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Article

Niche theory and its relation to morphology and phenotype in geographic space: a case study in woodpeckers (Picidae)

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Ecogeographic analyses have recovered common environmental trends with respect to morphology; however discrepancies among trends exist. Hypothesized reasons for these divergences vary, but most relate a taxon's morphology to its ecological niche. Morphology is known to diverge when species co-occur with competitors or predators and when species occur across different habitats and environments. A less understood divergence from ecogeographic trends is niche fixation, wherein species become locked into particular niches due to their community interactions or foraging ecology. A form of niche fixation has been hypothesized in the theory of interspecific social dominance mimicry (ISDM), in which mimics maintain relatively constant size ratios with models to perpetuate their mimicry. If true, mimics should display variation and trends in tandem with their models. Here, I use mass as a proxy for body size and examine ecogeographic trends in two sets of woodpeckers (Picidae): a Nearctic group which has been reported to interact via ISDM, and a Neotropical group which, based on similar appearances and overlapping distributions, is a potential ISDM system. I found ecogeographic trends suggestive of differential evolutionary responses, and I found evidence against niche fixation in the Nearctic clade. The Neotropical clade showed limited evidence for tandem size evolution between models and mimics, but inconsistencies in the size ratios between mimic and model populations. Here, I discuss the implications of observing divergent ecogeographic trends within mimicry systems, with specific emphasis on how environment, ecology, and community interactions guide evolution.

Keywords: Bergmann's rule, ecological niche theory, interspecific social dominance mimicry

Introduction

Three definitions of niche are broadly used to define species' interactions, ecologies, and spatial distributions: the Grinnellian niche (Grinnell 1917), where a taxon's distribution is limited to a suite of environments and habitats to which it is best suited morphologically and behaviorally; the Eltonian niche (Elton 1927), where a taxon's distribution depends heavily upon access to resources and related interactions with syntopic (i.e. co-occurring) taxa over resources; and the Hutchinsonian niche



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(Hutchinson 1957), where n number of biotic and abiotic variables are represented as n axes and a taxon's distribution is the spatial area corresponding to a hypervolume of suitable conditions on these axes. While all of these perspectives provide overlapping views, each offers its own specific insights on factors that may limit or constrain species ecologically. Of these definitions, the Hutchinsonian niche is the one most often presented as a broad definition for determining species' distributions and is often used to create 'scenopoetic' environmentally trained ecological niche models (Soberón and Peterson 2005, Soberón and Nakamura 2009, Peterson et al. 2011). Given that both amensal (i.e. antagonistic) and commensal (i.e. benefiting from co-occurrence) relationships can be hypothesized by a taxon's absence/presence in areas suitable for other taxa, spatial projections of the Hutchinsonian niche are often regarded as projections of the Grinnellian niche as well, and thus are considered a representation of the environments and the habitats that are suitable for a species (Soberón 2007, 2010, Peterson et al. 2011, Anderson 2017).

While such models of environment and basic land cover are sufficient for describing the basic ecological and spatial trends of species, their usefulness for describing biotic interactions is still debated. Some biotic interactions may not be informative for estimating distributions when assessed over broad geographic extents; conversely, these same interactions may be integral to a species' local occupancy and be predictive of occurrence over smaller spatial extents (i.e. the Eltonian noise hypothesis sensu Soberón and Nakamura 2009). Several recent studies have shown improvements in distribution models using explicit biological variables, demonstrating that distribution estimates can be improved by including data for co-occurring species or habitat information (Araújo and Luoto 2007, Heikkinen et al. 2007, Araújo et al. 2014, Cord et al. 2014, Atauchi and Peterson 2018). These models deal explicitly with the spatial correlation between a study taxon and different species or habitats, thereby addressing species' interactions at individual localities (Elton 1927, Vandermeer 1972, Soberón 2007). Using niche modeling techniques, commensal co-occurrence is detectable, but other ecogeographic interspecies interactions can be difficult to assess. One example of an important interspecies relationship that might affect a species' niche and is difficult to include in spatial models is mimicry. Multiple types of mimicry exist in nature, with two predominant categories: Batesian mimicry, where a taxon mimics one or more 'avoided' (i.e. aggressive, toxic, etc.) taxa to discourage depredation and/or aggression on itself despite lacking the properties discouraging amensal interactions (Bates 1861); and Müllerian mimicry, where multiple taxa with similar adaptations discouraging depredation and/or aggression evolve similar phenotypes (Müller 1879).

Woodpeckers (Aves: Picidae) appear to contain multiple recurrences of Batesian mimicry in the form of interspecies social dominance mimicry (ISDM). In these cases, a mimic is hypothesized to have evolved to copy the phenotype of a more aggressive co-occurring model species to facilitate

foraging while minimizing antagonistic interactions either with the model species or with the model species and third party observers (Wallace 1863, Diamond 1982, Prum and Samuelson 2012). Recent work has argued that ISDM systems are widespread in birds (Prum 2014), and that ISDM systems can have more than one sympatric mimic converging on the phenotype of a larger, more aggressive taxon (Benz et al. 2015). Preliminary analysis of mass within ISDM complexes has revealed a trending of mimics to be ca 55–60% of the mass of their models (Prum 2014). This indicates that selection on morphology may be concurrent with selection on phenotype, leading to the hypothesis that maintaining specific size ratios is imperative for maintaining mimicry dynamics (Prum 2014). The relationship is suggestive of an interlocked Eltonian niche dynamic that may lead to fixation in a species' niche, possibly for both the mimic and the model, with respect to maintaining a specific size ratio.

Spatial recovery of an Eltonian interaction is not new: previous studies have demonstrated character clines across contact zones in complexes that exhibit spatially localized sympatry (McNab 1971, Fjeldså 1983, Robinson and Wilson 1994, Kirschel et al. 2009, Grant 2013). These studies focus heavily on character displacement, and demonstrate that taxa diverge in specific character traits to reduce competition in sympatry. These systems, however, are not mediated by mimicry. ISDM systems are different in that competition leads to phenotypes and morphologies that allow syntopy. Even if species partition available resources from the outset, there appears to be an inherent benefit in converging on a dominant competitor's phenotype at a specific size ratio (Prum 2014). Thus, the difference in size between taxa may not be the maintenance of independently derived niches in the Grinnellian sense, but a novel Eltonian relationship reducing competition for non-dominant species.

ISDM systems represent opportunities to view the ecological niches of sympatric taxa while correcting for spatial trends. While a thorough ecogeographic study of *Picoides* sensu lato exists, it is scenopoetic in nature, and focuses on the relationships between observed morphological variation and known climatic conditions (James 1970). Re-examining these systems within an ISDM framework allows a restructuring of the questions, to ask if the response of the mimic conforms to the same environmental trends as the model or varies from the expectation under ISDM theory, thus revealing that other ecological needs may be mediating size through space. For example, if a species (mimic or model) maintains a similar size across all environments and habitats, it is possible that there is significant Grinnellian selection to maintain a morphology that is suited to a certain foraging behavior or habitat. Similarly, if a species' morphology varies greatly with respect to environment across space, we can deduce that this is a response to Hutchinsonian factors, and that certain morphological trends may exist to increase survival in local climates (Bergmann 1847, James 1970). Lastly, while we may not possess the capacity to discern interspecific

interactions according to the Eltonian niche for a model species, we should be able to determine whether mimic species are 'fixed' in a particular Eltonian relationship based on how closely they maintain a specific size ratio with their presumed model over geographic space. A well-defined Eltonian niche in this sense would erase evidence of other evolutionary drivers on the mimic due to high correlation with the geographic trends observed within the model taxa. The broad distributions of woodpeckers enable the close examination of these trends, as many mimics co-occur with their models across a wide range of environments and habitats, allowing for trends to be dominated by any of the three ecological niche definitions.

