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Research article

Non-adaptive processes explain chemical signal divergence in island lizards

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Understanding the processes that drive divergence in animal signals is central to behavioral and evolutionary ecology. While adaptive explanations have traditionally dominated, especially for traits involved in sexual signaling, the role of non-adaptive processes remains underexplored – particularly for vertebrate chemical signals. Here, we investigated chemical signal variation across multiple island populations of the Italian wall lizard *Podarcis siculus*. Using lipid and protein profiling of glandular secretions, microsatellite-based genetic distances, and socio-ecological variables, we tested competing hypotheses for signal divergence. Genetic and geographic distances were strong predictors of variation in chemical signal profiles, whereas environmental conditions (i.e. climate, habitat and food availability) and sexual size dimorphism offered little explanatory power. These findings suggest that stochastic mechanisms, such as genetic drift driven by historical isolation and restricted gene flow, have likely played a prominent role in shaping chemical signal diversity in this system. Our results underscore the importance of considering both non-adaptive and adaptive processes in signal evolution, particularly in geographically isolated systems with limited dispersal, such as island archipelagos.

Keywords: diet, island biology, lacertid lizards, non-adaptive evolution, pheromones, sexual selection

Introduction

Animal signals display remarkable diversity both among and within species (Espmark et al. 2000, Maynard Smith and Harper 2003). This sheer richness and complexity have long spurred interest in understanding the evolutionary origins of signal diversity (Johnstone 1997, Eliason 2018). While both adaptive (e.g. natural and sexual selection) and non-adaptive (e.g. genetic drift) processes can drive evolutionary change

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in signal design, research has traditionally favored adaptive explanations (Endler 1992, 1993, Dawkins and Guilford 1997), sometimes overlooking stochastic alternatives. This adaptationist bias is particularly evident in studies of chemical signaling, especially in vertebrates, where the roles of non-adaptive mechanisms has received relatively little attention (Johnston et al. 1999, Müller-Schwarze 2006, Symonds and Elgar 2008)

Lizards have relatively recently emerged as a promising model for studying chemical signal evolution in vertebrates. Many species possess specialized epidermal glands, typically active in adult males during the breeding season, which produce waxy secretions deposited into the environment as scent marks (Mouton et al. 2010, Mayerl et al. 2015). A growing body of research has documented substantial variation in the chemical composition of these glandular secretions, which play roles in species, population, and sex recognition, as well as in mediating social interactions, such as territory marking, male–male competition and mate choice (Weldon et al. 2008, Mason and Parker 2010, Apps et al. 2015, Martín and López 2015, 2024, Fleishman and Font 20194). Some of the most comprehensive efforts to explain the origins of this diversity have used macro-evolutionary, interspecific comparative approaches, suggesting that climatic, ecological and social factors may all contribute to shaping chemical signal design. For example, changes in the chemical composition of their glandular secretions may allow lizards to attain high signal efficacy under different climatic conditions (Martín and López 2013, Baeckens et al. 2018a, Campos et al. 2020, Zozaya et al. 2022). What lizards eat may also affect the chemical composition of their chemical signals (Kopena et al. 2011, 2014, García-Roa et al. 2017a), although broad comparative support for a dietary effect remains limited (Baeckens et al. 2017). In addition, stronger sexual selection may promote the evolution of more elaborate chemical signals (Baeckens et al. 2018b, Mangiacotti et al. 2023a), while reproductive character displacement may enhance signal divergence between sympatric species (Zozaya et al. 2019, Mangiacotti et al. 2021).

While much research has focused on adaptive explanations, the potential role of non-adaptive processes in shaping chemical signal diversity remains underexplored. Relatively few studies have explicitly tested whether stochastic processes, rather than selection, underlie observed patterns of chemical signal divergence. Yet accounting for stochasticity in signal divergence is important, especially in isolated systems with restricted gene flow, such as islands. Under these conditions, limited gene flow and demographic isolation amplify the effects of genetic drift, allowing genetic differentiation to accumulate over time – a process that can lead to trait divergence without direct adaptive significance (i.e. neutral divergence; Nei 2005). A strong correlation between signal distance and genetic distance based on neutral genetic markers would support such a scenario, yet direct empirical tests remain rare, particularly for chemical signals. Some prior work hints at this possibility: in common wall lizards *Podarcis muralis*, glandular secretion profiles mirrored neutral genetic structure (MacGregor et al. 2017), and in the Skyros wall lizard *Podarcis gaigeae*, secretion divergence aligned with genetic differentiation but not with mating preferences (Runemark et al. 2011). However, neither study formally contrasted non-adaptive and adaptive hypotheses, leaving the relative contributions of stochastic and selective processes unresolved.

In this study, we address this gap by investigating chemical signal variation among populations of the Italian wall lizard *Podarcis siculus* distributed across 11 nearby islands in the Adriatic Sea. The geographical isolation and limited connectivity of these land bridge islands have restricted gene flow over extended evolutionary timescales (Gorman et al. 1975, Podnar et al. 2005, Sikora et al. 2014), making them a valuable natural system to assess how genetic structure, spatial separation, and socio-ecological factors may shape signal divergence. Our objectives were twofold: 1) to quantify inter-populational diversity in the chemical composition of lizard epidermal gland secretions, and 2) to assess the extent to which this variation can be explained by genetic architecture, geographic distance, environmental conditions, or the strength of sexual selection. Notably, we analyze both the lipid and protein fractions of lizard glandular secretions, a combination rarely addressed together (but see Mangiacotti et al. 2023b), providing a comprehensive view of chemical signal divergence, and accounting for the distinct roles these components are thought to play in communication (Mayerl et al. 2015, Mangiacotti et al. 2023b). By integrating genetic and socio-ecological variables into a unified analytical framework, we directly test the often-overlooked role of non-adaptive processes (as opposed to adaptive ones) in shaping lizard chemical signals. If neutral evolution predominates, we predict that chemical signal divergence will correlate strongly with genetic and geographic distance, whereas associations with environmental or socio-ecological factors will be rather weak or absent.

Material and methods

Study system and field sampling

The Italian wall lizard *Podarcis siculus* is a medium-bodied lacertid native to much of the Mediterranean basin (Corti and Lo Cascio 2002, Podnar et al. 2005). The species is typically strongly sexually dimorphic and a dietary generalist, capable of adjusting its diet to local resource availability. Populations, particularly those on Adriatic islands, often differ markedly from one another in morphology, ecology, and diet (Clover 1979, Corti and Lo Cascio 2002, Herrel et al. 2008, Taverne et al. 2019, 2020, 2022). Like all *Podarcis* species, *P. siculus* possesses active epidermal glands that produce lipid- and protein-rich secretions used in intraspecific chemical communication (Mangiacotti et al. 2021, 2023b, 2023c).

