

Do ecogeographical rules explain morphological variation in a diverse, Holarctic genus of small mammals?

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Abstract

Aim: We use ecogeographical rules to understand the relationship between biogeography and morphological evolution in *Sorex* (Linnaeus, 1758) shrews. Specifically, we test for climatic correlations in body size (Bergmann's rule; larger species in colder habitats) and pelage brightness (Gloger's rule; darker species in more humid/warmer habitats).

Location: North America and Eurasia (Holarctic).

Taxon: *Sorex* spp. (Mammalia: Soricomorpha: Soricidae).

Methods: We compiled body size data for 51 species of *Sorex* and measured pelage brightness from museum specimens for 43 species. We sourced bioclimatic data across the geographical range of each species as well as specific to the museum specimen localities. For comparative purposes, we also estimated a *Sorex* phylogeny using existing sequence data. To test Bergmann's and Gloger's rules, we constructed phylogenetic least squares models considering latitude, altitude, and bioclimatic variables as predictors of interspecific variation in body size and pelage brightness across *Sorex*. We then performed these tests separately for the Palearctic and Nearctic lineages.

Results: *Sorex* exhibits wide variation in both body size and pelage brightness. In models of the entire genus and of the Nearctic clade, neither trait is significantly predicted by the variables tested. A decrease in pelage brightness in the Palearctic clade is significantly predicted by increasing mean annual temperature and annual precipitation, but only when considering climatic data specific to the measured specimen localities.

Main conclusions: *Sorex* does not conform to Bergmann's rule. This result aligns with intraspecific studies suggesting Bergmann's rule is less evident in smaller taxa, but it counters others that found support for the rule in North American and European assemblages. Different patterns in pelage evolution across the Nearctic and Palearctic clades may result from different historical climatic pressures; however, the significance of the relationship between climate and pelage evolution is dependent on the specificity of the climatic data. *Sorex* may be a useful focal taxon for exploring the relationship between intra- and interspecific ecogeographical patterns as well as the relative roles of morphological, behavioural, physiological, and life history characteristics in explaining the ability to persist in climatically challenging environments.

KEYWORDS

Bergmann's rule, Gloger's rule, Holarctic, *Sorex*

1 | INTRODUCTION

Understanding how environmental and climatic conditions have impacted the evolutionary history of lineages can help explain patterns of variation, adaptation, and diversity among extant taxa. *Sorex*, a species-rich genus of shrews (Mammalia: Soricomorpha: Soricidae; 78 species; IUCN 2017), contains some of the smallest living mammals, yet *Sorex* shrews have a broad, Holarctic distribution that reaches the northern-most aspects of the North American and Eurasian continental landmasses. Furthermore, *Sorex* shrews have extraordinary physiological characteristics. First, they have basal metabolic rates of, on average, more than 300% of those predicted for non-shrew mammals of their size, as well as greater average body temperatures than other shrews (Taylor, 1998). As a result of these high metabolic demands, *Sorex* shrews need to feed at least every few hours (Churchfield, 1990) and their body mass drops significantly in the winter (including reduction in brain size; Dehnel, 1949; Pucek, 1965; Lázaro, Dechmann, LaPoint, Wikelski, & Hertel, 2017). Second, unlike many other cold-adapted mammals, *Sorex* shrews are not known to hibernate or use torpor in the winter (Taylor, 1998). Third, they are primarily solitary and highly territorial, which excludes the use of group behaviours for thermoregulation (Rychlik, 1998).

Living at the extreme of physiological requirements makes *Sorex* shrews an ideal system to investigate whether and which morphological adaptations have evolved in small mammals to facilitate survival in environments that impose high energetic demands. Biologists have often employed the framework of ecogeographical “rules” to explain correlations between a taxon's biogeography and its ecology, physiology, and/or morphology (Lomolino, Sax, Riddle, & Brown, 2006). Examples of morphological ecogeographical rules include Bergmann's rule, which predicts that body size is greater in organisms that inhabit higher latitudes or colder climates (Bergmann, 1847); and Gloger's rule, which predicts that more heavily pigmented (darker) organisms are found in more humid climates (Gloger, 1833). While the generality, or even the applicability, of these rules across taxa or taxonomic levels is debated (Blackburn, Gaston, & Loder, 1999; Mayr, 1956; Meiri, 2010; Watt, Mitchell, & Salewski, 2010), they provide a useful set of testable predictions that can be employed to illuminate the relationship between the biogeography and the biology of a clade of organisms. In this paper, we test the predictions made by Bergmann's and Gloger's rules in *Sorex* shrews in an attempt to understand possible adaptations to the climatic conditions of their environments.

The original explanation for Bergmann's rule is that an increase in body size at higher latitude or in colder regions could assist with thermoregulation, as the overall surface-to-volume ratio of a larger

animal is smaller than that of a small animal (Bergmann, 1847). However, previous tests of Bergmann's rule in mammals have provided conflicting results. Intraspecific tests of Bergmann's rule suggest that small mammals are either less likely (Freckleton, Harvey, & Pagel, 2003; Meiri & Dayan, 2003) or not more likely (Ashton, Tracy, & de Queiroz, 2000) than large mammals to conform to the rule. For example, intraspecific studies in several species of *Sorex* shrews revealed that smaller individuals inhabit higher latitudes or colder habitats in both Palaearctic (*S. araneus*, *S. minutus*, and *S. caecutiens*) and Nearctic (*S. cinereus*) regions, the opposite of the prediction of Bergmann's rule (Ochocińska & Taylor, 2003; Vega, Mcdevitt, Kryštufek, & Searle, 2016; Yom-Tov & Yom-Tov, 2005).

Interspecific studies of Bergmann's rule in mammals have often used an assemblage approach: they correlate the mean body size of all taxa within squares of a geographical grid with latitude or temperature and generally encompass large and taxonomically diverse samples. These types of studies have found, for instance, that terrestrial mammals in both the Nearctic and Palaearctic generally follow Bergmann's rule (Blackburn & Hawkins, 2004; Rodríguez, López-Saundo, & Hawkins, 2006; Rodríguez, Olalla-Tárraga, & Hawkins, 2008). However, the few interspecific studies that have used a phylogenetic comparative approach have had more ambiguous findings. A broad-scale, interspecific study of Mammalia found support for Bergmann's rule (Clauss, Dittmann, Müller, Meloro, & Codron, 2013). Yet, at smaller taxonomic scales (i.e., ordinal and family levels), support for Bergmann's rule varies widely (Clauss et al., 2013; Gohli & Voje, 2016). In the Soricidae, body size was found to decrease with an increase in the maximum latitude of a species' range (i.e., the opposite of Bergmann's rule; Clauss et al., 2013). To our knowledge, there have not been any explicit interspecific tests of Bergmann's rule in *Sorex*, but it has been observed that some of the smallest *Sorex* species inhabit the highest latitudes (e.g., *S. uguanak*, Hope, Waltari, Payer, Cook, & Talbot, 2013; *S. minutissimus* and *S. minutus*, Ochocińska & Taylor, 2003).