Here, I compare two sets of ISDM woodpecker complexes to study these potential relationships, using mass as a proxy for overall body size. The first complex is restricted to the Nearctic, and consists of two phenotypically near identical, but distantly related, black-and-white woodpeckers formerly placed in *Picoides*: downy woodpecker *Dryobates pubescens* and hairy woodpecker *Leuconotopicus villosus* (Weibel and Moore 2002, 2005, Prum and Samuelson 2012, Prum 2014, Fuchs and Pons 2015, Shakya et al. 2017, Gill and Donsker 2018). These species are broadly sympatric across North America, from Alaska to far northwestern Mexico and Florida. Allopatric populations of the larger model taxon *L. villosus* exist in areas that lack *D. pubescens* from Mexico southwards through Panama (Jackson et al. 2002). The two species exhibit geographic variation in relation to overall size and mass, with documented trends associated with climate in *D. pubescens* (James 1970) and with southernmost *L. villosus* populations being smaller than northern populations (Jackson et al. 2002). *Dryobates pubescens* and *L. villosus* differ from each other with respect to foraging ecology, with *L. villosus* preferring larger branches and trunks than the smaller *D. pubescens* (Jackson and Ouellet 2002, Jackson et al. 2002). The foraging ecology of *D. pubescens* is similar to closely related taxa, but it differs from these species with respect to environment and habitat (Lowther 2000, 2001, Jackson and Ouellet 2002). *Leuconotopicus villosus* exhibits microhabitat preference for larger trunks and limbs throughout its North American range (Jackson et al. 2002) and it appears to excavate more than its close relative, Arizona woodpecker *L. arizonae* (Johnson et al. 1999).

The second ISDM system is restricted to the Neotropics, and contains multiple geographically overlapping black-and-white woodpeckers of the genera *Campephilus*, *Celeus*, and *Dryocopus* (del Hoyo et al. 2014, Prum 2014, Benz et al. 2015). Specifically, multiple species of large *Campephilus* woodpeckers all co-occur with smaller, similarly-patterned lineated woodpecker *Dryocopus lineatus* populations (del Hoyo et al. 2014). In southeastern Brazil, populations of cream-backed woodpecker *Campephilus leucopogon* and *Dryocopus lineatus* co-occur with another small black-and-white woodpecker that appears to be part of this mimicry dynamic as well. This species, the helmeted

woodpecker *Celeus galeatus*, is so similar in plumage to the previous two species that it was erroneously believed to be in the genus *Dryocopus* until recently (Benz et al. 2015). Phenotypic variation within *Dryocopus lineatus* appears to parallel larger sympatric *Campephilus* (del Hoyo et al. 2014, Prum 2014, Benz et al. 2015), and gives credence to the notion that phenotype is controlled by an Eltonian relationship. *Campephilus* woodpeckers vary in mass, and similar phenotypes are parapatric (i.e. minimally overlapping and replacing each other) in distribution, creating a mosaic of different models for the mimic species to copy. While we do not have nearly as much data relating to foraging ecology for large Neotropical woodpeckers as for *Picoides sensu lato*, the available information suggests that most *Campephilus* and *Dryocopus* forage in a similar manner, taking advantage of insects from the surface to fairly deep within the trunks of trees (Allen and Kellogg 1937, Skutch 1969, Short 1970, Kilham 1972, Winkler and Christie 2002, Malekan 2011). Given the paucity of data regarding most of these large Neotropical woodpeckers, I have focused on two of the most widely sampled *Campephilus* (pale-billed woodpecker *C. guatemalensis* of North and Central America and crimson-crested woodpecker *C. melanoleucos* of Panama and eastern South America) and their widespread presumed mimic, *Dryocopus lineatus* (which occurs from northern Mexico to Argentina). I have excluded other similarly plumaged *Campephilus* models and potential *Celeus* and *Dryocopus* mimics that are less well represented in museum collections, notably: powerful woodpecker *Campephilus pollens* (Andes Mountains); robust woodpecker *Campephilus robustus* (southern Brazil and adjacent Paraguay and Argentina); Guayaquil woodpecker *Campephilus guayaquilensis* (western Colombia, Ecuador, and Peru); *Campephilus leucopogon* (Bolivia, Paraguay, and Argentina); *Celeus galeatus* (southern Brazil and adjacent Paraguay and Argentina); and black-backed woodpecker *Dryocopus schulzi* (Bolivia, Paraguay, and Argentina).

If mimics are morphologically locked in an Eltonian niche with respect to their sympatric model taxa, then geographic trends of mimic mass should follow those of their models. While this correlation could also exist from similar Hutchinsonian dynamics, the magnitude of the ecogeographic trends can be assessed to see if it fits the predictions of Prum (2014). Different data trajectories between the taxa, however, will allow us to hypothesize what aspects of niche biology are affecting species' masses. If taxa are constrained by foraging ecology, their masses should be relatively constant due to ecological constraints on their foraging behavior and therefore weakly correlated to their environment. Conversely, if models are responding mostly to scenopoetic (Hutchinsonian) factors, then mass should significantly track environmental conditions. Using this framework, we can distill whether morphological character fixation is occurring within ISDM complexes, and we can begin to understand other aspects of niche dynamics with respect to basic community interactions.

Material and methods

Data were mined online and, after minimal reformatting, entered into a workflow for processing and analyzing these data in R that is available via the Dryad repository. As elucidated below, this pipeline takes the downloaded mass data and reduces the data by removing significant outliers, juvenile birds, etc. before combining it with data extracted from environmental data rasters and clustering points by biogeographic region. The code subsets and analyses both the Nearctic and Neotropical datasets, includes everything necessary to perform all statistical analyses, and includes the code to recreate every figure with the exception of Fig. 1.

