



## IS SPECIES GEOGRAPHIC OVERLAP CONSTANT ACROSS LATITUDE? A HOMAGE TO E. H. RAPOPORT

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**Abstract:** Eduardo H. Rapoport's seminal book, *Areography*, was significant for the foundation of macroecology and development of geographical ecology. Indeed, one of the most studied macroecological patterns is the so-called Rapoport's rule – the tendency of species geographic ranges to be smaller towards lower latitudes. However, several of Rapoport's pioneering ideas have been rarely studied or completely overlooked. Related to the ecogeographical rule that carries his name, he proposed the existence of a latitudinal geographical trend in the overlap of species ranges of the same genus: the constant overlap hypothesis. Such constancy, he argued, appears despite the existence of both latitudinal gradients in species richness and range size. This overlap pattern has not, to our knowledge, being revisited and tested. Here, we intend to honor his legacy by revisiting this particular hypothesis. Using current data for the original rodent genera that Rapoport studied and for phyllostomid bat genera, we applied this framework along with modern macroecological tests to evaluate the overlap among species of the same genus across latitude. We conducted correlation and linear regression analyses to describe this pattern and compared our results to a null model of simulated range construction and placement. Based on the observed vs. simulated pattern comparison, we found that Rapoport's original idea of a constant overlap across latitudinal bands is actually the expected pattern under the conditions of our null model. This may suggest that range cohesion and size, the only range properties kept in the null model, are sufficient to explain the overlap patterns among species of the same genus across latitude. We discuss our findings in light of potential biological and methodological explanations. In doing so, we highlight the enduring legacy that E. H. Rapoport had and will continue to have on our investigations of geographical ecology and macroecology.

**Keywords:** diversity gradients; geographic range; macroecology; null models; Rapoport's rule.

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## INTRODUCTION

*“The geographical areas of distribution are the Chinese-lantern shadows produced by the different taxa on the continental screen: it is like measuring, weighing, and studying the behaviour of ghosts”* (Rapoport, 1982, p. 1)

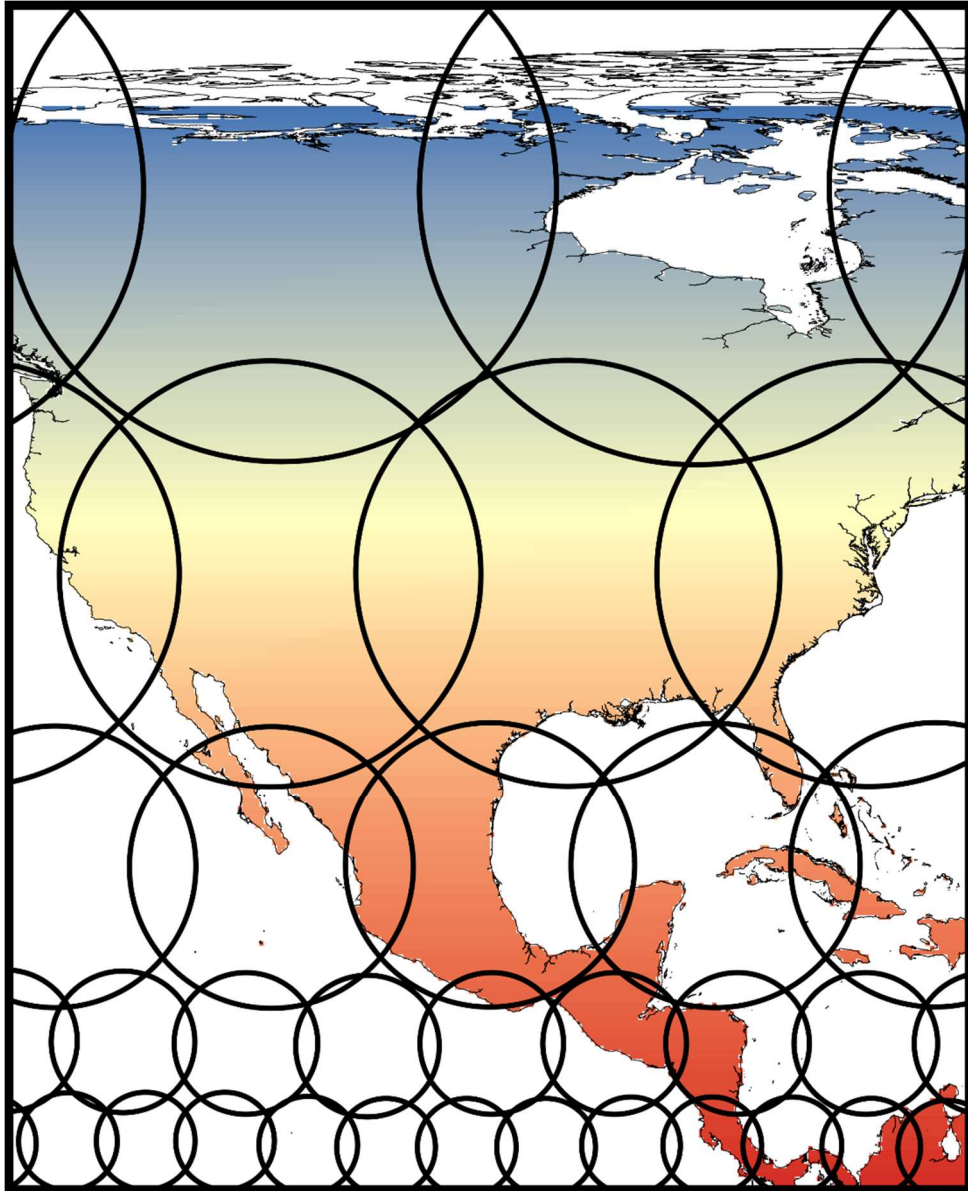
Eduardo Hugo Rapoport (1927-2017) was certainly one of the most influential Latin American ecologists and biogeographers. His recent passing leaves an unfillable void in both disciplines. Areography (1975, 1982), his seminal and exceptionally original book served as a foundation for the development of macroecology being even considered as the first modern treatment of the discipline (after Robert H. MacArthur's Geographical Ecology [1972], Ruggiero & Hawkins 2006). Indeed, one of the most studied macroecological patterns is the so-called Rapoport's rule (Stevens 1989) – the tendency of species geographic ranges to be smaller towards lower latitudes. Such ecogeographical rule (Gaston *et al.* 2008) was originally proposed to explain the latitudinal diversity gradient (LDG) under a climatic mechanism where species' range sizes were associated with tolerance to climatic variability (Stevens 1989). Regardless of its efficacy in explaining the LDG (Šizling *et al.* 2009) or its actual status as a 'rule' (Gaston *et al.* 1998), Rapoport's rule continues to be studied and its investigation has generated important insights into the mechanisms determining the observed patterns of diversity and distribution of taxa (Arita *et al.* 2005, Pintor *et al.* 2015).