We sampled 342 adult lizards from 12 sites in Croatia (11 islands and one mainland location; Fig. 1) during two field trips, with an average of 29 individuals per site (range = 22–34; Supporting information). Lizards were captured by hand

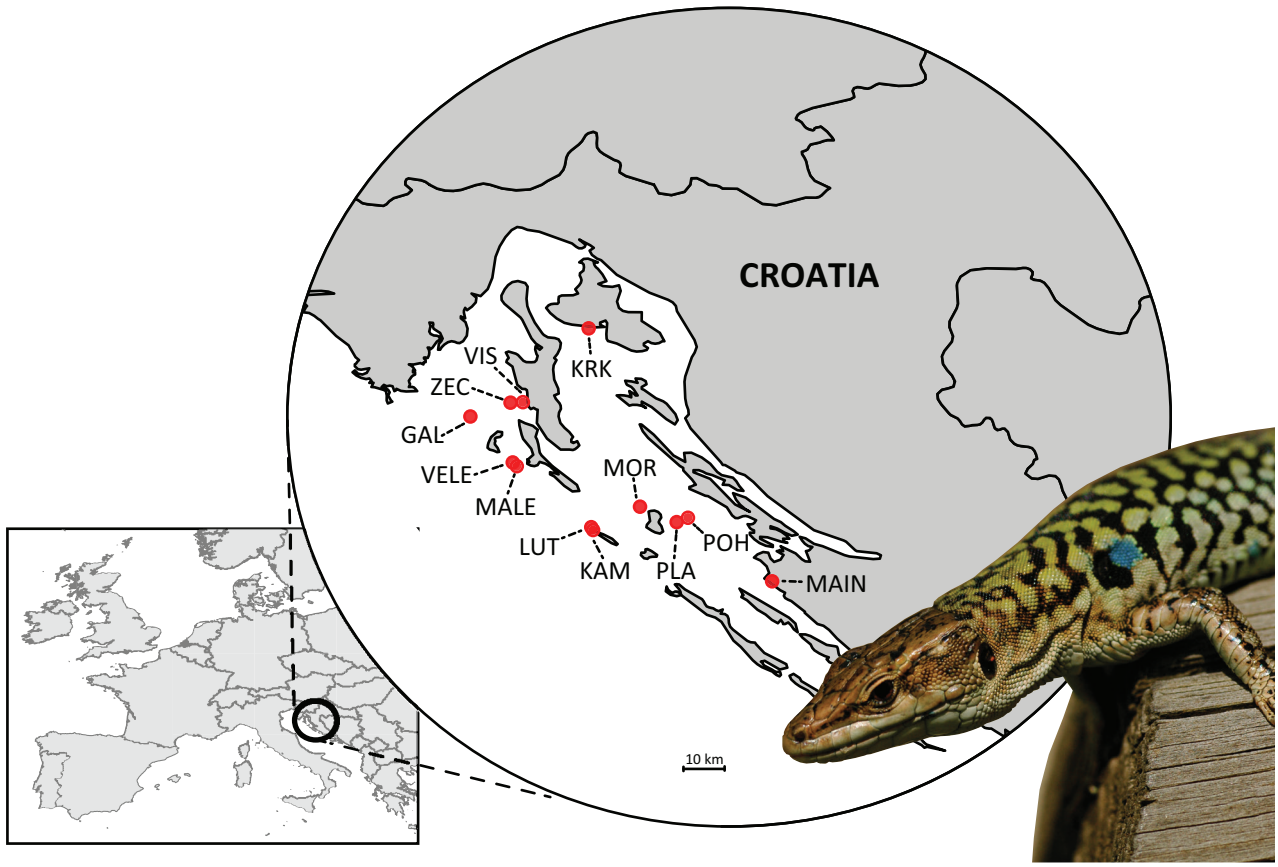

Figure 1. Map of the study area in the Adriatic Sea, showing the geographic distribution of the 12 sampled populations of *Podarcis siculus* (picture on the right), including one mainland site and eleven islands along the Croatian coast. Each population is labelled with a unique three- or four-letter code corresponding to the Supporting information.

or noose. Upon capture, each lizard's snout–vent length (SVL) was measured using digital calipers (Mitutoyo, precision = 0.01 mm), and a ~ 5 mm tail tip was collected and preserved in 95% ethanol for DNA extraction. Epidermal gland secretions were sampled from a random subset of 10 males per site by gently pressing around the femoral pores. Secretions were collected into glass vials with inserts, sealed with Teflon-lined caps, and stored at −20°C until chemical analysis. To assess the availability of potential invertebrate prey for lizards, we conducted sweep netting through vegetation along ten 10-m transects at each site (as in Herrel et al. 2006). Each sweep sample was individually bagged and frozen for later identification and quantification.

Chemical analysis of epidermal gland secretions

To characterize the lipophilic fraction of epidermal gland secretions, we used gas chromatography–mass spectrometry (GC-MS) following established protocols (Martín and López 2006, 2015, García-Roa et al. 2018). This analysis yielded a lipid abundance matrix comprising 79 distinct compounds, though most were sparsely represented across individuals. For downstream analyses, we grouped these compounds into 11 major chemical classes (Supporting information) (Gabirot et al. 2010, Baeckens et al. 2017, 2018a), in order to avoid possible bias due to zero-inflation (Martın-Fernandez et al. 2003, Templ et al. 2016). In addition, given that individual compounds may have specific signaling roles independent of class-level trends, being the true target of evolutionary pressures (Martín and López 2024), we compiled a secondary matrix focusing on five functionally relevant compounds: cholesterol, cholestanol, campesterol, provitamin D3 and α-tocopherol. These compounds are known to contribute to social signaling in lacertid lizards (Martín and López 2014, García-Roa et al. 2017b, Mangiacotti et al. 2023b) and were consistently present across all sampled populations (Supporting information).