Georeferenced mass data were downloaded directly from VertNet (a database of vouchered biodiversity records and their associated metadata, <www.vertnet.org>; Supplementary material Appendix 1) on 17 November, 2016. Data were parsed to include only the relevant study taxa that possessed greater than ten georeferenced occurrences with recorded mass (i.e. specimen records with coordinates and mass information available; Supplementary material Appendix 1–2). These data were imported into R 3.4.4 (R Core Team) and manipulated with the packages

ggplot2 (Wickham 2009), maptools (Bivand and Lewin-Koh 2017), raster (Hijmans 2017), and rgdal (Bivand et al. 2017). Given the numerous outliers that existed in the mass dataset, all species were restricted to non-juvenile birds with masses within two standard deviations of the mean for that species. This procedure clipped extreme outliers, while preserving the tails of the distribution where true morphological variation may be represented. Thus, all specimens < 10 g and all *Dryobates pubescens* > 40 g were removed from the dataset. Specimens under < 10 g were removed to ensure that no juvenile or immature birds were included, while the 40 g threshold was enforced for *D. pubescens* as this is larger than any known populations and indicative of probable identification or weighing error in the collections (Jackson and Ouellet 2002). One additional record (KU95783) was removed as it was the only record from its geographic area and physiologically appears to be a fledgling (heavy molt, smooth ovary, unossified skull, collected 22 May 2003), despite being > 10 g and not being labeled as a juvenile within the database. 81.8% of records had a posted coordinate uncertainty, with an average uncertainty of 8.2 km. Points with uncertainties of greater than 25 km were removed from the dataset to limit the effects of potentially inaccurate coordinates; this step

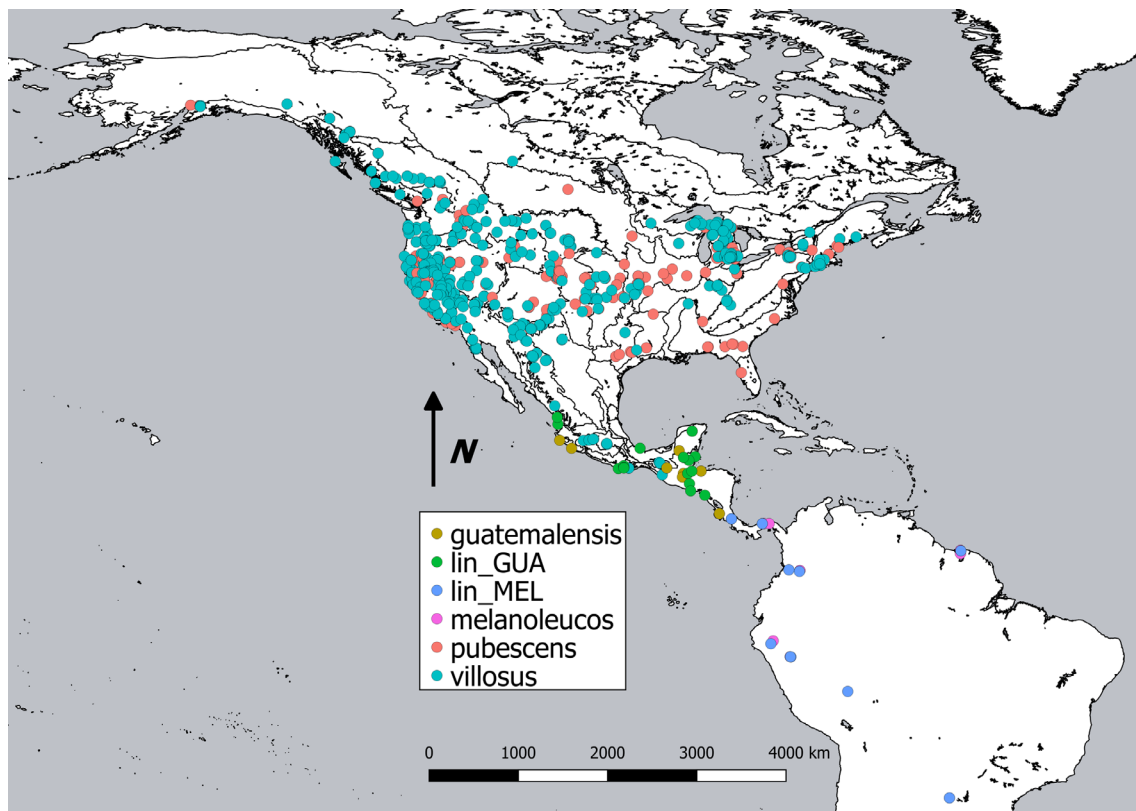


Figure 1. A map of georeferenced specimen records that were used in this study for *Campephilus guatemalensis*, *C. melanoleucos*, *Dryocopus lineatus*, *Dryobates pubescens*, and *Leuconotopicus villosus*. The annotations of 'lin-GUA' and 'lin-MEL' correspond to populations of *D. lineatus* that are sympatric with *C. guatemalensis* and *C. melanoleucos*, respectively. Polygons overlaid on North America are Bird Conservation Region boundaries (Bird Studies Canada and NABCI 2014). Map created using data layers from NaturalEarthData.com and QGIS 2.8.6 (QGIS Development Team 2018).

affected only *Dryobates pubescens* and *Leuconotopicus villosus*, and reduced the number of points used for each by 15 and 34 points, respectively.

Climatic data for these species were drawn from five datasets of two factors from the WORLDCLIM 1.4 database (Hijmans et al. 2005) that have been shown to affect bird distributions in North America (Root 1988): average temperature of the warmest quarter, average temperature of the coldest quarter, average rainfall in the driest quarter, average rainfall in the wettest quarter, and cumulative precipitation. The WORLDCLIM 1.4 data covers the time period of 1960–1990, which temporally encompasses 23% of the specimen data used explicitly (whereas the WORLDCLIM 2.0 database temporally includes only 11% of all specimen data). A total of 81% of the records come from 1990 or earlier. While morphological changes in populations have been documented within time periods as short as 30 yr (Brown and Brown 2013), I evaluated all records with the WORLDCLIM 1.4 dataset as insufficient data exist to determine if localized mass evolution is occurring in these woodpeckers as the climate warms. The WORLDCLIM 1.4 data exists in a 2.5 arcminute grid, which is 4.6 km at the equator, compared to the average spatial uncertainty of specimen records of 8.2 km. Such spatial inaccuracies may affect the extraction of environmental data for the localities, but these effects were considered minimal due to the spatial corrections that were employed and due to the broad distributions of the species studied in depth (del Hoyo et al. 2014).

Specimen records that possessed 'NA' values for climate factors (i.e. records from outside the extent of the environmental data rasters) were removed from the analysis. In addition to these layers, another layer of 'environmental variation' was created by means of principal components analysis (PCA; Jolliffe 2002) of climatic conditions at occurrence localities using the built-in R function 'princomp' (R Core Team). Analyses were made with PC1 (which explained 57.5% of the variance, mostly driven by the annual precipitation and precipitation of the wettest quarter) and PC2 (which explained 22.4% of the variance, mostly driven by the mean temperature of the warmest quarter).