Undoubtedly, the most important contribution of E. H. Rapoport to macroecology and geographical ecology was the realization that understanding large-scale patterns of diversity requires the explicit consideration of species' geographical areas of distribution. Indeed, geographic gradients in species richness are determined by the overlap of species geographic ranges that are ultimately defined by the size, shape, and position of such ranges (Gotelli *et al.* 2009). This reasoning has allowed, for example, integrating two previously divorced approaches, site-based (*i.e.*, focusing on properties of species assemblages) and species-based (*i.e.*, focusing on individual species and their aggregate properties),

to reveal the processes responsible for the assembly and distribution of biological communities (Arita *et al.* 2008, Guisan & Rahbek 2011). We have come a long way since Rapoport introduced us to the importance of studying species geographic ranges. However, like other farsighted ecologists, Rapoport provided us with considerable insights on how to study nature, some of which have rarely been explored or even forgotten altogether. In the context of this special issue, we take the opportunity to honor E. H. Rapoport's life and work by revisiting and evaluating a particularly intriguing hypothesis he raised in Areography (1975, 1982).

Unlike Rapoport's rule (Stevens 1989), several other 'macroecological ideas' pioneered by E. H. Rapoport have been surprisingly overlooked. For example, he hypothesized the existence of a constant geographic range overlap across latitude among species of the same genus (Rapoport 1975, 1982, Figure 1). Such latitudinally constant overlap runs counter to Rapoport's own expectations: "...it is obvious that [species' range] overlap tends to increase at any increment given to the ranges or when species density augments" (Rapoport, 1982, p. 174). This counterintuitive pattern, which he found for three rodent genera, motivated Rapoport to ask "Does an optimum overlap exist, something like a strategy of 'giving and receiving' among species?" (Rapoport, 1982, p. 176). Interestingly, a similar 'giving and receiving among species' idea appears at Brown and Maurer's original proposal for the macroecological approach (Brown & Maurer 1989). Indeed, the original goal of macroecology was to "understand the assembly of continental biotas in terms of how the physical space and nutritional resources of large areas are divided among diverse species" (Brown & Maurer, 1989, p. 1145). Such division of the physical space among species is directly related to their degree of overlap and thus with the observed gradients in species richness (Brown 1995, Villalobos *et al.* 2014). Despite its potential relevance for understanding geographic diversity gradients, the constant overlap hypothesis has not been, to the best of our knowledge, evaluated since Rapoport introduced it in 1975.

