevated toxicity in northern *Ta. granulosa* populations suggests more predation on newts by snakes, and therefore stronger selection on newts. Increased newt movement and activity where optimal microhabitats are more exploitable in both space and time, for example in less-seasonal environments (Hochberg & Van Baalen, 1998; Licht & Brown, 1967) could contribute to this pattern, as individuals that move often expose themselves to predators more frequently (Lima & Dill, 1990).

Conversely, elevated TTX resistance in Northern CA populations of *Th. sirtalis* suggests stronger predation on newts. The favourable climatic conditions experienced by snakes in northern

California may increase activity and movement and increase the likelihood a snake encounters a toxic newt. In some places, newts comprise a small proportion of a garter snakes' diet (Durso et al., 2021) so snakes that are more active are likely to opportunistically encounter newts more than snakes that are less active. Moreover, snakes can be active close to year-round in the warmer parts of their range, which results in more overlap with newts that are primarily active in winter and spring. Newts should experience stronger selection when their predators are more active and when predator–prey overlap is at its greatest. In fact, some northern CA populations of predators and prey exhibit functionally mismatched phenotypes (Hanifin et al., 2008). However, these snake populations overlap with the greatest richness of *Taricha* species. This discrepancy highlights the power of studying this coevolutionary system from a multi-species assemblage perspective. *Thamnophis sirtalis* in northern CA that exhibit elevated TTX resistance are likely experiencing strong reciprocal selection, but the strength of that reciprocal selection may not be fully attributable to the toxin levels of sympatric *Ta. granulosa*. Rather, these very active snakes could potentially encounter multiple *Taricha* species all with some degree of toxicity, which could explain some mismatches in the geographic mosaic.

4.2 | Community context influences predator and prey phenotypes

Variation in prey and predator composition covaried with toxin and resistance phenotypes in *Ta. granulosa* and *Th. sirtalis*. *Thamnophis sirtalis* co-occurring with more newt species exhibited elevated TTX resistance, and *Ta. granulosa* co-occurring with more snake species exhibited elevated toxicity, though this pattern was not statistically significant. We have assumed that more diverse communities of interacting predators and prey would have the potential to encourage more predator–prey interactions, and thus reinforce reciprocal selection, though this hypothesis has yet to be empirically tested. However, population densities of all *Thamnophis* and *Taricha* species would need to be known before determining the relationship between community diversity and encounter rates. One ecological hypothesis of the geographic mosaic of coevolution is that traits of interacting species are only matched in some communities (Thompson, 1999). Phenotypic mismatches across space can be attributed to external ecological factors, or evolutionary constraints (Hague et al., 2018; Thompson, 1986). Toxicity and resistance are not matched where the most resistant snakes occur, which suggests processes other than reciprocal selection between *Ta. granulosa* and *Th. sirtalis* contribute to exaggerated phenotypic evolution (Hanifin et al., 2008). In northern CA, *Th. sirtalis* interacts with multiple *Taricha* species which may relax selection on *Ta. granulosa*, but strengthen selection on *Th. sirtalis* (Feldman et al., 2009). This bias towards predators suggests the effect of newt toxicity is additive when snakes occur with more than one newt species. TTX stereoisomer profiles do not appear to exhibit species-specific differences

(Hanifin et al., 2022), so the evolutionary response to dangerous prey may be exaggerated when consuming multiple *Taricha* species. The effect of multiple TTX-resistant predators on *Ta. granulosa* may likewise be additive, as toxicity tended to increase in environments with richer *Thamnophis* predator guilds. Not all garter snakes are resistant enough to TTX to consume *Taricha* newts without consequence (Feldman et al., 2009; Motychak et al., 1999; Reimche et al., 2020); while *Th. sirtalis* has the most exaggerated resistance, multiple co-occurring *Thamnophis* species engage in their own unique evolutionary dynamics when and where they interact with toxic newts (Reimche et al., 2020). Interacting species with relatively matched toxicity and resistance (Hanifin et al., 2008) may be responsible for exaggerating landscape patterns of resistance or toxicity in areas where specific predators have functionally escaped reciprocal selection, such as *Th. sirtalis* in northern California (Hanifin et al., 2008). In this context, the idea of diffuse coevolution (i.e. coevolution occurring between guilds rather than species) between *Thamnophis* and *Taricha* guilds should be explored with much more rigour. While traditionally applied to plant–herbivore or host–parasite systems (Iwao & Rausher, 1997; Levin et al., 1990), an explicit test of how our system conforms to a traditional model of specific versus diffuse coevolution may offer insights into the evolutionary pressures shaping phenotypes at the interface of coevolution.

Our findings suggest that climatic and community variation act in tandem to facilitate the coevolutionary mosaic between newts and snakes. Hotspots throughout the range of the newt–snake interaction align with less-seasonal habitats, and habitats with more newt prey and snake predator richness. More information on how environmental factors affect predator–prey overlap could reveal the specific mechanisms by which the environment contributes to the geographic structure of this coevolutionary mosaic. The diversity of prey and predator guilds also contribute to the exaggeration of the phenotypic interface of coevolution in a manner consistent with a multi-species assemblage, but more data on population densities and encounter rates are needed to describe precise links between community contexts and reciprocal selection. Nevertheless, climate, community and selection jointly contribute to the geographic mosaic of coevolution, suggesting that coevolution is very sensitive to local ecological contexts that reinforce the evolutionary consequences of species interactions.

AUTHOR CONTRIBUTIONS

Edmund D. Brodie III conceived the study. Michael T. J. Hague, Amber N. Stokes, Chris R. Feldman, Charles T. Hanifin, Edmund D. Brodie Jr and Edmund D. Brodie III collected the data. Anthony L. Gilbert and Savanna Cabrera synthesized the data. Anthony L. Gilbert performed the analysis and wrote the first draft. All authors contributed to editing and revision.

ACKNOWLEDGEMENTS

We thank P. Cook, S. McPeck, C. Stahlmann Roeder and V. Formica for their comments on previous versions of this manuscript. We are also indebted to the dozens of students over the last three decades

that have made this work possible. This project was funded by an NSF OPUS to EDBIII (#065391526).

CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hmgqnk9nq> (Gilbert et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Population data used in analysis.

How to cite this article: Gilbert, A. L., Cabrera, S., Hague, M. T. J., Stokes, A. N., Feldman, C. R., Hanifin, C. T., Brodie, E. D. Jr, & Brodie, E. D. III (2023). Phenotypic outcomes of predator-prey coevolution are predicted by landscape variation in climate and community composition. *Functional Ecology*, 37, 2170–2180. <https://doi.org/10.1111/1365-2435.14360>