Nearctic woodpeckers were overlaid on the Bird Conservation Region (BCR; Bird Studies Canada and NABCI 2014, Fig. 1) shapefile to aggregate records by ecologically similar areas. This dataset includes 66 expert-defined ecological regions that are inclusive of regional bird communities in similar habitats. Ecoregions are numbered from northwest to southeast and cover the entirety of the Canada, the United States, and Mexico. As this region is inclusive of the study area for *Dryobates pubescens* and *Leuconotopicus villosus*, all records that fell outside of defined BCR regions were removed from the analysis. Overviews of these data revealed that most United States records affected by this step were in the pelagic zone of the Great Lakes, likely representing erroneous coordinates or coordinates that appear pelagic due to a lack of precision and/or accuracy. This procedure also excluded populations of *L. villosus* from the Bahamas and from Guatemala

southwards; these exclusions do not affect the comparisons as none of these populations are sympatric with *D. pubescens*, and therefore exist in different picid communities. Data that remained for these species were concentrated in the western and central United States; there was little data from eastern North America away from New England and Michigan, especially for *L. villosus* (Fig. 1). The reasons for this regional bias are complex, but include a lack of georeferencing and mass data for older specimens and individual collections' data sharing policies (some museums do not share data or only serve partial datasets online that may exclude coordinates or mass).

Neotropical species' ranges were estimated using generic kernels limited by major biogeographic regions around the species' known distributions following the methods of Cooper and Soberón (2018). These estimates were intentionally made broader than range maps available online to account for potential regions of dispersal within the mimic and model taxa (Ridgely et al. 2007). These dispersal areas were 'clipped' to major biogeographic barriers (i.e. mountains, rivers, etc.) or placed a significant distance (e.g. 100 km) from known occurrences in homogeneous terrain. Points of each species were then overlaid on the map to determine which populations are sympatric, with these points used for mass comparisons. Any points outside of this kernel – whether of the model or the mimic – were ignored to ensure the study was focusing on a concise geographic area of known occurrence and to avoid potentially misidentified or mislabeled specimens. *Dryocopus lineatus* records were separated into two populations, those sympatric with *Campephilus guatemalensis* (i.e. northern) and those sympatric with *C. melanoleucos* (i.e. southern), for geographically-corrected comparisons of mass.

After data cleaning, 1241 georeferenced specimen records with mass remained, specifically: 27 *Campephilus guatemalensis*, 13 *Campephilus melanoleucos*, 457 *Dryobates pubescens*, 31 *Dryocopus lineatus* (northern), 14 *Dryocopus lineatus* (southern), and 699 *Leuconotopicus villosus* (Supplementary material Appendix 1). Sufficient data existed for the Nearctic dataset for an analysis of covariance (ANCOVA; Dalgaard 2008) and linear model (LM) analyses to be performed with respect to environmental variables. While residuals were left-skewed, ANCOVA can be robust to some violations of non-normality (Moore and McCabe 2003). Given the paucity of data from most of the Neotropical system, adjacent populations were compared using Wilcoxon tests (Dalgaard 2008) and boxplots, with regressions performed only on latitude (based on the importance of this variable for Nearctic species). I also performed LM models of these species to determine if any trends were apparent with the available data. I directly compared all regression slopes using Welch's *t*-tests (Dalgaard 2008). Values are presented with a confidence interval of ± 2 standard errors.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.d6d5011>> (Cooper 2018).

Results

Analysis of Nearctic woodpeckers

Geographic comparisons of the Nearctic black-and-white woodpeckers that account for habitat, latitudinal trends, and climatic correlates revealed that mass of *D. pubescens* and *L. villosus* vary with Bird Conservation Region (BCR), but *D. pubescens* is always smaller than its model, *L. villosus* (Wilcoxon rank sum test, $W=28.5$, $p < 0.005$, mimic/model ratio = 0.39; Fig. 2). Regressions of average mass per BCR confirm that mass of *D. pubescens* increases as mass in *L. villosus* increases ($R^2=0.46$). The slope of this relationship (i.e. the slope of mimic/model ratios in multiple populations

of *Dryobates* and *Leuconotopicus*; 0.18 ± 0.08) rejects the hypothesis of trending in tandem that would be expected for these species given the reported slope of the mimic/model ratios (0.56 ± 0.04) for ISDM complexes suggested by Prum (2014) (Welch's t -test, $t=-8.52$, $df=29.56$, $p < 0.05$; Fig. 3). An analysis of covariance determined that both species increase in mass as latitude increases, but the two species possess distinct slopes with respect to latitude ($F_{(2,1153)}=8138$, $p < 0.005$). The relationships, while correlated, are operating independently (Fig. 4). Regression equations calculated for the data revealed that both latitude and the mean temperature of the coldest quarter explained much of the variance within the data for *L. villosus* only, with latitude (*D. pubescens*: $R^2=0.07$; *L. villosus*: $R^2=0.58$) performing