To analyze the proteinaceous component of the secretions, we used sodium dodecyl sulphate–polyacrylamide gel electrophoresis (SDS-PAGE), using previously described methods (Mangiacotti et al. 2017, 2019, 2021). From the individuals previously analyzed for lipids, five samples per population (60 in total) were randomly selected, defatted using n-hexane, and extracted in PBS prior to electrophoresis. Gels were scanned at high resolution (1200 dpi), and lanes were processed in R ver. 3.5.2 (www.r-project.org) using custom functions and code adapted from (Mangiacotti et al. 2019). Each lane was converted into an electrophoretogram representing color intensity along the molecular weight gradient, serving

as a quantitative proxy for protein composition (Alberts 1991, Mangiacotti et al. 2019, 2021, 2023a, 2023b). Profiles were aligned and normalized before analysis and standardized into 300 within-lane relative intensity values for direct comparison across samples (Mangiacotti et al. 2019, 2021, 2023a, 2023b).

Genetic analysis

To estimate genetic differentiation among populations, we extracted genomic DNA from tail tip samples of 240 lizards (20 individuals per site), following the protocol of (Huyghe et al. 2010). Microsatellite genotyping was conducted across 11 loci. As *Podarcis siculus*-specific primers were unavailable, we used primers developed for closely related congeners. Eight loci (Pmeli-02, -04, -08, -13, -14, -15, -16, -19) originated from *Podarcis melisellensis* (Huyghe et al. 2009), while three additional loci (B3, B4, B6) were adopted from *Podarcis muralis* (Nembrini and Oppliger 2003). This cross-species amplification strategy is commonly used when flanking regions of microsatellite loci are conserved across taxa, allowing for sufficient polymorphism and resolution (Canales-Aguirre et al. 2010). PCR amplification and genotyping followed the methods described in (Huyghe et al. 2010). While genome-wide markers may provide higher resolution, the use of microsatellites offers a cost-effective and sufficiently informative approach for assessing broad-scale population structure, which is appropriate for the objectives of this study.

Genetic distances between populations were calculated using Nei's standard genetic distance (Nei 1987) as implemented in the R package 'poppr' (Kamvar et al. 2014). To visualize genetic relationships, we constructed a dendrogram based on the resulting distance matrix, supported by 1000 bootstrap replicates at a threshold cut-off of 50% for node support (Supporting information).

Sexual size dimorphism

In *Podarcis siculus*, males are typically larger than females (Corti et al. 2011, Sacchi et al. 2023). Such male-based sexual size dimorphism is generally attributed to intrasexual selection favoring larger males in the context of territoriality and male–male competition (Braña 1996, Cox et al. 2003, Sacchi et al. 2015). To quantify the strength of sexual size dimorphism (SSD) across populations, we calculated the ratio of mean male to mean female snout–vent length (SVL) using measurements from all captured individuals at each site (Supporting information, Smith 1999, Janicke and Fromonteil 2021). This size ratio served as a population-level proxy for the intensity of sexual selection and was incorporated into downstream analyses.

Environmental conditions

To characterize environmental conditions across sites, we compiled data on topography, climate, land cover, and prey availability. A 20 km buffer was applied around the mainland site to approximate the surface area of the largest island (Krk, 411 km^2), ensuring comparability across localities. Island boundaries and extents were defined using Croatian administrative data from GADM (ver. 4.1, released on 16 July 2022, https://gadm.org/).

- Topography. Mean elevation and elevation range (minimum-maximum) were extracted for each site from the NASA Shuttle Radar Topography Mission Global dataset (1-arc-second resolution, ±30 m; www.earthdata.nasa.gov) (Supporting information).
- Climate. We obtained downscaled 30-year climate data (1990–2020) from ClimateEU ver. 4.63 model (Marchi et al. 2020 p. 202). From this dataset, we calculated the annual mean temperature, total annual precipitation, and their respective standard deviations (SDs) to account for seasonal variability (Supporting information).
- Land cover**.** Land cover information was derived from CLC+Backbone 2018 dataset (10 m resolution; https://land.copernicus.eu), which categorized land into 11 classes, eight of which were represented at our study sites. For each site, we calculated the relative coverage of each category (Supporting information). Given that permanent herbaceous vegetation, matching the ecological requirement of *P. siculus* (Corti and Lo Cascio 2002, Corti et al. 2011), was dominant across sites, we distilled land cover into two variables: 1) relative abundance of herbaceous vegetation (as a proxy for suitable habitat), and 2) the Shannon index of land cover categories (as a proxy for habitat heterogeneity).
- Prey availability. To estimate food resources, we categorized all invertebrates from our sweep-netting surveys (Study system and field sampling) to order level under a digital microscope. This produced a matrix of relative abundance across 18 taxonomic groups (Supporting information). From these data, we calculated a Shannon index of prey diversity for each site, following (Baeckens et al. 2017).

Our composite environmental dataset matrix finally included ten variables: two topographic (mean elevation, elevation range), four climatic (mean temperature, temperature SD, total precipitation, precipitation SD), two land cover (herbaceous cover, land cover diversity), prey diversity, and island size (log-transformed). The variables included in the environmental matrix were standardized to ensure equal weighting in the computation of the distance matrix.

Statistical analyses

To assess population-level differences in chemical signal composition, we first applied ordinary least squares linear models for high-dimensional multivariate response variables (Collyer et al. 2015, Collyer and Adams 2024), implemented via the 'RRPP' package ver. 2.0.0 in R (www.r-project.org, Collyer and Adams 2018). These models estimate variance attributable to population identity using a randomized residual permutation procedure (ter Braak 1992, Collyer et al. 2015, Collyer and Adams 2018). We conducted separate models for lipids and proteins, using three response matrices:

1) lipid chemical classes (now abbreviated as 'L11'), 2) relative abundances of five socially relevant lipids (abbreviated as 'L5'), and 3) normalized electrophoretic profiles (abbreviated as 'NEP') for protein content. All matrices were centered-log-ratio transformed to account for compositional structure (Aitchison 1982, van den Boogaart and Tolosana-Delgado 2013, Mangiacotti et al. 2019, 2023a, 2023b). Each model was permuted 999 times to generate empirical F distributions.

We next evaluated whether chemical signal divergence among populations could be explained by genetic, geographic, environmental, or sexual dimorphic differences. For this, we used multiple regression on distance matrices (MRM), a method suited for modelling relationships where both response and predictor variables are pairwise distances (Legendre et al. 1994, Legendre and Legendre 1998, Lichstein 2007). The MRM framework involves unfolding the upper triangle of symmetric matrices into one-dimensional vectors of pairwise distances (d_{ij}) followed by a linear regression of response distances against predictor distances (Legendre and Legendre 1998, Lichstein 2007). However, due to the non-independence among pairwise comparison, standard inference methods are invalid (Legendre et al. 1994, Lichstein 2007).