Gloger's rule ties the evolution of pelage coloration to environmental and climatic conditions. Pelage coloration can have many functions in mammals, including communication, crypsis, and physiological regulation (Caro, 2005). Based on morphological characteristics of the eye, shrews are thought to have poor visual acuity (Braníš & Burda, 1994), so pelage coloration is unlikely to play a role in communication with conspecifics. In addition, due to their small size, shrews are not thought to use pelage coloration in aposematic predator deterrence (Caro, 2013). However, cryptic coloration could help shrews avoid predators via environmental background-matching (Atmeh, Adruszkiewicz, & Zub, 2018; Vignieri, Larson, & Hoekstra, 2010). Differences in pelage coloration may also be important for physiological regulation in shrews, as lighter pelage can reflect or scatter radiation and dark



fur can provide melanin-based bacterial or parasite resistance in wet and warm regions (Burt & Ichida, 2004; Caro, 2005). Few mutations are required to evolve dark coloration in mammals (Nachman, Hoekstra, & D'Agostino, 2003), so dark coats could evolve rapidly as a response to environmental pressures. Shrews face both physiological and predatory challenges and often carry high parasite loads (Churchfield, 1990). Because these detrimental factors can be magnified by climatic conditions, the evolution of pelage coloration in response to climatic variation is a viable adaptive strategy in *Sorex*.

Previous tests of both Bergmann's and Gloger's rules in vertebrate clades have provided inconsistent findings (Freeman, 2016; Kamilar & Bradley, 2011), so the rich discussion and speculation surrounding these rules makes them an intriguing starting point for a study of *Sorex* morphological evolution. In this paper, we assess both Bergmann's and Gloger's rules in *Sorex* shrews using phylogenetic least squares regression models that consider bioclimatic variables as predictors of variation in body size and pelage brightness. *Sorex* shrews are hypothesized to have a Palearctic origin (Dubey, Salamin, Ohdachi, Barrière, & Vogel, 2007) and to later have diverged into two monophyletic clades, one Palearctic and one Nearctic (Fumagalli et al., 1999). Therefore, we repeat our phylogenetic tests in each of these two monophyletic clades to explore geographical patterns in greater detail. We also present a calibrated phylogeny of *Sorex*, which we use in our comparative analyses. This clade-focused approach to testing ecogeographical rules will help us understand morphological evolution in shrews and, more generally, gain context for interpreting the equivocal support for ecogeographical patterns in mammals.

2 | MATERIALS AND METHODS

2.1 | Inferring a *Sorex* phylogeny

For the purposes of our comparative analyses, we estimated a *Sorex* phylogeny. We used BEAST 2 2.4.7 (Bouckaert et al., 2014; Drummond & Bouckaert, 2015) and mitochondrial (cytochrome b, *cytb*; cytochrome c oxidase subunit I, *co1*) and nuclear (breast cancer type I protein, *brca1*; apolipoprotein b, *apob*) DNA sequences that were available on GenBank for 56 *Sorex* species. We generally used the list of *Sorex* species currently recognized by the International Union for the Conservation of Nature (IUCN 2017) to guide our species designations; however, we amended our list to account for recent revisions not yet incorporated in the IUCN list. We considered *S. minutissimus* and *S. yukonicus* as one species (Cook et al., 2016; Hope et al., 2010) and *S. bedfordiae* and *S. excelsus* as one species (Chen et al., 2015); we considered only *S. navigator* of the recent split of the *S. palustris* species group (Hope, Panter, Cook, Talbot, & Nagorsen, 2014); and we did not use sequences from the coastal clade of *S. monticolus* as these are probable hybrids (Demboski & Cook, 2001). We chose *Anourosorex yamashinai*, *Blarina brevicauda*, *Cryptotis parva*, and *Neomys fodiens* as outgroup taxa, although we did not explicitly designate them as such in our phylogenetic inference. For each species, we attempted to choose three sequences of

each gene, with each sequence stemming from a different study; however, this was not always possible. A list of sequences with taxonomic authorities for each species is provided in Appendix S1 in the Supporting Information. For each species, we aligned the sequences for a particular gene using MAFFT_{LOCAL} 7.271 (Katoh & Standley, 2013) in ALIVIEW 1.17.1 (Larsson, 2014) and combined them into one consensus sequence for the gene, using International Union of Pure and Applied Chemistry (IUPAC) ambiguity codes to represent polymorphisms. Then, we used the same software to align the set of consensus sequences for each locus. We cropped each alignment to the following lengths: *cytb*, 1140 base pairs (bps); *co1*, 657 bps; *brca1*, 390 bps; and *apob*, 502 bps. Because we did not have all four sequences for all 60 species included in the alignments (56 *Sorex* and 4 outgroup taxa), and because some sequences did not extend the full length of the locus, our alignments were incomplete: *cytb*, 59 taxa included, 4% missing bps; *co1*, 28 taxa included, 56.2% missing bps; *brca1*, 40 taxa included, 34.1% missing bps; and *apob*, 45 taxa included, 27.8% missing bps.