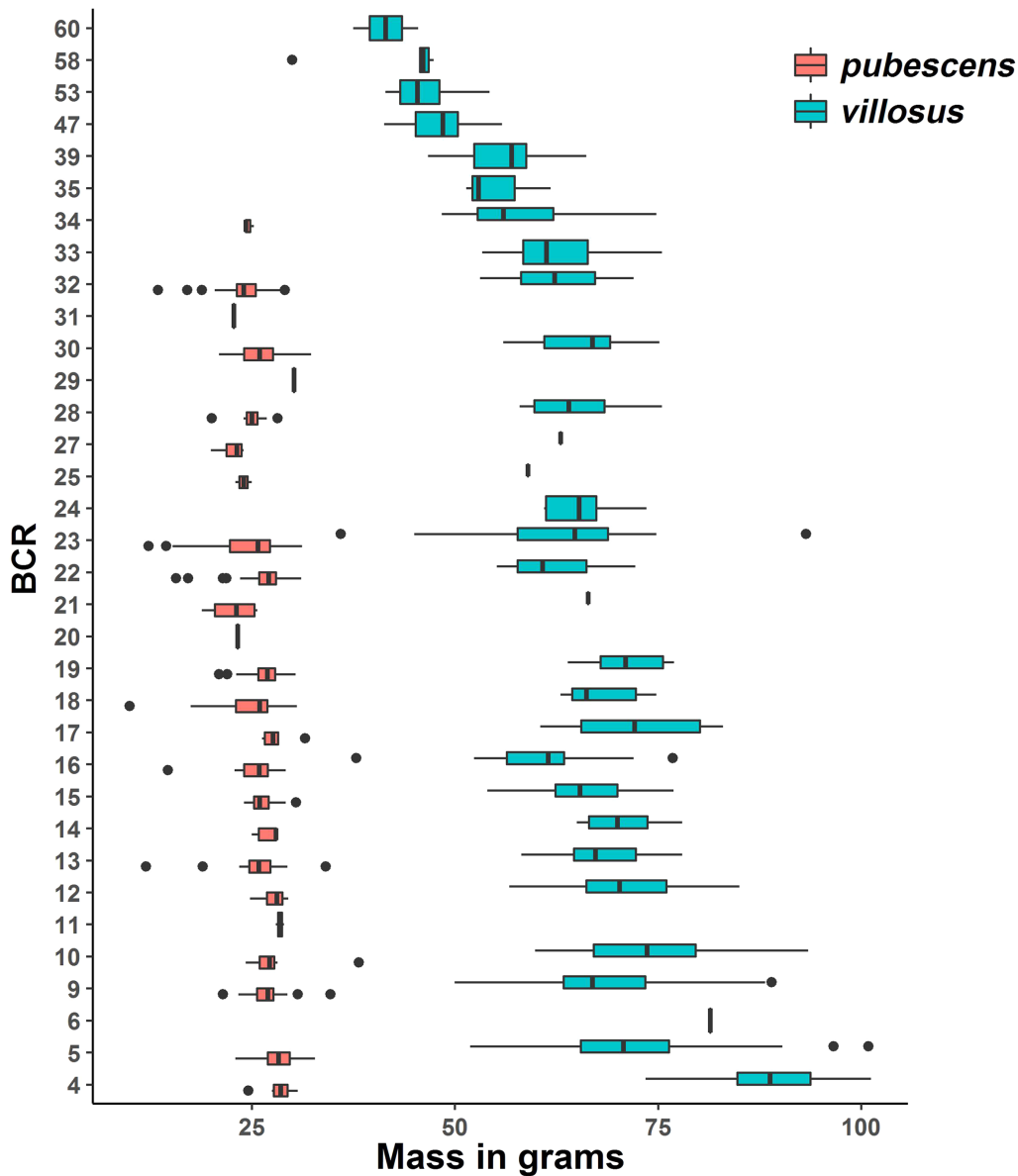


Figure 2. Boxplots of mass of *Dryobates* and *Leuconotopicus* across different Bird Conservation Regions (BCRs). BCRs are numbered roughly from northwest (BCR2 = western Alaska) towards the southeast (BCR60 = Sierra Madre de Chiapas).

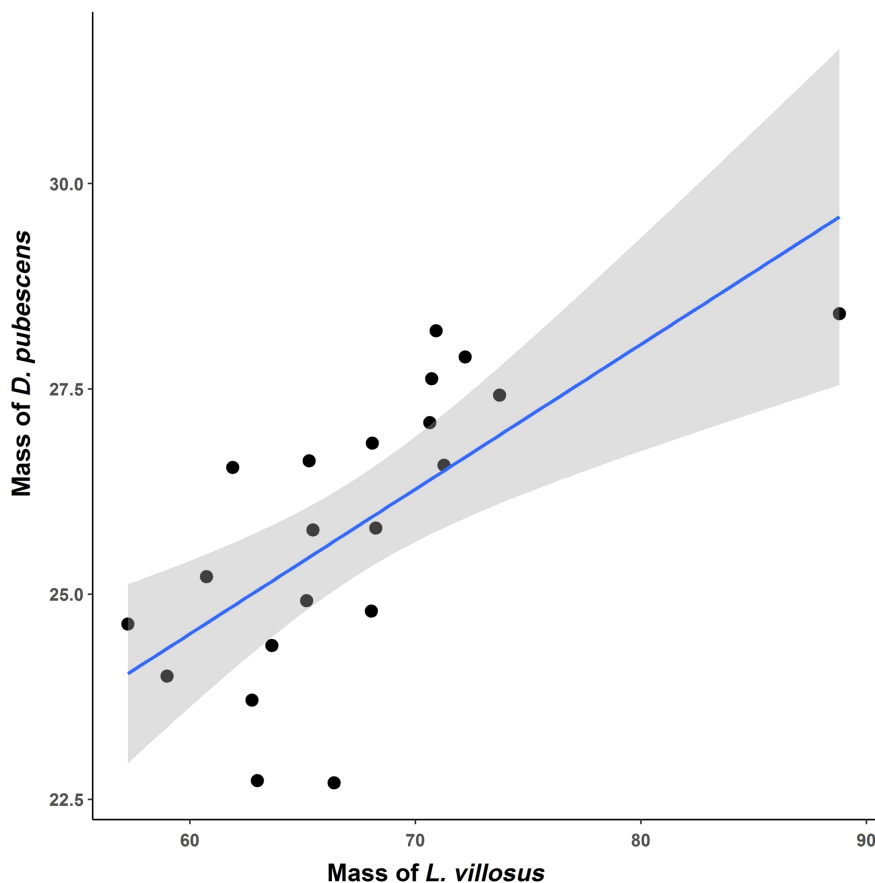


Figure 3. A regression of the mass of *Dryobates pubescens* and *Leuconotopicus villosus*. Each point represents the average of each species in a particular Bird Conservation Region (BCR); thus, the graph shows the relation in body size between *D. pubescens* and *L. villosus* by geographic area. The equation for the line is $y = (0.18 \pm 0.08)x + (13.93 \pm 5.88)$ with an adjusted $R^2 = 0.46$.

better than regressions with respect to coldest temperature (*D. pubescens*: $R^2 = 0.03$; *L. villosus*: $R^2 = 0.32$) or overall environmental variation (principal component 1: *D. pubescens*: $R^2 < 0.01$; *L. villosus*: $R^2 = 0.05$; principal component 2: *D. pubescens*: $R^2 = 0.03$; *L. villosus*: $R^2 = 0.16$). Longitudinal analyses performed poorly in describing overall geographic variation (*D. pubescens*: $R^2 = 0.04$; *L. villosus*: $R^2 = 0.06$).

Analysis of Neotropical woodpeckers

The difference in size between *Campephilus guatemalensis* and *C. melanoleucos* was found to be insignificant (Wilcoxon rank sum test, $W = 231$, $p = 0.11$), with *C. guatemalensis* averaging 95% the size of *C. melanoleucos*. Both species were significantly larger than their sympatric populations of *Dryocopus lineatus*, with *C. guatemalensis* (Wilcoxon rank sum test, $W = 826$, $p < 0.005$) possessing a mimic/model ratio of 0.67 and *C. melanoleucos* (Wilcoxon rank sum test, $W = 8.29$, $p < 0.005$) possessing a mimic/model ratio of 0.80. Similarly, the population of *Dryocopus lineatus* sympatric with *C. guatemalensis* is significantly smaller than the population of *D. lineatus* sympatric with *C. melanoleucos* (Wilcoxon rank sum test, $W = 38$, $p < 0.005$, ratio = 0.79; Fig. 5).

General examinations of mass in comparison to latitude of the Neotropical woodpeckers recovered a dichotomy, with a response demonstrated by northern populations but not by southern populations. The overall trend of *D. lineatus* was a large increase in mass going southward, with the smallest birds near 25°N and the largest birds near 10°S. Similarly, *Campephilus guatemalensis* was largest near the southern end of its distribution in northern Costa Rica, where they appear to be locally sympatric or parapatric with the northernmost populations of *Campephilus melanoleucos* (eBird 2012). Dividing the *Dryocopus lineatus* populations allowed for comparisons of the slopes from within each geographic region, revealing that latitudinal trends are roughly parallel between *Campephilus* and *Dryocopus* (Fig. 6). The strongest relationship was recovered for *C. guatemalensis* ($R^2 = 0.33$), with lesser responses observed for *C. melanoleucos* ($R^2 = 0.24$) and northern populations of *D. lineatus* ($R^2 = 0.27$). Almost no trend was recovered for southern *D. lineatus* ($R^2 = 0.02$). Both relationships were found to be indistinguishable using *t*-tests (Welch's *t*-tests, northern: $t = -0.927$, $df = 26.04$, $p > 0.05$; southern: $t = -1.42$, $df = 12.20$, $p > 0.05$), but the relationships between *C. guatemalensis* and *D. lineatus* were significantly different when compared using ANCOVA