To address this, we adopted a Bayesian implementation of MRM using the 'brms' package ver. 2.21.0 in R (www.r-project.org, Bürkner 2017, 2021), incorporating a multi-membership random effect (Bürkner 2018) to account for the dependency of d_{ij} values on population identity. At the population level, we extracted mean chemical signal profiles from the earlier RRPP models and computed pairwise Euclidean distances between centered-log-ratio transformed profiles for lipids (L5, L11) and proteins (NEP) (Aitchison 1982, van den Boogaart and Tolosana-Delgado 2013), yielding the response matrices for lipids (dL5, dL11) and proteins (dNEP).

Predictor matrices included genetic distance (dGEN), geographic distance (dGEO), environmental distance (dENV), and sexual size dimorphism distance (dSSD). Genetic distances were calculated using Nei's standard genetic distance from microsatellite genotyping, and geographic distances were computed as the haversine great-circle distances using the 'terra' package ver. 1.7-71 (Hijmans 2024). Environmental distances were based on pairwise Euclidean distances between standardized environmental profiles. All distance matrices were z-standardized prior to model fitting.

For each response matrix (i.e. dL5, dL11, dNEP), we fitted four competing univariate models, each including one predictor variable (dGEN, dGEO, dENV or dSSD). Model support was assessed using the posterior probability that slope estimates exceeded zero. Predictive performance was compared using expected log pointwise predictive density (*elpd*) calculated via leave-one-out cross-validation (Vehtari et al. 2017), implemented in the 'loo' package ver. 2.7.0 (Vehtari et al. 2024). Models were ranked by *elpd* scores, and model comparisons were made using differences and associated standard errors. We used MRM models also to assess pairwise dependence among predictors.

All MRM models were run with default flat priors, using three chains with 4000 iterations each (2000 warm-up, thinning = 2). Convergence was evaluated via visual inspection of trace and density plots (Bürkner 2017). Posterior estimates were summarized as the half-sample mode (Bickel and Frühwirth 2006) and 95% highest density intervals (Turkkan and Pham-Gia 1993), calculated via the 'modeest' ver. 2.4.0 (Poncet 2019) and 'HDInterval' ver. 0.2.4 (Meredith and Kruschke 2022) packages in R (www.r-project.org).

Results

We found significant among-population divergence in both lipid and protein components of the glandular secretions across all datasets (L11, L5, NEP), with population effects explaining substantial variance in each case (all p values ≤ 0.001; Table 1). Specifically, population identity accounted for ~25% of variation in lipid chemical classes (L11), ~ 37% in the five local signaling lipids (L5), and ~ 25% in normalized electrophoretic profiles (NEP).

Among the L11 classes, steroids, waxy esters, and tocopherols contributed most to population-level differences (Fig. 2, left). Within the L5 matrix, cholesterol, provitamin D_3, and campesterol were the most variable compounds (Fig. 2, right). Protein profiles were generally consistent in peak position along the molecular weight gradient but varied in peak intensity among populations (Fig. 3). Most profiles showed a dominant peak in the 15–20 kDa region, although the number and height of peaks differed across sites.

Visualizing the datasets in phylomorphospace (Revell 2012, 2024) revealed that L11 and NEP shared similar population-level clustering patterns, while L5 followed a somewhat distinct distribution. All three datasets showed partial alignment with both genetic structure and geographic configuration of the sampled populations (Fig. 4).

Bayesian MRM models supported these trends: chemical distances (dL5, dL11, dNEP) increased with both genetic and geographic distances, with slope estimates strongly favoring positive associations (Table 2, Fig. 5A). The largest effect

Table 1. Results of ordinary least squares linear models testing for among-population variation in the lipid and protein composition of lizard glandular secretions. Shown are the summarizing outputs for the three datasets: L11 (relative abundances of 11 major lipid chemical classes), L5 (relative abundances of five key lipid compounds known to function in lizard communication and present in all populations), and NEP (normalized electrophoretic profiles of the protein fraction). Reported are the proportion of variance explained (R^2), observed f values with associated numerator and denominator degrees of freedom (subscripts), and p-values based on 999 permutations.

Response matrix	R^2	$f_{num,den}$	p
Lipids (major chemical classes, L11)	0.252	$3.301_{11,108}$	≤ 0.001
Lipids (individual compounds, L5)	0.375	$5.900_{11,108}$	≤ 0.001
Proteins (NEP)	0.283	$1.719_{11,48}$	≤ 0.001