Within BEAST 2, we loaded the four alignments as separate partitions, linked the site and clock models for *cytb* and *co1*, and linked the tree for all partitions. We assigned each gene alignment the substitution model with the lowest Akaike information criterion (AIC) as determined by JMODELTEST 2.1.7 (Darriba, Taboada, Doallo, & Posada, 2012; Guindon & Gascuel, 2003). We assigned *cytb* and *co1* a GTR+I+ Γ substitution model (Tavaré, 1986) and *brca1* and *apob* HKY+ Γ (Hasegawa, Kishino, & Yano, 1985) and GTR+ Γ substitution models respectively. We set all partitions to interpret the IUPAC ambiguity codes as informative characters and assigned a Yule process tree prior to the linked tree. We employed uncorrelated relaxed lognormal molecular clock models (Drummond, Ho, Phillips, & Rambaut, 2006) with diffuse exponential priors for all partitions. To calibrate the tree, we constrained the dates of the ancestor originate nodes of *Sorex* and the putative Nearctic *Sorex* clades (i.e., we selected the “use originate” option when setting the node constraints). We did not, however, constrain those groups to be monophyletic. The oldest fossil assigned to *Sorex* is from the European Land Mammal Age MN 4 (16.9–16.0 Ma; Córcoles Formation; Szyndlar & Alférez, 2005; Paleobiology Database, accessed October 2017), so we placed a lognormal prior with a mean of 16.0 and a standard deviation of 1.0 on the parent of the putative *Sorex* ancestor. Probable Nearctic *Sorex* fossils first appear in the Clarendonian North American Land Mammal Age (13.6–10.3 Ma; Dove Spring Formation; Whistler & Burbank, 1992; Paleobiology Database, accessed October 2017). We placed a normal prior with a mean of 10.0 and a standard deviation of 1.0 on the parent of the putative Nearctic *Sorex* ancestor. The BEAST 2 XML file that contains the final alignments and all settings for model parameters and priors is provided in the Supporting Information.

To estimate the *Sorex* tree, we ran four independent Markov chain simulations of 70 million generations each, logged a tree every 10 thousand generations for a total of seven thousand trees per chain, and updated the trace file every one thousand generations. We assessed convergence of each chain with TRACER 1.6.0 (<http://>

tree.bio.ed.ac.uk/software/tracer/) to ensure the effective sample size for each parameter was greater than 200. We then combined the trees from each chain using LogCombiner (part of the BEAST 2 package), discarding the first 50% of each chain as burn-in to obtain a posterior distribution of 14,003 trees. We used TreeAnnotator (part of the BEAST 2 package) to calculate a maximum clade credibility (MCC) tree from this distribution and FIGTREE 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) to visualize this tree. We then further sampled the posterior distribution to obtain a set 3,500 trees to supplement the MCC tree in hypothesis testing. The MCC tree is provided in the Supporting Information.

2.2 | Morphological data collection

We collected body mass data from either PanTHERIA (Jones et al., 2009; our preferred source), museum records, or field guides for 44 *Sorex* species. For seven species included in our tree, only head-body length was available as an overall body size measurement. We inferred the body masses of these species by fitting a linear model to the body mass and head-body length data set for *Sorex* from PanTHERIA. More information about this model is provided in Appendix S2 in the Supporting Information. Our final data set included body mass data for 51 *Sorex* species.

To measure pelage brightness, we took photographs of one to 12 museum skin specimens of 43 *Sorex* species included in our tree with either a Canon EOS Mark II 5D or a Mark III 7D camera with a Canon EF 24-105 mm or 100 mm lens. To avoid confounding sources of brightness variation due to possible differences between the sexes or seasonal moult cycles, we only photographed female specimens collected between the months of June and September. A list of museum specimens is provided in Appendix S3 in the Supporting Information. Prior to each photography session, we manually set the white balance of the camera with the grey side of a CAMERA TRAX 2.3 in. 24ColorCard, and we included the colorblock side in every photograph of the session. To avoid automatic colour adjustments to photographs by camera software, we imported the RAW files into Adobe Photoshop Camera Raw and saved them as TIFF files in the Adobe RGB 16-bit colour space. We then colour-corrected (linearized and equalized; Stevens, Stoddard, & Higham, 2009) each photo using the PictoColor inCamera plugin for Adobe Photoshop CS6. To ensure reflectance equivalence among photographs, we verified that the values of the greyscale row of the colour card remained consistent in all photographs. As a measure of pelage brightness, we recorded the mean of the RGB distribution across a broad selection of the dorsal torso pelage, using the free-form selection tool in Photoshop (see Figure S3.1 in the Supporting Information).

2.3 | Bioclimatic and geographical data collection

To gather bioclimatic and geographical data for each species, we first downloaded geographical range maps for each species from the IUCN (IUCN 2017). We then used the 'sp', 'rgeos', 'rgdal', and

'raster' packages (Bivand, Keitt, & Barry, 2016; Bivand, Pebesma, & Gomez-Rubio, 2013; Bivand & Rundel, 2017; Hijmans, 2016; Pebesma & Bivand, 2005) in R version 3.4.3 (R Core Team, 2017) to extract average values over each species' range for mean annual temperature, mean temperature of the coldest quarter, annual precipitation and altitude from the WorldClim 1.4 data set at a resolution of 2.5 arc-minutes (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The raw data for temperature variables in the WorldClim data set are multiplied by 10, so we divided them by 10 before including them in our analyses. We used the same software to extract mean actual evapotranspiration (AET) across each species' range from the United Nations Global Resource Information Database (Ahn, 1994; Ahn & Tateishi, 1994). These average values across each species' range were used as bioclimatic predictors of the morphological variables. We also used the 'gCentroid' function of the 'rgeos' package (Bivand & Rundel, 2017) to extract the approximate latitude of the centroid of each species' range, which was used as a predictor of body size.

Our pelage data set contained considerably fewer samples per species than the general sources of information used to estimate other trait averages (e.g., body size data from PanTHERIA), and the specimens we used had associated locality data. Therefore, we also extracted bioclimatic predictor variables (mean annual temperature, annual precipitation, and AET) for just the specific localities of the specimens from which we collected pelage data. If museum records did not list latitude and longitude coordinates, we used the 'geo-code' function from the 'dismo' package for R version 3.4.3 (Hijmans, Phillips, Leathwick, & Elith, 2017) to find coordinates. For mean annual temperature and annual precipitation, we averaged the values within a radius of 10 km of the specimen locality; for AET, we averaged the values within a 100 km radius, due to the lower resolution of this data set. Then, we averaged the variables extracted for each species to derive a species average.

2.4 | Tests of ecogeographical rules

Bergmann's rule predicts that body size will increase with increasing latitude or elevation because temperature decreases with these variables. We tested this prediction with four different regression models, each considering a different predictor of body mass: latitude (at the centroid of the species' range), and averages over each species' range of elevation (the altitude variable from WorldClim) mean annual temperature and mean temperature of the coldest quarter (as seasonal changes may have a greater influence on morphological evolution than annual averages). Following Gloger's rule, we predicted that animals with darker pelages are found in more humid (warmer and wetter) habitats. As measures of humidity are difficult to obtain, we tested Gloger's rule considering environmental variables that are highly correlated with humidity: mean annual temperature, mean annual precipitation, and AET. We tested two models for each predictor variable: one using predictor variable data that were averaged across the species' full range, and the other using average predictor variable data from just the localities of the museum



specimens from which we measured pelage brightness. To reduce variable skewness, we log-transformed body mass, mean annual precipitation, AET, and elevation prior to analyses in R version 3.4.3 (R Core Team, 2017).