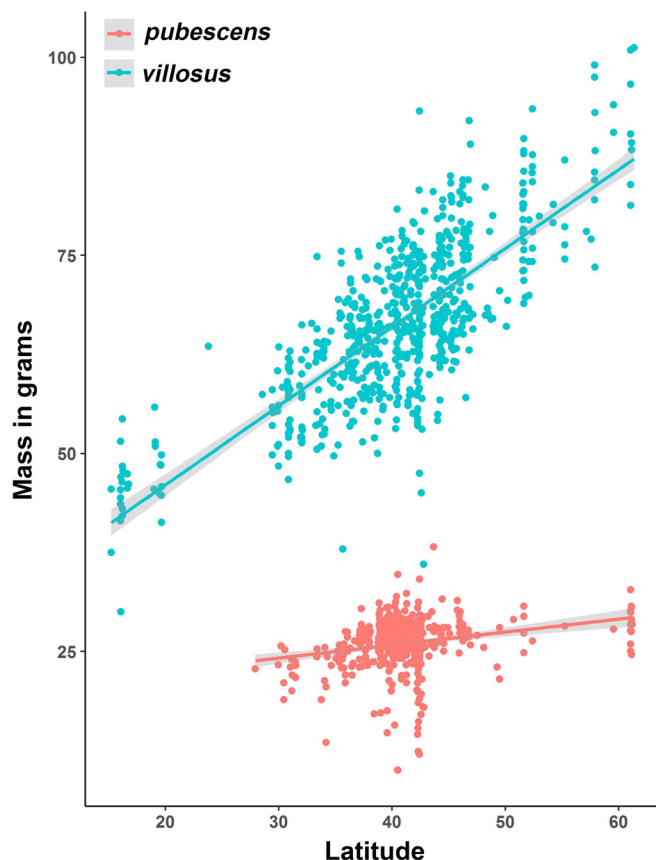


Figure 4. Relationship of mass to latitude for *Dryobates pubescens* and *Leuconotopicus villosus*. The equations for the lines are as follows: *D. pubescens* = $(0.16 \pm 0.06) x + (19.23 \pm 2.40)$, adjusted $R^2 = 0.07$; *L. villosus* = $(1.00 \pm 0.06) x + (26.11 \pm 2.64)$, adjusted $R^2 = 0.58$.

($F_{(2,55)} = 98.99$, $p < 0.005$) while remaining indistinguishable for the southern group ($F_{(2,24)} = 1.58$, $p = 0.23$).

Discussion

Implications of differential morphological selection

Within North American *Picoides* sensu lato, *L. villosus* varies significantly with respect to latitude, and is similarly correlated to temperature. The results indicate that variation in *L. villosus* body mass is an adaptation to climate, and that *L. villosus* is not morphologically constrained within a specific Grinnellian niche. Indeed, *L. villosus* populations vary in their foraging ecology and morphology across their distribution, with two major genetic clades occurring in North America (Klicka et al. 2011). The south and west clade displays greater amounts of genetic variation than its north and east counterpart, with ecological niche reconstructions indicating greater stability through time for the south and west populations (Klicka et al. 2011). Both clades demonstrate variation in foraging style based on regional abiotic

and biotic factors (Jackson et al. 2002). *Leuconotopicus villosus*' mimic, *Dryobates pubescens*, stands in contrast, with much smaller magnitude responses to environmental factors. While variances in size (using other variables as proxies) are well documented within *D. pubescens* (James 1970), the magnitude of these trends is shallow compared to *L. villosus*. At present, there is no published phylogeographic analysis for *D. pubescens* to compare to the structure observed in *L. villosus*. *Dryobates pubescens* shows greater consistency in foraging ecology than *L. villosus* throughout its distribution, preferentially foraging on small limbs, weeds, and branches (Jackson and Ouellet 2002). The apparently constrained variation in *D. pubescens* contrasts with the major trends observed in *L. villosus*; this contrast is maintained in the foraging literature, where the foraging styles of *L. villosus* are more variable (Kiesel 1972, Jackson and Ouellet 2002, Jackson et al. 2002). The plasticity of *L. villosus* with respect to foraging, phenotype, and morphology may be partially attributable to the different picid communities in which it occurs over its distribution, but more research is required. Local responses to picid competition have been documented in *D. pubescens*, but these responses appear to be related to direct access to resources and less related to foraging plasticity (Williams and Batzli 1979, Peters and Grubb 1983).

The social behaviors of *Dryobates pubescens* and *Leuconotopicus villosus* also diverge from the expectation within a mimicry-dominated system, with *L. villosus* acting more aggressively towards *D. pubescens* than would be expected under a strict ISDM hypothesis (Leighton et al. 2018). The lack of evidence for adhering to an ISDM dynamic and the lack of major size variation within *D. pubescens*' distribution suggests that it may occupy a more specific Grinnellian niche (with respect to foraging ecology) that causes a constraint in body size. While the overall size ratio between models and mimics may be beneficial to the formation of ISDM systems, the evolutionary pressure to maintain these systems is apparently not as strong as other ecological pressures on morphological evolution in *D. pubescens* and *L. villosus*.

Within the large Neotropical woodpeckers, *Dryocopus lineatus* as a whole showed little evidence for clines with respect to latitude or environment variation. Central and South American populations have greater masses than those found in northern Central and North America. *Dryocopus lineatus* were significantly larger in areas where they overlap with a larger model taxon, a possible indication that *D. lineatus* is tracking the mass of its models. There were insufficient data to determine if the trending of a 67–80% size of mimic to model was maintained throughout the Neotropics (in contrast to the $55\text{--}60\% \pm 3.8\%$ by Prum 2014), but the size of *D. lineatus* is correlated with larger *Campephilus* at a local scale (i.e. within each *Campephilus*' individual distribution). This is especially apparent in North and Central America, where there appears to be a significant trending towards larger body size as one moves south. *Dryocopus lineatus* demonstrates an apparent lack of body size change in the southern portion of its distribution, but this is potentially clouded