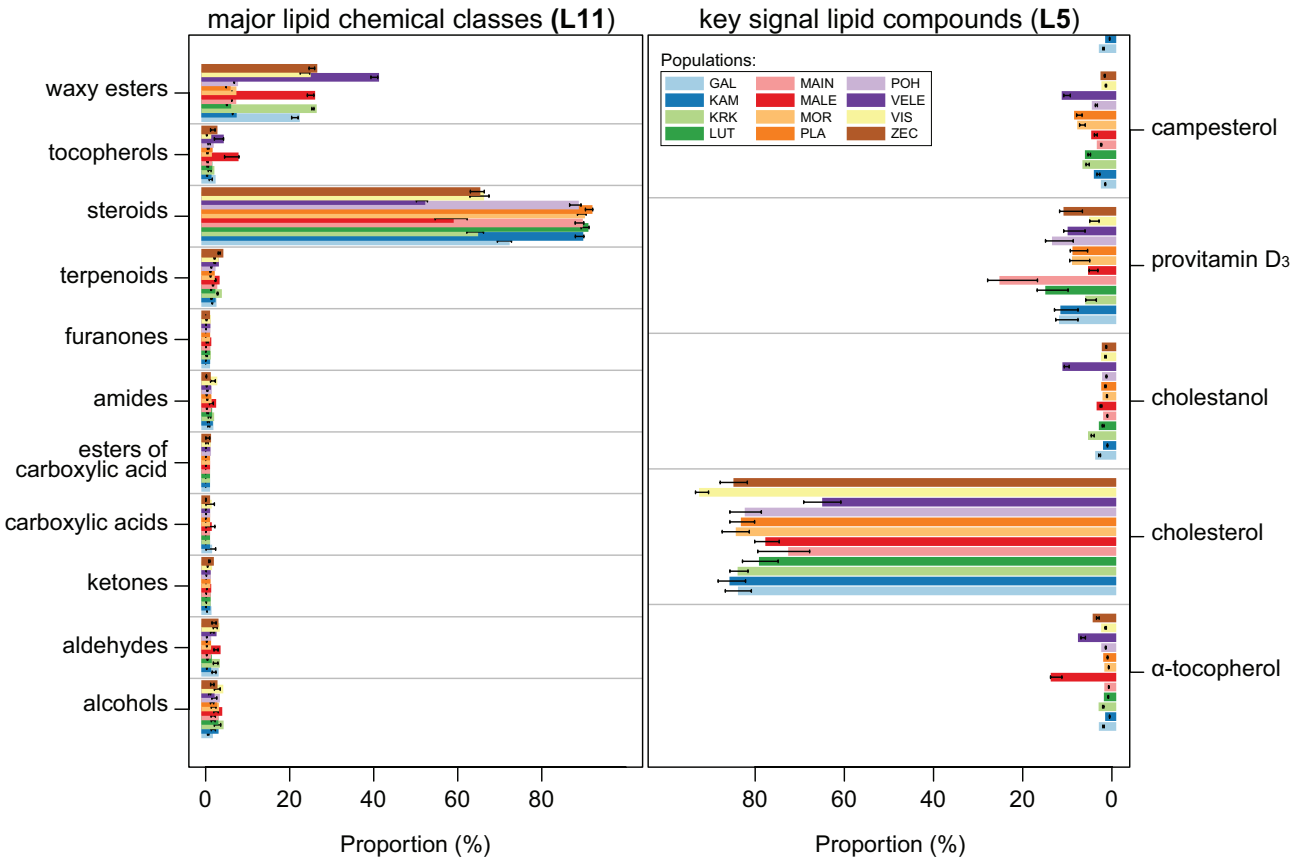

Figure 2. Population-level variation in the lipid composition of *Podarcis siculus* glandular secretions. Bar heights represent the relative abundance of (left) 11 major lipid chemical classes (L11) and (right) five key signaling lipid compounds (L5). Values are predicted averages per population. Black error bars represent the 95% confidence interval of the mean.

was found for genetic distance predicting divergence in L5 (slope = 0.571), followed by L11 (0.318) and NEP (0.221). Geographic distance had comparable effects on L11 (0.324) and NEP (0.353) and was nearly as strong as genetic distance for L5 (0.569). In contrast, sexual size dimorphism had only a weak influence, marginally affecting protein profiles (Table 2, Fig. 5A), and environmental distance showed no detectable effect on any response variable.

Model comparisons based on expected log pointwise predictive density (*elpd*) ranked the genetic and geographic models highest, although their relative performance varied by dataset (Table 3, Fig. 5B). For L11 and L5, the genetic model had the best predictive fit, but differences with the geographic model were not statically robust (*elpd* difference ± 1 SE overlapped zero). For NEP, the geographic model performed best overall, outperforming all alternatives. Across datasets, environmental and sexual size dimorphism models consistently ranked lowest (Table 3, Fig. 5).

Finally, pairwise MRM models applied to the predictor matrices (dGEN, dGEO, dSSD, dECO) revealed a strong positive correlation between genetic and geographic distances (slope = 0.63 ± 0.13; Supporting information), whereas all other pairwise associations received weak support.

Discussion

Among-population variation in the chemical composition of *Podarcis siculus* glandular secretions was best explained by genetic and geographic divergence, while environmental conditions (i.e. topography, climate, land cover, prey availability) and (a proxy for) sexual selection offered little to no explanatory power. Genetic and geographic distances were themselves correlated, consistent with expectations for island systems where dispersal is limited and gene flow is restricted (Wright 1943, MacArthur and Wilson 1967). These patterns point to a relevant role for stochastic processes, such as genetic drift, in shaping chemical signal divergence across the studied populations. Rather than reflecting local adaptation to environmental or social conditions, the observed variation in chemical signal profiles appears to largely mirror neutral genetic structure and spatial separation.

Evidence for a role of non-adaptive processes, particularly stochastic mechanisms, in explaining chemical signal divergence in *P. siculus* aligns well with theoretical predictions from island biogeography. This perspective suggests that geographic isolation, limited dispersal, small population sizes, and historical contingency can promote substantial

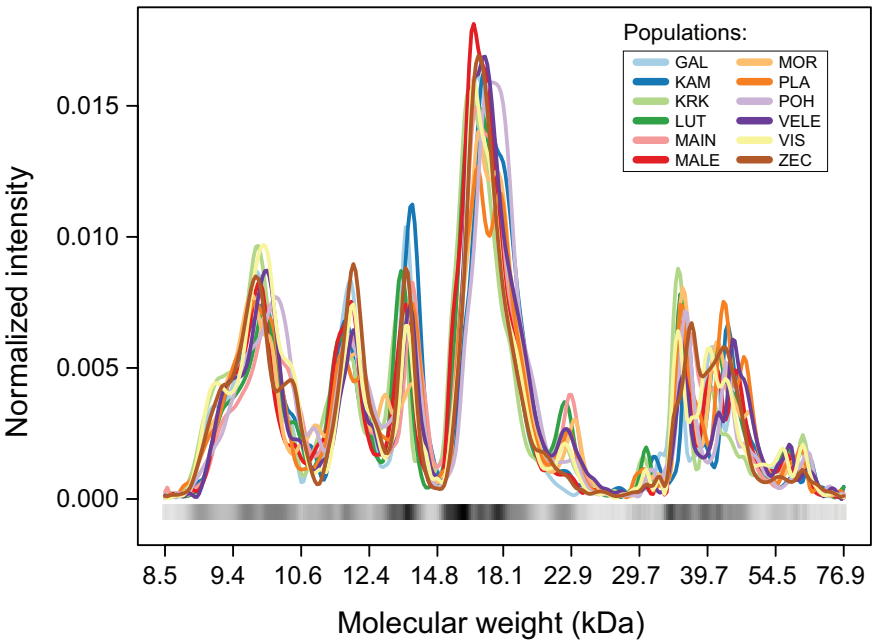

Figure 3. Population-level protein composition of *Podarcis siculus* glandular secretions. Colored lines represent normalized electrophoretic profiles (NEP) for each population. Shading in the horizontal bar indicates the degree of between-population variation across the molecular weight gradient, with darker regions reflecting higher divergence.