Each model consisted of a phylogenetic least squares regression (Felsenstein, 1985; Garland & Ives, 2000; Grafen, 1989) assuming a Brownian motion model of evolution with one predictor variable. To account for possible Type I error inflation due to multiple testing, we adjusted our chosen significance value of 0.05 with a Bonferroni correction (Quinn & Keough, 2002) equal to the number of predictor variables tested (four for tests of Bergmann's rule and six for tests of Gloger's rule). We conducted the analyses for the entire *Sorex* genus, just the Palaearctic clade, and just the Nearctic clade. Several *Sorex* species belong to one of the two monophyletic clades but are present in the geographical area of the other (*S. arcticus*, *S. minutissimus*, *S. camtschatica*, *S. leucogaster*, *S. portenkoi*, *S. tundrensis*, and *S. maritimensis*); these were included in their evolutionary clade, not their geographical clade. In addition, we were unable to obtain AET data for the Nearctic species *S. jacksoni* and *S. pribilofensis* due to their small ranges, so they were removed from the AET model. We performed analyses using the 'ape', 'geiger', 'phytools', and 'nlme' packages (Harmon, Weir, Brock, Glor, & Challenger, 2008; Paradis, Claude, & Strimmer, 2004; Pinheiro, Bates, DebRoy, & Sarkar, 2016; Revell, 2012) in R version 3.4.3 (R Core Team, 2017). Data sets for tests of both Bergmann's rule and Gloger's rule are provided in the Supporting Information. No permits or institutional approvals were required for any aspect of this study.

3 | RESULTS

3.1 | *Sorex* phylogenetic relationships

The MCC tree of 56 *Sorex* species strongly supported the Palaearctic and Nearctic bifurcation at the base of the *Sorex* genus (Figure 1). Within *Sorex*, 62.7% of nodes were supported with posterior probabilities of 95% or greater, and 81.4% of nodes had greater than 80% support.

3.2 | Tests of Bergmann's and Gloger's rules

Sorex shrews have body sizes that span a full order-of-magnitude (Figure 2), a wide range of pelage brightness values (Figure 3), and they inhabit diverse environments. These include very wet environments and very cold environments, although no species in our sample inhabits both wet and cold environments (Figures 2–4). Of the species included in our sample, the Olympic shrew (*S. rohweri*) of the Nearctic Pacific Northwest inhabits the wettest environment, which has a mean annual precipitation of over 2000 mm/yr. In contrast, the Inyo shrew (*S. tenellus*) lives in the overall driest range occupied by *Sorex*, at 218 mm/yr in California and Nevada. The Barren ground shrew (*S. ugyunak*) inhabits the coldest environment in northern Alaska with an average temperature of -12°C ; its range is also particularly dry at 220 mm/yr. Two shrew species of the southern

Nearctic (*S. milleri* and *S. saussurei*) inhabit the warmest ranges, with average temperatures of just over 17°C . The largest species of *Sorex* is the Marsh shrew (*S. bendirii*, 15.8 g) from the Pacific Northwest, and the smallest species is the Eurasian least shrew (*S. minutissimus*, 2.5 g), which belongs to the Palaearctic clade but has a Holarctic distribution. The darkest *Sorex* species is *S. bendirii* and the lightest is *S. tenellus* (Figures 2 and 3).

The observed variation in *Sorex* body size was not explained by centroid latitude, or averages across species' ranges of elevation, mean annual temperature, or mean temperature of the coldest quarter (Table 1; Figure 2). Of the predictor variables tested, the significance of elevation mean annual temperature, and mean temperature of the coldest quarter were dependent on the phylogenetic hypothesis used in the models for all *Sorex* and for just the Nearctic clade (Table 1). We also did not find any significant patterns relating body size to our predictor variables in either the Palaearctic or Nearctic clades when they were analysed separately.

Mean annual temperature, mean annual precipitation, and mean AET all failed to explain variation in pelage brightness across *Sorex* and in the Nearctic subclade (Table 2; Figure 3). This was the case for predictor variables averaged across species' ranges as well as for predictor variable averages from specimen localities. Tests of a relationship between annual precipitation or temperature and pelage brightness, however, were dependent on the phylogeny (Table 2).

In the Palaearctic subclade, tests using climatic data specific to measured specimen localities demonstrated significant correlations between darker pelage and both warmer temperatures and increased precipitation, as predicted by Gloger's rule. Annual precipitation had a considerably larger effect than mean annual temperature (Table 2). However, similar tests that instead incorporated climatic data averaged over each species' entire range found only non-significant trends between these variables and pelage brightness. Models testing effects of range-averaged mean annual temperature and AET were particularly dependent on assumed phylogenetic relationships.

4 | DISCUSSION

Sorex shrews are morphologically diverse and occupy geographical regions with extreme climatic conditions, but the relationship between their morphology and geography is complex and nuanced. Neither Bergmann's rule nor its reverse (smaller individuals in colder climates) was supported in any of our tests. This challenges findings of previous interspecific and intraspecific studies (the reverse of Bergmann's rule in some *Sorex* species and in Soricidae, Clauss et al., 2013; Ochocińska & Taylor, 2003; Yom-Tov & Yom-Tov, 2005; Vega et al., 2016). Only Palaearctic *Sorex* conform to the pattern predicted by Gloger's rule, and the significance of the relationships between pelage brightness and climate in Palaearctic *Sorex* is dependent on the method of climatic data compilation. *Sorex* shrews are unique among mammals in some aspects of their behaviour, physiology, and biogeography. Therefore, their morphological responses to environmental pressures may