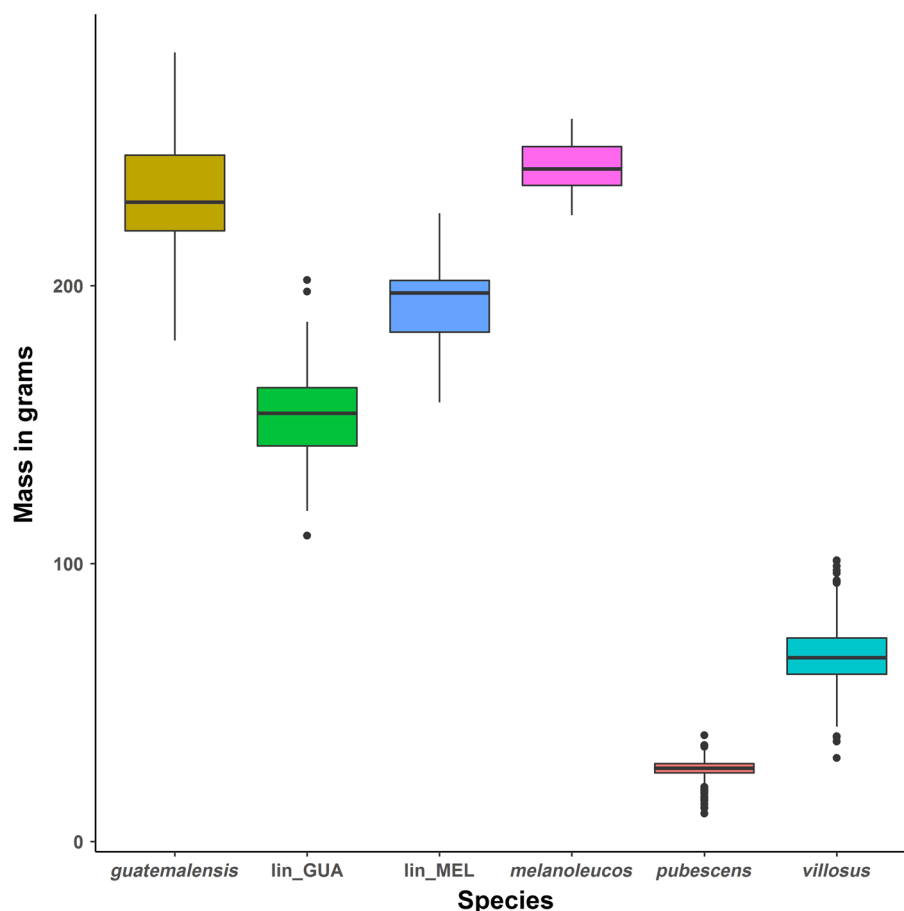


Figure 5. Mass comparisons of *Campephilus guatemalensis*, *C. melanoleucos*, *Dryocopus lineatus*, *Dryobates pubescens*, and *Leuconotopicus villosus*. The annotations of 'lin-GUA' and 'lin-MEL' correspond to populations of *D. lineatus* that are sympatric with *C. guatemalensis* and *C. melanoleucos*, respectively.

by a lack data for regional analyses with other *Campephilus* woodpeckers. The southernmost populations of *D. lineatus* occur outside of the distribution of *C. melanoleucos*, and are sympatric with *C. robustus* and *Celeus galeatus*, where they may be subject to a different selection regime for size. Both northern and southern populations of *D. lineatus* assessed in this study are ca one standard deviation above the average size ratio reported by Prum (2014), bringing into question how consistent size differences must be to indicate ISDM systems.

Notes on ecogeographic trends

Previous studies have recovered a similar trend for size gradation across latitude and environment in Nearctic woodpeckers, with these trends being attributed (at least in part) to Bergmann's rule (i.e. the trending of species to have larger body masses in colder climates; Bergmann 1847, James 1970). Despite this, more expansive studies of tropical and Nearctic taxa have failed to show universality of Bergmann's rule, suggesting that more than environment is affecting the size of some taxa (Zink and Remsen 1986, Freeman 2017). One hypothesis is that these changes are more closely related

to a taxon's foraging according to the Grinnellian niche (Zink and Remsen 1986) or to the Eltonian niche (McNab 1971). Zink and Remsen (1986) discuss this with birds specifically, noting that ecological factors other than temperature may lead to species possessing larger ranges at high latitudes, thereby mirroring the effects of temperatures. For example, Nearctic woodpeckers may possess larger territories in the north because food is less plentiful at some times of year; larger birds may be better adapted for foraging across these larger territories (Jenkins 1981). Misinterpretation of these correlations may occur with some work on Bergmann's rule in North America, where wing length has been used as a proxy for overall bird size despite these characters not necessarily being linked (James 1970, Zink and Remsen 1986). Furthermore, other work has shown that taxa may exhibit an ecological release at higher latitudes not just as a response to environment, but as a response to community structure. McNab (1971) discussed several mammalian predators that exhibit larger sizes in different geographical regions, but that these trends are sometimes restricted to areas in which related dominant taxa do not occur. The effects of community composition and food availability on species size should

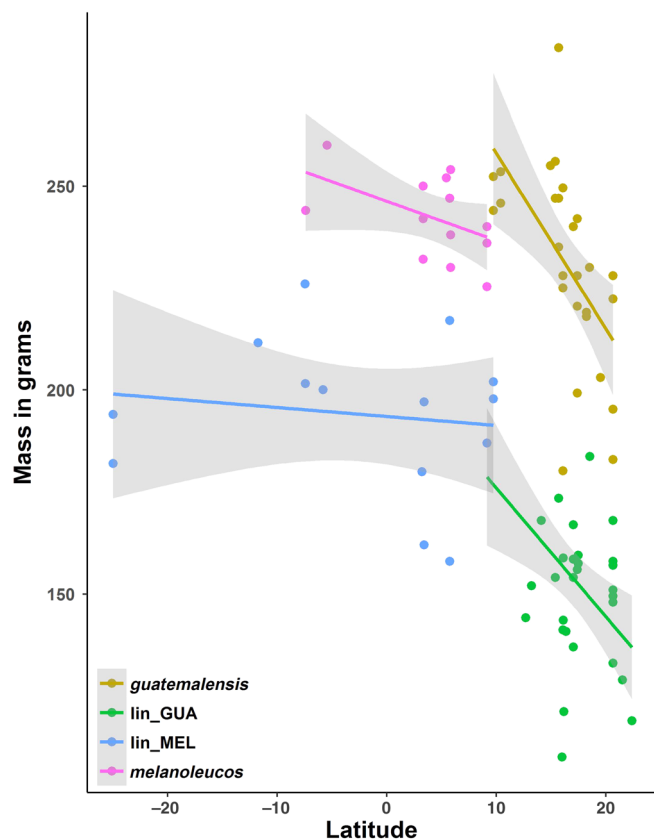


Figure 6. Linear regressions of mass to latitude for *Campephilus guatemalensis*, *C. melanoleucos*, and *Dryocopus lineatus*. All taxa possess larger birds in the southern parts of their distribution. Equations for the regressions are as follows: *Campephilus guatemalensis* = $(-4.30 \pm 2.46) x + (301.08 \pm 41.04)$, adjusted $R^2 = 0.33$; *C. melanoleucos* = $(-0.96 \pm 1.04) x + (246.29 \pm 6.70)$, adjusted $R^2 = 0.24$; *Dryocopus lineatus* (northern or 'lin-GUA') = $(-3.16 \pm 1.94) x + (207.60 \pm 33.40)$, adjusted $R^2 = 0.27$; *D. lineatus* (southern or 'lin-MEL') = $(-0.22 \pm 0.92) x + (193.48 \pm 10.74)$, adjusted $R^2 = 0.02$.

be further investigated in birds, especially in species that have broad latitudinal ranges (e.g. *Leuconotopicus villosus*).