phenotypic divergence through non-adaptive mechanisms alone (MacArthur and Wilson 1967, Losos and Ricklefs 2009). In such contexts, random genetic drift – amplified by historical founder effects and restricted gene flow – can cause populations to gradually accumulate phenotypic differences, even in traits traditionally assumed to be shaped by strong selection (Wright 1943, Mayr 1954, Barton 1996). Chemical signals, composed of complex lipid and protein mixtures, may be prone to such divergence if stabilizing selection is weak or inconsistently applied across populations. That said, our findings do not imply that drift is the only force influencing signal evolution in this system. A strong correlation with neutral genetic structure supports a role for stochastic processes (Charlesworth et al. 2003), but does not rule out the possibility of linked selection – where selection acts on genomic regions near those underlying signal traits – or that genetically similar populations may occupy ecologically similar environments. However, in our dataset, genetic distances were not strongly correlated with environmental or socio-sexual variables (Supporting information), making parallel ecological effects an unlikely driver of the observed patterns in chemical profiles. Regardless, the combined evidence – spanning the alignment of chemical and genetic structure, the weak influence of environmental and social predictors, and the geographic context of isolated island populations – supports the conclusion that drift and isolation have been key contributors in shaping signal divergence. Our results build on earlier studies suggesting a role for stochastic processes in lizard chemical signal divergence (Runemark et al. 2011, MacGregor et al. 2017), but extend those findings by explicitly comparing competing hypotheses across a broader set of populations. In doing so, we offer compelling evidence that non-adaptive processes, too, can play a substantial role in shaping chemical signal divergence in island systems.

Our observation of a minimal role for abiotic and biotic factors in explaining chemical signal divergence in *P. siculus* contrasts with dominant adaptive models of signal evolution, which predict that environmental and social selection should shape signal design to optimize efficacy and function. Yet in our (albeit correlative) study, neither climatic variables, habitat structure, prey diversity, nor sexual size dimorphism showed consistent associations with divergence in either lipid or protein profiles. These 'negative' results are nonetheless informative, suggesting that local adaptation has not been a major driver of chemical signal differentiation at the spatial and ecological scale examined here. Several non-exclusive explanations could account for this pattern. First, the relative ecological similarity among Adriatic islands may limit the opportunity for – or strength of – divergent selection. Compared to interspecific studies spanning broader climatic or ecological gradients (Baeckens et al. 2018a, Campos et al. 2020, Zozaya et al. 2022), intraspecific comparisons among island populations likely involve more subtle environmental variation, for which phenotypic responses may be limited or selection pressures too weak to generate consistent divergence. Second, even if adaptive responses exist, they may be masked by the overriding influence of stochastic processes, such as genetic drift and founder effects. In systems with small population sizes and restricted gene flow, these processes can dominate trait evolution and obscure the effects of weak or inconsistent selection (Barton 1996, Charlesworth et al. 2003). For instance, Kolbe et al. (2012) demonstrated that

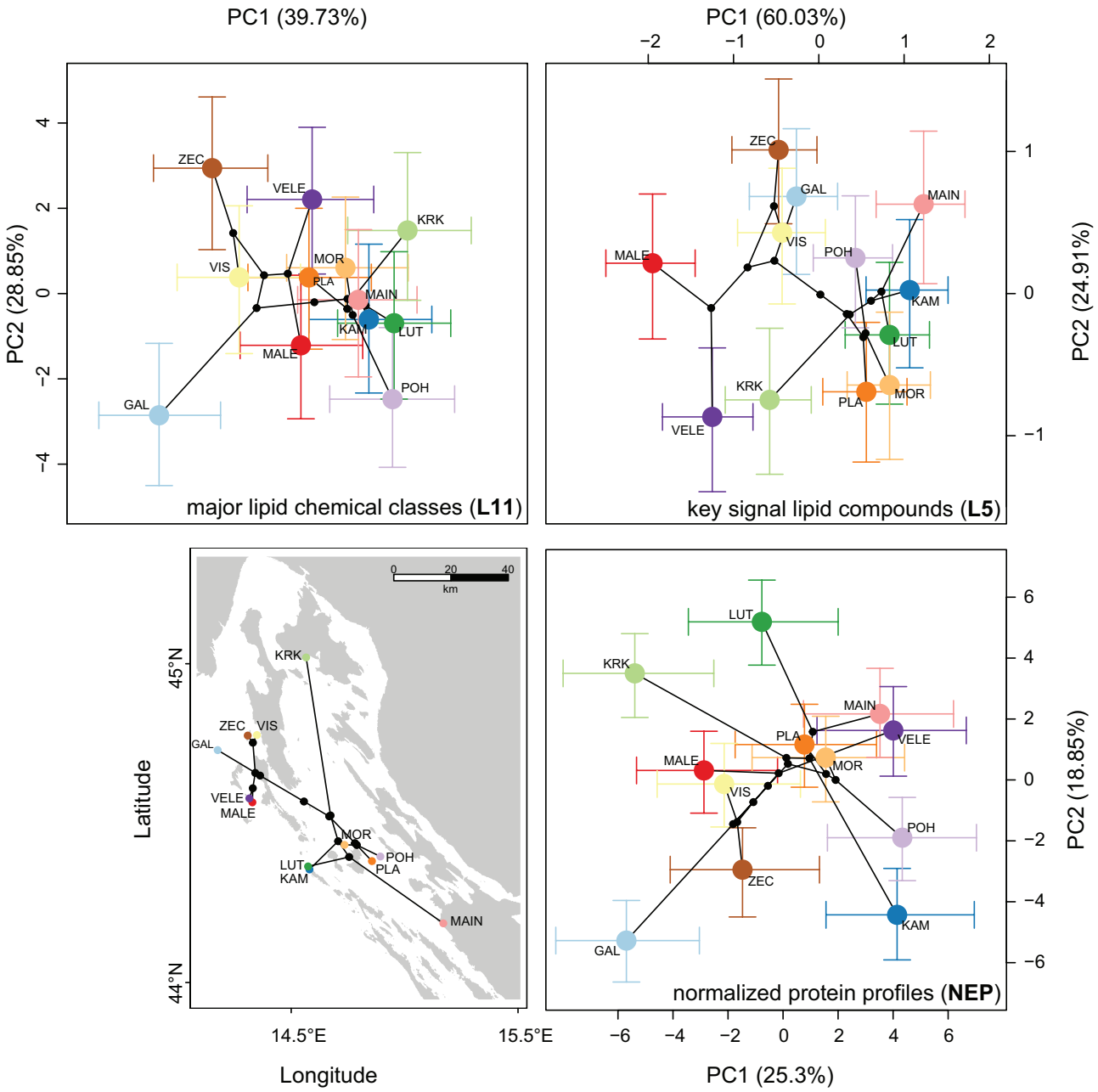

Figure 4. Phylomorphospace visualization of population-level chemical profiles. Clockwise from the top-left: principal component (PC) projections for lipid chemical classes (L11), key lipid compounds (L5), and normalized protein profiles (NEP). Grey lines denote 95% confidence intervals. Bottom-left panel projects geographic locations into phylomorphospace, illustrating the relationship between genetic structure and spatial distribution.