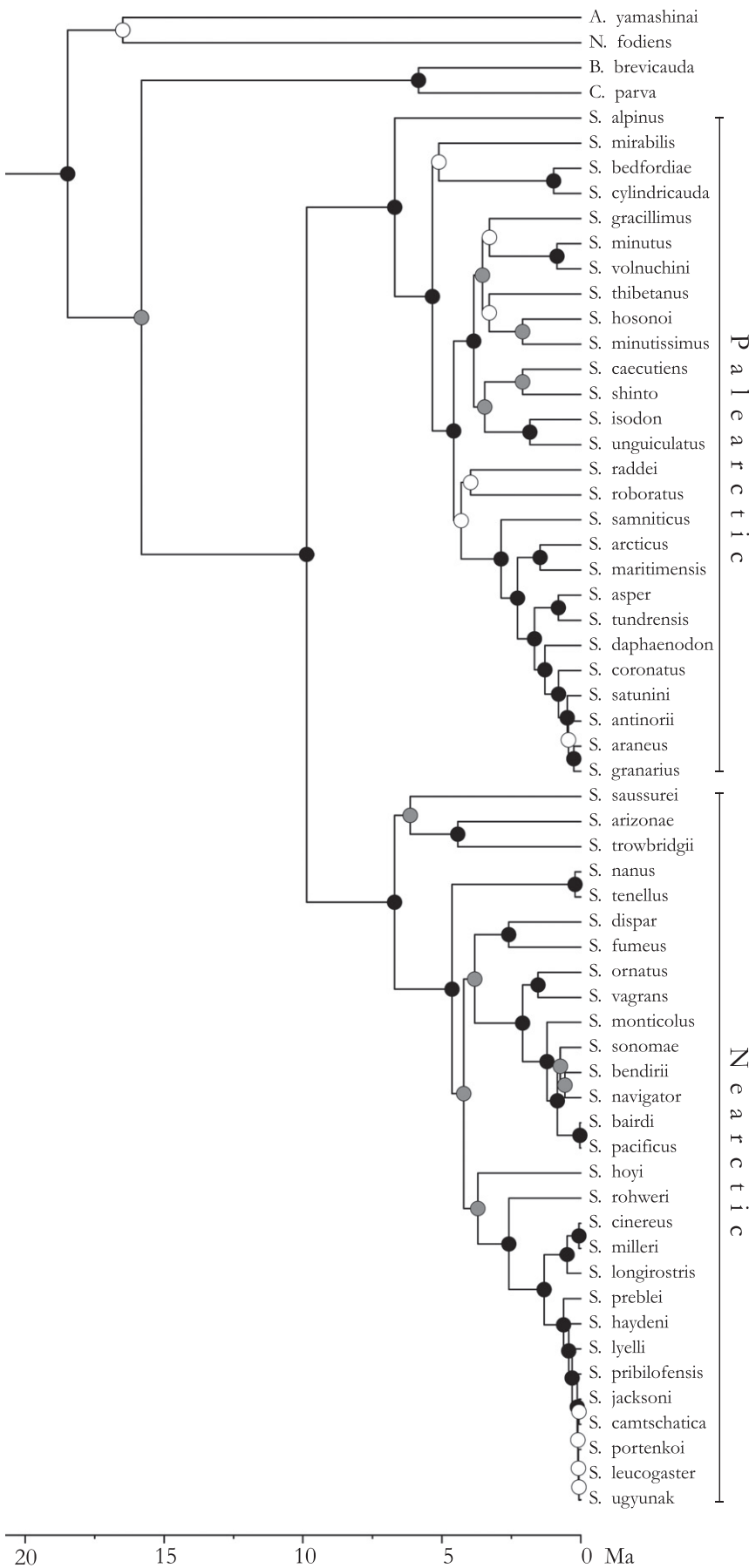


FIGURE 1 Maximum clade credibility tree from a Bayesian phylogenetic inference (BEAST 2) of *Sorex* species with Soricidae outgroups. The monophyletic Palaeartic and Nearctic sub-clades are labelled to the right of the figure. Circles on nodes indicate posterior probabilities: black indicates nodes with greater than 0.95, grey greater than or equal to 0.8, and white less than 0.8. The scale is in millions of years before present time (Ma)