I have corrected for a potential ecological release affecting body size (as noted by McNab 1971) by selecting a complex in which one mimic is nearly entirely syntopic with one model taxon, and it appears that the trending towards Bergmann's rule demonstrated by *Dryobates* and *Leuconotopicus* is a response to multiple environmental and ecological conditions. Confirming the findings of Zink and Remsen (1986), I found that temperature and environmental variation do not explain variability as well as latitude, thus implying that other factors (e.g. day length, seasonal food productivity) not included in environmental data may be affecting woodpeckers' masses. For the Neotropical taxa, it appears that ecological selection will outweigh purely environmental selection for body mass in the widespread *D. lineatus* in the northern hemisphere, thus resulting in the latitudinal trends paralleling sympatric *Campephilus* presented herein (Fig. 6). Furthermore, while

longitudinal trends could exist with respect to mass (mirroring trends observed in phenotype in North America attributed to Gloger's rule, i.e. that darker and more pigmented populations occur in more humid environments; Gloger 1833, Roulin and Randin 2015), I failed to recover any strong trends. Analyses of such trends can be confounded by the geography of the Americas, wherein many ecoregions (e.g. BCR 4: the Northwestern Interior Forest) exist without similar habitats to their south and many habitats are distributed in north-south bands (e.g. BCR18: the shortgrass prairie, Bird Studies Canada and NABCI 2014). This can cause a covariation of longitudinal trends with latitudinal and environmental trends within analyses. Finer scale sampling is needed to allow for the analysis of species within latitudinal transects to correct for this covariation.

Expansion of research

Trends such as Bergmann's rule are often related to firm responses to environment (i.e. Hutchinsonian niches), and have less often been examined in relation to other ecological niche definitions. Examining a species' foraging ecology and community interactions in tandem with environmental and latitudinal trends sheds light on a species' ecological evolution on multiple scales. This research has demonstrated character disjunction within complexes of organisms with Eltonian dynamics, and reinforces that ecological selection driven by a taxon's community and specific ecology may be differentially affecting aspects of a taxon's morphology and phenotype.

It is possible that the macroevolutionary scaling of mimicry presented by Prum (2014) is true across broad spatial areas, and that this trend is an example of the Eltonian noise hypothesis in that fine-scale relationships are clouded by the macro-scale analyses (Soberón and Nakamura 2009). Larger comparative analyses of size in purported ISDM systems in specific regions will reveal whether other species are 'locked' into specific morphospaces to mimic dominant sympatric taxa or if such ratios only exist when species are examined across their entire co-distribution. If the ratio holds true only at coarse scales, then it is possible that certain size ratios are more amenable to the development of mimicry even if this ratio does not have to be strictly maintained through time or across geographic space to perpetuate the mimicry dynamic. Parallel analyses should compare pairs of taxa with similar phylogenetic and ecological relatedness that co-occur broadly and do not share similar phenotypes to provide a null comparison of sympatric ecogeographic variation in systems lacking mimicry. If results are similar to those found in mimicry systems, then communities' ecomorphological evolution as a whole are likely being driven by other abiotic and biotic factors (García-Navas et al. 2018).

Future work with ecogeographic clines should focus on multi-character assessments that take into account aspects of functional morphology (e.g. bill length) as well as gross mass, phenotype, and community interactions. Fine scale data,

such as those that are available from consistent local collecting and banding operations, will permit analyses of micro-habitat evolution and insights into how different community members respond to environmental changes (James 1970). Combining these data with known interspecific interactions will provide an idea of how a species' habitat and community are affecting its ecological niche and, therefore, its evolutionary trajectory.

While phenotype was not quantified in this study, there are five presently recognized subspecies of *Dryocopus lineatus*, many of which possess plumage characteristics paralleling sympatric *Campephilus* species (del Hoyo et al. 2014, Gill and Donsker 2018). Perhaps the most striking example of this local adaptation is in western South America, where the notably browner subspecies *D. lineatus fuscipennis* co-occurs with the distinctively brownish *Campephilus guayaquilensis* (Ridgely and Greenfield 2001). No population level genetic analysis of *D. lineatus* exists, so it is unknown to what extent these geographic phenogroups interbreed or experience selection to maintain their local *Campephilus*-like phenotype. Bioacoustics also were not included in this study, but are an important aspect of proposed ISDM systems. Visual signaling is integral to ISDM theory and is undoubtedly occurring in wild picids, but birds also must be detecting each other acoustically as well (Prum 2014). Many non-ISDM species are known to mimic the vocalizations of potential competitors or predators, while other species have apparently converged on similar vocalizations by means of natural selection (Kelley et al. 2008). Vocal convergence should be quantified in ISDM systems as well to understand to what extent mimics diverge from their close relative and converge on their presumed models (M. B. Robbins and Anon. reviewer pers. comm.).

Ecological niche research, thus far, has focused on factors determining overall distribution and macro-scale patterns of interaction with other species, mainly through competition. Less research has focused on the finer-scales of niche evolution dynamics, be it local niche conservatism or niche differentiation across geographic space within a single clade or taxon (Holt 2009). Recent papers have focused on quantifying differences between species ecological niches on the whole to determine if species are diverging (Warren et al. 2008, McCormack et al. 2009, Glor and Warren 2011), with the consensus now being that niches are generally conserved through time (Peterson et al. 1999, Peterson 2011, Petitpierre et al. 2012) but that secondary contact can encourage character divergence in sympatry (Jang and Gerhardt 2006, Kirschel et al. 2009). Regiospecific studies of widespread, polytypic species (such as *Dryobates pubescens*, *Dryocopus lineatus*, and *Leuconotopicus villosus*) incorporating morphological and genetic data will provide an opportunity for understanding if ecogeographic variation is truly conservative, Brownian (i.e. stochastic and random) in nature, or the result of highly selected regional niche evolution in response specific community and environmental factors (Holt 2009, Klicka et al. 2011).

Conclusions

Studies of ISDM are limited, and likely do not reflect the full extent of the phenomenon either within the class Aves or beyond. This form of mimicry is complex in that it can evolve in a two-observer system and does not necessarily require a third party observer to cause evolutionary pressure within the system. As I have shown here, mimics do maintain smaller sizes than their models, but what size is necessary for effective mimicry is still undetermined. In the Neotropics, a parallel ecogeographic relationship in size between *Dryocopus lineatus* and overlapping species of *Campephilus* exists, suggesting that community members influence each others' physical traits (and, therefore, morphological evolution via their Eltonian niches). Observed trends within this group seem to counter Bergmann's rule, at least in the case of *Campephilus guatemalensis* and *Dryocopus lineatus*, for reasons that are unknown. Conversely, Nearctic taxa follow Bergmann's rule but differ significantly in their responses to abiotic factors, demonstrating that mimics and models can possess correlated phenotypic evolution contemporaneously with disjointed morphological evolution. This comparison of sympatric Nearctic taxa shows that while similar environmental trends in body mass can exist concurrently for mimics and models, the magnitude of their responses may be a reflection of the relative importance of selection with respect to abiotic factors, their communities, and/or their foraging regimes. While mass ratios differed from the ISDM expectation in a pair of Neotropical woodpeckers, the trending towards larger mimics in areas with larger models also holds true, and highlights the need for more research on Eltonian dynamics.

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Supplementary material (Appendix JAV-01771 at <www.avianbiology.org/appendix/jav-01771>). Appendix 1–2.