founder effects produced persistent morphological divergence in *Anolis* lizards, despite strong selection in experimental island populations, highlighting how non-adaptive processes can shape trait variation even under directional selection. Third, our ecological and social proxies may not fully capture the selective pressures relevant to chemical signaling. For instance, while we quantified prey availability, this may not fully reflect dietary intake, although lacertids are generalist feeders and often track available resources (Arnold 1987, Díaz 1995). Likewise, variables such as predation pressure and the intensity of intraspecific competition, which could plausibly affect investment in signaling traits (Donihue et al. 2020, Baeckens et al. 2025a), were not directly measured in this study. Also, although we were able to limit sampling to just two field trips, unmeasured environmental or physiological variation across field trips could have introduced noise that obscured ecological signals. Future studies would benefit from conducting all sampling within a single, temporally consistent field trip to minimize such potential confounding effects. Fourth, sexual selection may act more on the quantity of specific, condition-dependent compounds than on the overall relative composition of the secretions, as assessed in

Table 2. Coefficient estimates from Bayesian multiple regression on distance matrices (MRM) models, each incorporating a single predictor: genetic distance (dGEN), geographic distance (dGEO), sexual size dimorphism distance (dSSD), or environmental distance (dENV). For each model, the intercept (β_0) and slope (β_1) are reported with the following summary statistics: half-sample mode (HSM), 95% highest density credible interval (95% HDI), and the posterior probability that the slope is greater than zero (p). Coefficients with p > 0.95 are highlighted in bold, indicating strong evidence for a positive effect.

				95% HDI		
Response	Predictor	Coefficient	HSM	lower	upper	p
Lipid distance (major chemical classes, dL11)	**dGEN**	β_0	0.016	−0.854	0.840	0.520
		$\boldsymbol{\beta_1}$	0.318	0.191	0.442	**1.000**
	dGEO	β_0	0.039	−0.902	0.818	0.494
		$\boldsymbol{\beta_1}$	0.324	0.140	0.448	**0.999**
	dSSD	β_0	0.038	−0.809	0.855	0.517
		β_1	−0.117	−0.393	0.232	0.311
	dENV	β_0	0.058	−0.893	0.817	0.499
		β_1	0.141	−0.167	0.410	0.788
Lipid distance (individual compounds, dL5)	**dGEN**	β_0	0.032	−0.738	0.692	0.497
		$\boldsymbol{\beta_1}$	0.571	0.389	0.712	**1.000**
	dGEO	β_0	0.055	−0.824	0.763	0.508
		$\boldsymbol{\beta_1}$	0.569	0.374	0.750	**1.000**
	dSSD	β_0	−0.057	−0.663	0.584	0.485
		β_1	0.009	−0.383	0.321	0.457
	dENV	β_0	−0.067	−0.702	0.675	0.475
		β_1	0.104	−0.249	0.447	0.662
Protein distance (dNEP)	**dGEN**	β_0	−0.044	−0.605	0.695	0.509
		$\boldsymbol{\beta_1}$	0.221	0.011	0.420	**0.989**
	dGEO	β_0	0.047	−0.655	0.659	0.489
		$\boldsymbol{\beta_1}$	0.353	0.150	0.586	**0.999**
	dSSD	β_0	−0.090	−0.777	0.742	0.478
		β_1	0.241	−0.116	0.655	0.901
	dENV	β_0	−0.070	−0.794	0.649	0.496
		β_1	−0.041	−0.427	0.281	0.325

our study. Consequently, its contribution to signal divergence may be underestimated in our analyses. Finally, although we used neutral genetic divergence as a proxy for non-adaptive stochastic processes, we cannot entirely rule out the possibility that selection on loci linked to chemical signaling traits contributed to the observed divergence, particularly if such selection covaries with genetic structure due to shared demographic history. To resolve these possibilities, future work should integrate more direct ecological and behavioral measurements with genomic tools that can detect selection on candidate loci. Experimental assays evaluating the efficacy and social function of divergent chemical profiles will also be essential for clarifying when – and under what conditions – ecological variation shapes lizard chemical communication.

Even if the divergence in chemical signals among *P. siculus* island populations seem largely to have arisen through stochastic processes, this does not necessarily imply that the resulting variation is functionally obsolete. Lizards, including *Podarcis* species, are known to detect subtle differences in conspecific glandular secretion composition using scent alone (Martín and López 2015, 2024). It is therefore plausible that the variation we document, even if non-adaptive in origin,

Table 3. Model comparison results for Bayesian multiple regression on distance matrices (MRM), ranked by expected log pointwise predictive density (elpd) for each response variable: lipid classes (L11), key lipid compounds (L5), and protein profiles (NEP). Models are listed in descending order of elpd. Reported values include the standard error of the elpd estimate (SEelpd), the difference in elpd relative to the best model (Δelpd), and the standard error of that difference (SE(Δelpd)).