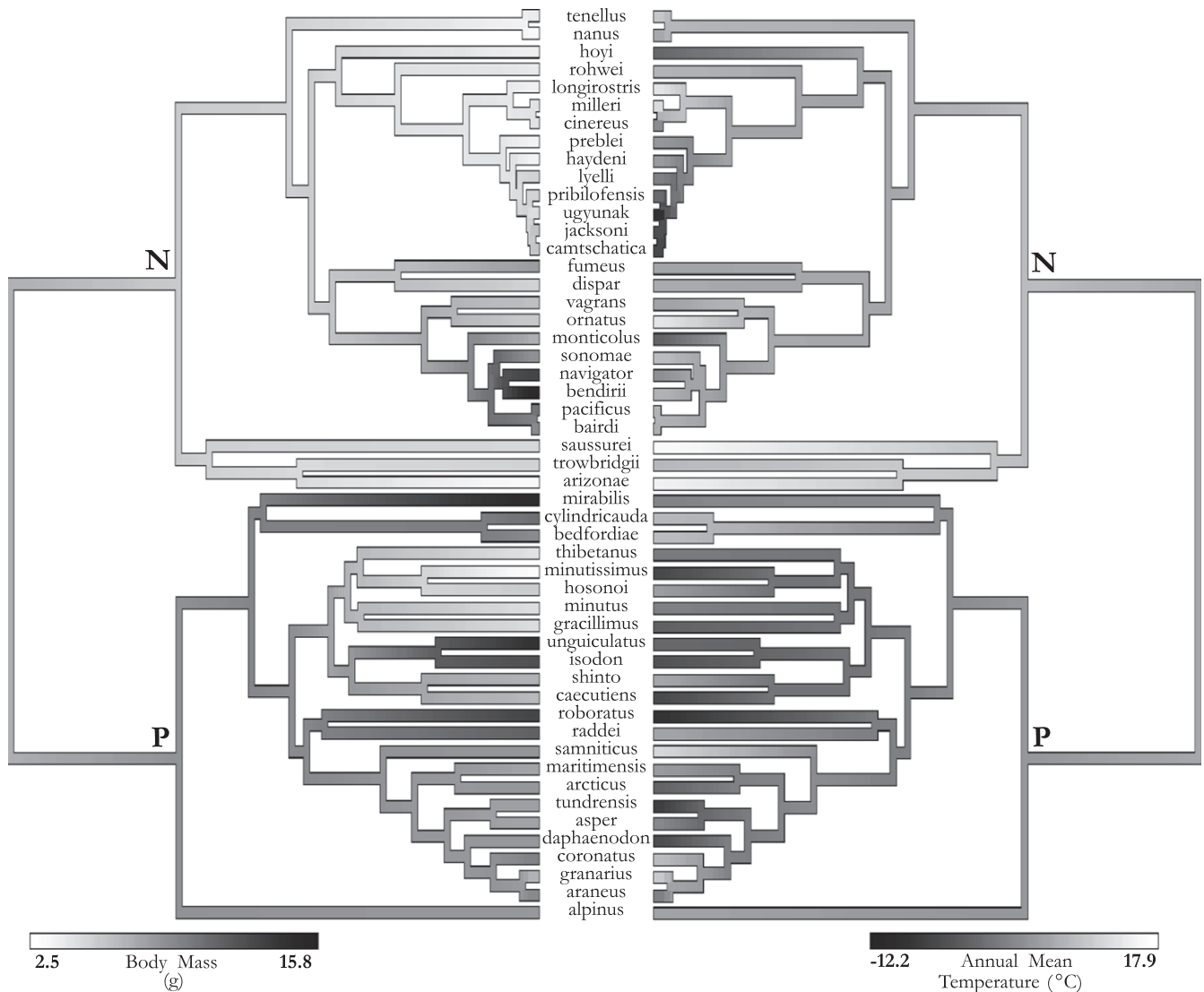


FIGURE 2 Body size (left) and mean annual temperature (right) reconstructed on the *Sorex* phylogeny using the fastML method for the ‘contMap’ function in the ‘phytools’ package (Revell, 2012) in R version 3.4.3 (R Core Team, 2017). The Nearctic clade is labelled “N,” and Palearctic clade is labelled “P.” Body mass is a species average, and mean annual temperature is the average from across each species’ range

not match those common to other clades, as suggested by these rules. Our results are compatible with previous findings that ecogeographical patterns among mammals are inconsistent.

The lack of an interspecific ecogeographical pattern in *Sorex* body size may be because these shrews have evolved other ways to adapt to cold climates. The small size of shrews—particularly their reduction in body mass in the winter—is thought to reduce energy requirements in seasonally harsh climates (Ochocińska & Taylor, 2003), and their necessary reliance on small prey due to their small size may be advantageous in cold climates, when the arthropod community is also of particularly small size (Churchfield, 2002). The winter pelage of some *Sorex* species is longer and denser than their summer pelage, and this could provide additional insulation regardless of body size (Ivanter, 1994). However, carrying a heavy coat presents additional challenges for very small mammals (e.g., it may not be possible to increase pelage density in proportion to the

temperature drop in winter or length without affecting locomotion; Stuedel, Porter, & Sher, 1994). Plasticity in morphological traits, like a seasonal reduction in body size or increase in coat density, can have a stabilizing effect on selection in the local environment of a taxon (Ghalambor, McKay, Carroll, & Reznick, 2007; Wright, 1931), which might in turn constrain adaptive evolution of body size in *Sorex*.

Furthermore, *Sorex* shrews may be adapted to cold environments through behavioural, life history and ecological strategies. Because of their territoriality, *Sorex* shrews likely do not nest with or gain heat from conspecifics (Taylor, 1998), but some species put considerable effort into making nests and may spend more time in these nests during the winter (Churchfield, 1990), when they might also be insulated by the snow pack. *Sorex* species also have larger litters than other shrew species (Taylor, 1998) and, in many species, low population densities (Churchfield, 1990). Thus, *Sorex* species

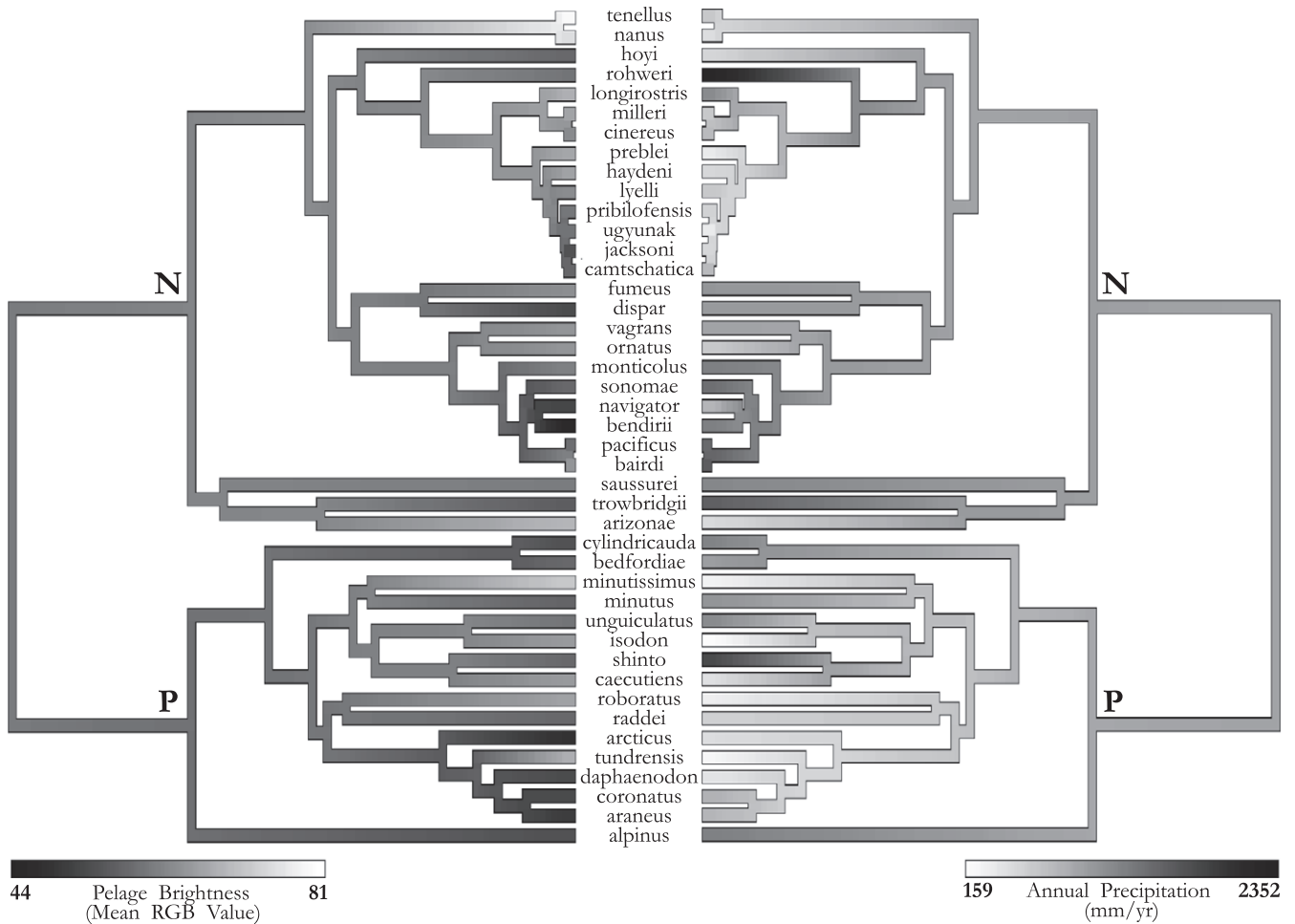


FIGURE 3 Pelage brightness (left) and annual precipitation (right) reconstructed on the *Sorex* phylogeny using the fastML method for the ‘contMap’ function in the ‘phytools’ package (Revell, 2012) in R version 3.4.3 (R Core Team, 2017). The Nearctic clade is labelled “N,” and Palearctic clade is labelled “P.” The visual grey scale range for pelage brightness is extended beyond the actual RGB measurements to emphasize differences. The actual RGB measurements are the scale labels. Lower RGB values indicate a darker pelage; the RGB measurements are averages of a sample of museum specimens for each species; annual precipitation is the species average of the annual precipitation from the measured specimen localities