Ever since Darwin, coexistence is thought to be more restricted among species of the same genus than among those of distinct genera, given the



**Figure 1.** Schematic representation of Rapoport's model of latitudinally constant overlap under species richness and range size gradients. Circles represent species ranges and the background map illustrates a species richness gradient. Redrawn from Rapoport (1975).

greater ecological similarity among species of the same genus due to their evolutionary relationships (Darwin 1859, Webb *et al.* 2002). Rapoport did not mention this Darwinian premise when proposing the constant overlap hypothesis, but he certainly had it in mind, as evidenced several times throughout his book when discussing his findings. For example, specifically regarding species overlap, he mentions that “[c]ases of 100% overlap in some species of the same genus clearly tell us that they have suffered competitive exclusion and therefore displacement of ecological niches...” (Rapoport, 1982, p. 178). Thus, we can infer that Rapoport's

constant overlap hypothesis is based on the Darwinian premise with the resulting expectation that species of the same genus should not overlap completely and present similar overlap across latitude irrespective of their trends in range size and species richness within that gradient. This expectation was indeed what he found for three rodent genera (*Microtus*, *Eutamias* [*Neotamias*] and *Sciurus*) distributed across North America. However, we do not know if this is a general pattern applicable to other taxa or merely a fortuitous finding by Rapoport. Therefore, several questions remain open. For example, is the

constant overlap across latitude present in other mammalian genera? Is this pattern consistent across the Americas? What is the probability of finding such pattern when considering the expectations of modern macroecological approaches (e.g., null simulation models; Gotelli *et al.* 2009)?

Here, we evaluate Rapoport's constant overlap hypothesis and try to answer the aforementioned questions by applying modern macroecological approaches. More specifically, we re-evaluated the hypothesis for the three rodent genera that Rapoport originally studied as well as for 11 genera of New World leaf-nosed bats (Chiroptera: Phyllostomidae). The bat family Phyllostomidae is one of the most species-rich and the most ecologically diverse family of mammals (Simmons & Conway 2003). Also, current knowledge on their geographical and evolutionary patterns is abundant (Villalobos *et al.* 2013). In fact, Phyllostomidae has been defined as the major contributor to the latitudinal diversity gradient of the whole order Chiroptera in the New World (Stevens 2004), which in turn drives the overall gradient for mammals across the globe (Kaufman 1995, Buckley *et al.* 2010). Regarding range size, New World bats also present evidence for the original Rapoport's rule with a decrease in range sizes towards the equator (Lyons & Willig 1997, Arita *et al.* 2005). Therefore, the availability of geographical data as well as our knowledge of the species richness and range size gradients of Phyllostomidae, make this family an ideal group for testing Rapoport's constant overlap hypothesis.

## MATERIAL AND METHODS

### *Distributional data*

We obtained species range maps (*i.e.*, extents of occurrence) for three rodent genera (*Microtus*, *Eutamias* [*Neotamias*] and *Sciurus*) and the bat family Phyllostomidae from the IUCN database (2015). Since Rapoport's publication of *Areography*, species taxonomic and distributional information has changed. For example, what he considered as *Eutamias* species from North America are now considered as *Neotamias* (Retrieved May 05, 2017, from the Integrated Taxonomic Information System on-line database,

<http://www.itis.gov>). However, aside from this change, preliminary analyses on the rodent genera showed that the distributional patterns found by Rapoport remain qualitatively similar (e.g., species absent from particular latitudinal bands, see below). For the Phyllostomidae, we considered those genera that had at least five species in total and thus may present richness and range size gradients as well as allowing for robust statistical analyses. These genera were *Anoura* (6 species), *Artibeus* (11), *Carollia* (6), *Dermanura* (9), *Glossophaga* (5), *Lonchophylla* (10), *Lonchorhina* (5), *Lophostoma* (7), *Micronycteris* (9), *Platyrrhinus* (17), *Sturnira* (16). For all rodent and bat genera, we followed IUCN (2015) taxonomy. Range maps were projected onto a Behrmann equal-area projection in order to have a more accurate estimation of species range area. Processing of species range maps was done in R 3.3.3 (R Core Team 2017), using the following packages: *maptools* (Bivand & Lewin-Koh 2015), *raster* (Hijmans 2015), *rgdal* (Bivand *et al.* 2014), *rgeos* (Bivand & Rundel 2015), *sp* (Pebesma & Bivand 2005), and *spdep* (Bivand & Piras 2015).