Response	model	*elpd*	SE*elpd*	Δ*elpd*	SE(Δ*elpd*)
Lipids (major chemical classes, L11)	Genetic	−49.672	5.025	0.000	0.000
	Geographic	−53.565	4.920	−3.893	4.365
	Environmental	−61.028	4.334	−11.357	4.651
	SSD	−61.980	4.516	−12.308	4.610
Lipids (individual compounds, L5)	Genetic	−66.501	5.236	0.000	0.000
	Geographic	−69.025	5.682	−2.524	4.964
	SSD	−86.498	4.702	−19.997	4.621
	Environmental	−86.623	4.814	−20.123	4.513
Proteins (NEP)	Geographic	−78.763	5.893	0.000	0.000
	Genetic	−82.594	5.310	−3.832	2.630
	SSD	−82.886	5.740	−4.123	3.625
	Environmental	−84.196	5.482	−5.433	3.619

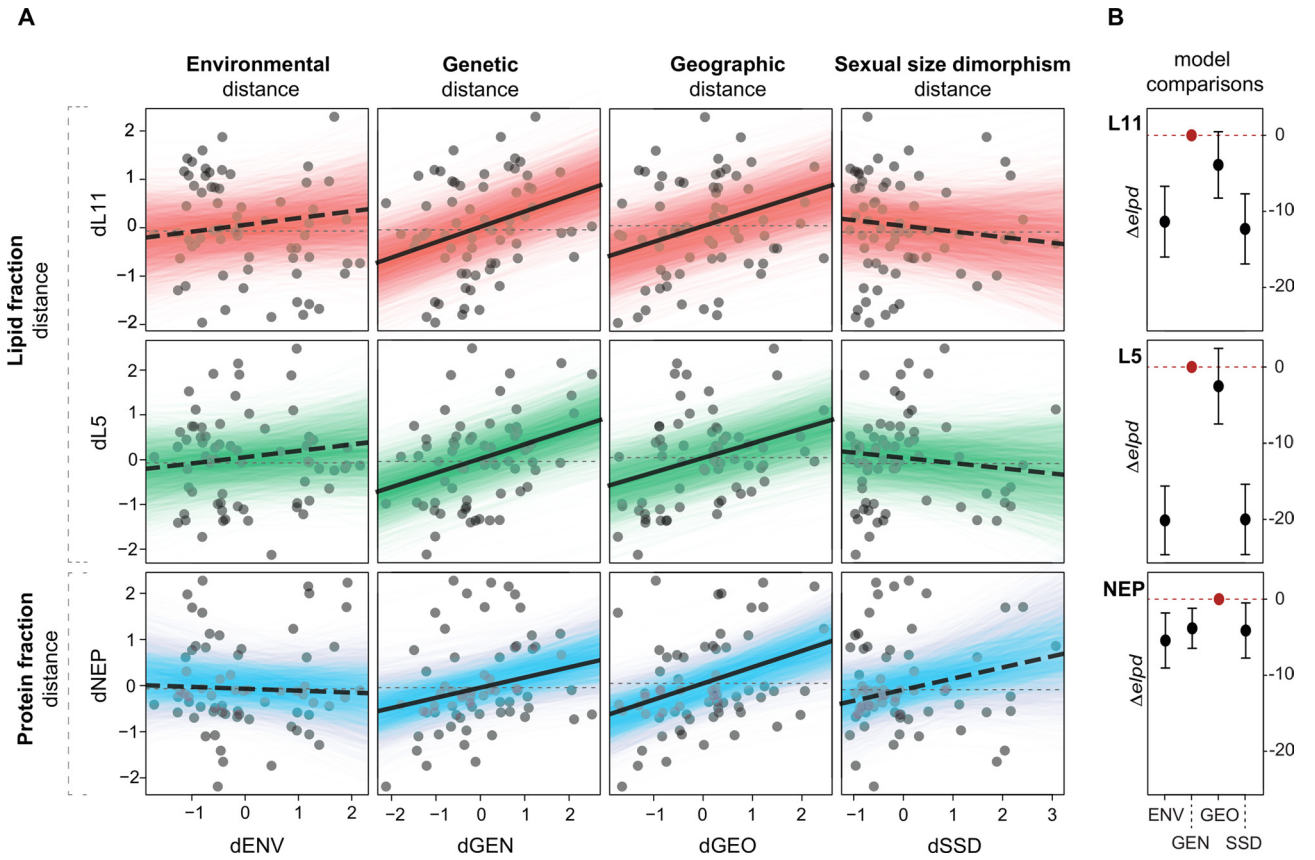

Figure 5. Model results assessing predictors of chemical signal divergence. (A) shows regression fits from Bayesian multiple regression on distance matrices (MRM), with each row corresponding to a different chemical response: (top row) lipid chemical classes (dL11), (middle) key lipid compounds (dL5), and (bottom) normalized protein profiles (dNEP). Columns depict models using single predictors (left-to-right): environmental distance (dENV), genetic distance (dGEN), geographic distance (dGEO), and sexual size dimorphism distance (dSSD). Black dots represent observed pairwise values; bold black lines indicate posterior half-sample mode regression fits; thin colored lines show posterior draws; dotted lines denote a lack of a significant relationship. (B) summarizes model performance via leave-one-out cross-validation: Δelpd scores are shown for each model and response variable, with the best-performing model per set highlighted in red.

could still influence social interactions such as mate recognition or population-level discrimination (Gabirot et al. 2010, 2012, 2013, MacGregor et al. 2017). While opportunities for interpopulation encounters are presumably rare due to the geographic isolation of islands, the capacity to detect and respond to chemical differences may nonetheless help reinforce reproductive barriers in the event of secondary contact. In this way, signal divergence that initially arises through stochastic processes may still carry functional consequences, shaping behavioral interactions and potentially influencing longer-term evolutionary outcomes.

Overall, our results highlight that stochastic processes can be relevant drivers of phenotypic divergence, even in communication traits often assumed to be shaped primarily by selection. In isolated systems such as island archipelagos, the signatures of genetic drift and historical contingency may dominate over adaptive responses to ecological and social variation. By explicitly testing both non-adaptive and adaptive hypotheses across multiple populations, our study contributes to a more balanced view of how chemical communication evolves – one that recognizes the interplay of contingency and determinism in evolution, from recent population divergence to deeper evolutionary timescales.

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Author contributions

Simon Baeckens: Conceptualization (lead); Investigation (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **José Martín**: Formal analysis (lead); Investigation (equal); Writing – review and editing (supporting). **Zoran Tadić**: Project administration

(equal); Writing – review and editing (supporting). **Emma Van den Camp**: Investigation (equal); Writing – review and editing (supporting). **Roberto Sacchi**: Funding acquisition (equal); Writing – review and editing (supporting). **Raoul Van Damme**: Funding acquisition (lead); Investigation (equal); Project administration (equal); Writing – review and editing (equal). **Marco Mangiacotti**: Data curation (lead); Formal analysis (lead); Investigation (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from Zenodo: https://doi.org/10.5281/zenodo.15497079 (Baeckens et al. 2025b).

Supporting information

The Supporting information associated with this article is available with the online version.

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