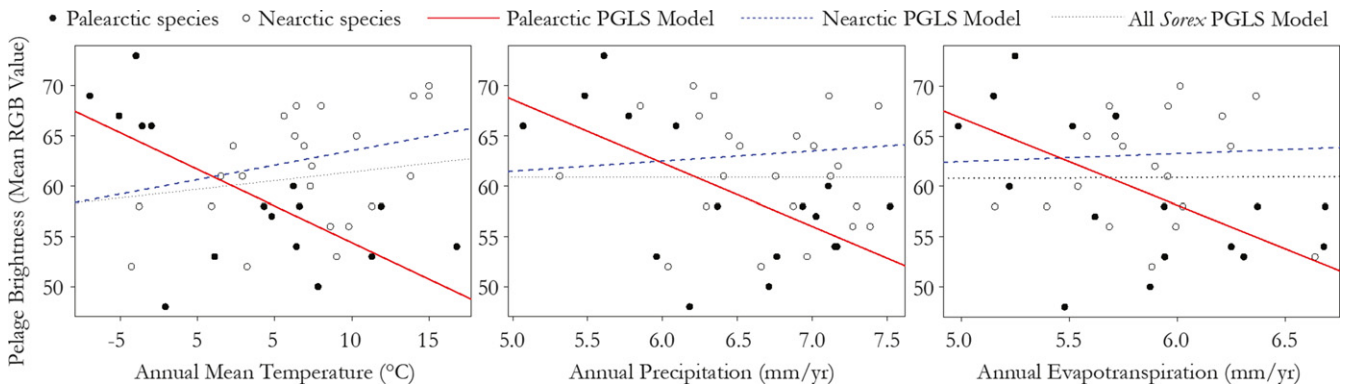


FIGURE 4 *Sorex* pelage brightness values plotted against mean annual temperature, annual precipitation, and actual evapotranspiration, demonstrating differing patterns in Palearctic and Nearctic clades. The RGB measurements are averages from a sample of museum specimens for each species; climatic variables for each species are averages of values extracted for the specific localities of the measured museum specimens. Regression lines are plotted using the coefficients of the corresponding PGLS models

TABLE 1 Results from PGLS models testing Bergmann's rule across the *Sorex* genus, Palearctic *Sorex* species, and Nearctic *Sorex* species. The response variable in all models is body mass. Results are shown for tests incorporating the MCC tree. Statistical significance for the MCC tree is considered at $\alpha \leq 0.0125$ due to Bonferroni correction. The “%” column is the percentage of the hypothesis tests against the 3,500 trees in the posterior distribution that had p -values > 0.05

Predictor	Value	SE	p -value	%
All <i>Sorex</i>				
Latitude	0.000	0.003	0.989	93%
Elevation	-0.033	0.034	0.332	65%
Mean Annual Temperature	0.001	0.004	0.748	73%
Mean Temperature of Coldest Quarter	0.002	0.003	0.563	67%
Palearctic <i>Sorex</i>				
Latitude	0.007	0.006	0.230	97%
Elevation	-0.089	0.091	0.335	98%
Mean Annual Temperature	-0.011	0.008	0.206	96%
Mean Temperature of Coldest Quarter	-0.007	0.005	0.159	93%
Nearctic <i>Sorex</i>				
Latitude	-0.001	0.004	0.780	95%
Elevation	-0.029	0.043	0.507	75%
Mean Annual Temperature	0.004	0.006	0.557	76%
Mean Temperature of Coldest Quarter	0.003	0.004	0.376	69%

may persist in harsh climates through classic r -selection (Pianka, 1970). *Sorex* communities are relatively species-diverse, and niche-partitioning is often size-related (Churchfield, Nesterenko, & Shvarts, 1999; Churchfield & Sheftel, 1994), so size evolution may be constrained by the available niche space within the community. Notably, *Sorex* body temperatures can cause hyperthermia in high ambient temperature (Sparti & Genoud, 1989), so *Sorex* may not be adapted to colder environments as much as they are excluded from warmer environments.

Gloger's rule has been subjected to fewer rigorous tests in mammals than Bergmann's rule. Similar to the results in this study, assessments of Gloger's rule across mammal species have reported conflicting results. Artiodactyls (Stoner, Caro, & Graham, 2003), some carnivorans (Ortolani & Caro, 1996), and primates (Kamilar & Bradley, 2011; Santana, Alfaro, Noonan, & Alfaro, 2013; Santana, Lynch Alfaro, & Alfaro, 2012) have been found to conform to Gloger's rule, while other carnivoran clades (Ortolani & Caro, 1996) and lagomorphs (Stoner, Bininda-Emonds, & Caro, 2003) have not. Gloger's rule has been poorly studied in small mammals, but pelage brightness has been found to significantly decrease with increasing rainfall within *Mus musculus*, as would be predicted by Gloger's rule (Lai, Shi-roishi, Mori-waki, Motokawa, & Yu, 2008). We found significant support for Gloger's rule in the Palearctic *Sorex* clade, but not in the Nearctic clade. Some Nearctic species that live in climatic extremes also seem to match the expectations of Gloger's rule (e.g., the light-

TABLE 2 Results from PGLS models testing Gloger's rule across the *Sorex* genus, Palearctic *Sorex* species, and Nearctic *Sorex* species. The response variable in all models is mean RGB value across the dorsal pelage. Results are shown for tests incorporating the MCC tree. Statistical significance for the MCC tree tests is considered at $\alpha \leq 0.0083$ due to Bonferroni correction. The Actual Evapotranspiration (AET) models contain two fewer Nearctic species because their ranges are too small to calculate AET from our data set. The “%” column is the percentage of the hypothesis tests against the 3,500 trees in the posterior distribution that had p -values > 0.05

Predictor	Value	SE	p -value	%
All <i>Sorex</i>				
Mean Annual Temperature (range)	0.199	0.150	0.192	75%
Mean Annual Temperature (localities)	0.172	0.225	0.450	78%
Annual Precipitation (range)	-0.653	2.877	0.822	64%
Annual Precipitation (localities)	-0.007	2.177	0.998	62%
Actual Evapotranspiration (range)	2.298	3.311	0.492	91%
Actual Evapotranspiration (localities)	0.108	2.551	0.966	98%
Palearctic <i>Sorex</i>				
Mean Annual Temperature (range)	-0.525	0.248	0.052	56%
Mean Annual Temperature (localities)	-0.728	0.212	0.004*	0%
Annual Precipitation (range)	-7.915	3.992	0.067	97%
Annual Precipitation (localities)	-6.304	1.860	0.004*	0%
Actual Evapotranspiration (range)	-9.391	4.359	0.049	46%
Actual Evapotranspiration (localities)	-8.665	3.523	0.028	1%
Nearctic <i>Sorex</i>				
Mean Annual Temperature (range)	0.240	0.189	0.218	81%
Mean Annual Temperature (localities)	0.287	0.293	0.336	83%
Annual Precipitation (range)	-0.064	3.710	0.986	73%
Annual Precipitation (localities)	1.011	2.902	0.731	71%
Actual Evapotranspiration (range)	3.442	4.315	0.433	93%
Actual Evapotranspiration (localities)	0.809	3.319	0.810	99%

coloured *S. tenellus* in a dry climate and the dark-coloured *S. bendirii* in a wet climate); however, the phylogenetic models do not indicate that this correspondence occurs more than would be expected due to chance or phylogenetic similarity.

What are potential causes of the observed differences in pelage brightness trends between the Palearctic and the Nearctic clades? *Sorex* shrews inhabit a broad range of climates, and the different geographical distributions of the two clades might provide clues to the processes that led to their diversification. It has been suggested that Pleistocene glacial cycling led to taxonomic and ecological diversification within the Nearctic *S. cinereus* species complex, including

the evolution of xeric- and mesic-adapted clades (Hope, Speer, Demboski, Talbot, & Cook, 2012). It is possible that Pliocene–Pleistocene geologic events impacted the ecological diversification of other clades within the *Sorex* lineage. For instance, differences in Pleistocene glacial extents between the Palaearctic and Nearctic (Hewitt, 2000) might have created different selective pressures and thus differentially influenced morphological diversification of the two *Sorex* clades. As the geographical histories of the Palaearctic and Nearctic clades further diverged, they likely continued to face different evolutionary pressures (e.g., different climatic gradients), which could have ultimately led to their distinct their ecogeographical patterns. Because of their diverse geographical and geological histories, Holarctic taxa are particularly useful for understanding the impact of environmental change on evolutionary processes and their resulting phenotypic variation (Bernatchez & Wilson, 1998). *Sorex* may be a useful taxon for further investigating impacts of climatic change on diversification.

The analyses and results presented here demonstrate the difficulties inherent in testing ecogeographical rules at the interspecific level. For example, a conservative bias against the predicted pattern can arise from averaging variables across the entire range of a species (Blackburn & Hawkins, 2004). Our results exposed this bias in the tests of Gloger's rule in the Palaearctic *Sorex* that used either averaged or locality-specific climatic data. To counter this effect, some studies have used a spatial approach (i.e., each data point represents the mean body mass of all taxa that inhabit a square of a geographical grid) and tested ecogeographical patterns in assemblages rather than lineages (Gaston, Chown, & Evans, 2008). This assemblage approach was used by previous studies that found a general pattern that Holarctic mammals follow Bergmann's rule (Blackburn & Hawkins, 2004; Rodríguez et al., 2006, 2008). However, models that employ an assemblage approach do not consider phylogenetic relationships, which are necessary for direct testing of hypotheses of adaptive evolution in response to environmental variation. This is critical because the suggested mechanisms that underlie ecogeographical rules are framed as morphological adaptations that allow individuals to persist in their climatic conditions.

In addition, testing patterns across a wide range of taxa can elide biologically relevant complexity. For instance, there is some support for Bergmann's rule in Mammalia across broad spatial extents in North America (Blackburn & Hawkins, 2004; Rodríguez et al., 2008), but (1) mammal species diversity decreases as latitude increases, and (2) the increase in average mammal size at higher latitude seems to be largely a result of fewer species (and only a small number of larger species; e.g., figure 2 in Rodríguez et al., 2008). Importantly, the mammalian latitudinal diversity gradient is highly influenced by bats (Buckley et al., 2010; Wilson, 1974), which are generally small mammals. Therefore, an overall increase in average mammalian body mass at high latitudes or in cold climates may say more about clade-specific biological constraints of small mammals to living in colder climates (e.g., the energetic constraints of flight in bats), and little about whether or not the body size of taxa living in

high latitudes increased adaptively in response to climatic conditions. The results presented here illustrate the usefulness of clade-focused, comparative approaches to understand ecomorphology, adaptive evolution, and ecogeography.

The typical interspecific studies of correlations between morphological and ecological evolution could be greatly improved by instead constructing phylogenetic regression models in which each tip is an individual, not a clade, within a sample that spans multiple species. This approach would solve the problem of averaging data (often from multiple sources) across the entire range of a species and would simultaneously test intra- and interspecific correlations. Voucher specimens from existing museum collections that document the full geographical extent of a species would be of critical importance in this type of study. We suggest that *Sorex* would be an ideal clade for this type of analysis, which could be compared with the results presented here and with previous intraspecific studies (Ochocińska & Taylor, 2003; Vega et al., 2016; Yom-Tov & Yom-Tov, 2005).


Sorex shrews continue to be an enigmatic, surprisingly diverse group of mammals. Despite their reputation for morphological homogeneity, they vary considerably in body size and pelage brightness and reach extremes in these traits and in their climatic conditions. We find that climatic conditions partly explain the pelage brightness diversity in *Sorex* shrews, but only within the Palaearctic clade and when the climatic data are sourced from the specimen localities. The wide variance and seasonal plasticity in *Sorex* morphological traits, and their unique physiological, life history, and ecological characteristics make these mammals an interesting focal taxon for future mechanistic investigations of the relationships between biogeography and adaptive evolution of morphological traits.

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