### *Species distributional overlap*

We followed the original protocol of Rapoport to calculate the distributional overlap among species of the same genus across latitude. First, we divided the geographic domain of each species group (Rodentia and Phyllostomidae) into parallels spaced in four degrees. For the rodent genera, we followed Rapoport's original divisions from 8° to 72° of latitude in North and Central America, rendering 16 latitudinal bands. For the Phyllostomidae, we divided the Americas from -34° to 30° in 4° latitudinal bands, which rendered 16 latitudinal bands (Figure 2). Second, we measured the area (in Km<sup>2</sup>) of each species within each latitudinal band. Third, we calculated the area of overlap among species of the same genus within each latitudinal band. Fourth, we estimated the percentage of overlap with respect to the areas of species within latitudinal bands. For this fourth step, we used Rapoport's formula for intrinsic percentage overlap (O\*) within each latitudinal band, defined as:

$$O^* = \frac{\sum_{i=1}^n O_{i,j}}{\sum_{i=1}^n a_i} \times 100$$

where  $\sum_{i=1}^n O_{i,j}$  is the sum of the overlaps between species pairs ( $i$  and  $j$ ) and  $\sum_{i=1}^n a_i$  is the sum of the areas of species. Note that the use of latitudinal bands to measure and describe species range patterns is similar to the one proposed by Stevens (1989) for documenting Rapoport's rule, generally known as Stevens' method (Ruggiero & Werenkraut 2007). Accordingly, Stevens' method consists of averaging the latitudinal extent (*i.e.*, the length of the north-south axis) of all species recorded at each latitudinal band and then correlating these average range sizes with latitude (Stevens 1989, Ruggiero & Werenkraut 2007). One of Rapoport's assumptions was that species showed a positive latitudinal trend in range size (along with a negative trend in species richness). However, he did not check for such range size trend (*i.e.*, Rapoport's rule, after Stevens [1989]) in his studied rodent genera. Therefore, we also evaluated the existence of Rapoport's rule in the rodent genera as well as in the Phyllostomidae genera using Stevens' method.

### **Statistical analyses**

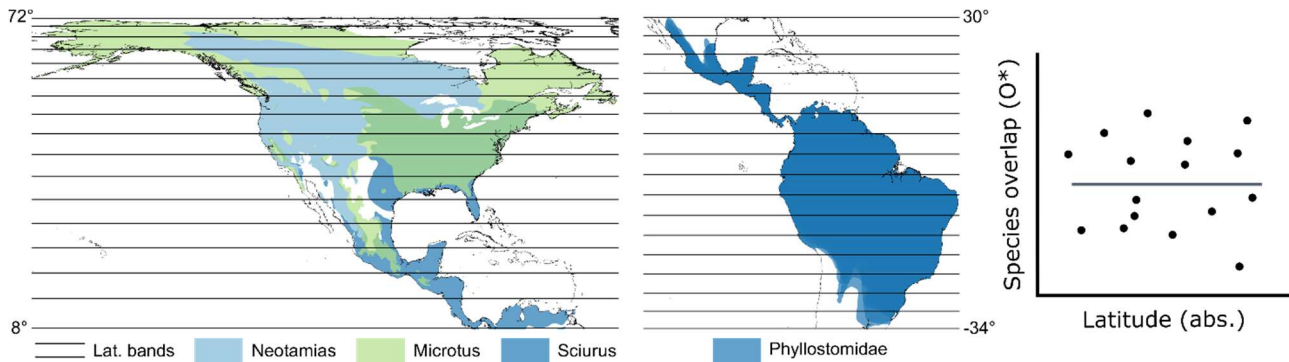
Rapoport did not apply any formal statistical test to confirm his findings on species overlap. Therefore, we decided to apply a similar approach to that used in testing for Rapoport's rule, namely Stevens' method, to test for an association between overlap among species within latitudinal bands and the latitudinal position of those bands (*i.e.*, their midpoint). We evaluated such association using correlation and regression analyses. We used Spearman's rank correlation coefficients ( $\rho$ ) to describe the strength of the association between the two variables, as suggested by early studies on Rapoport's rule (Ruggiero 1994, 1999). Also, we used linear regression and its associated slope and coefficient ( $R^2$ ) to describe the relationship between the two variables and its strength. Under Rapoport's constant overlap hypothesis, we expect that both correlation and regression analyses show no significant association and relationships (Figure 2). We applied the same analyses to describe the relationship between range size and latitude. In this case, support for original Rapoport's rule would come from significantly positive correlation and linear relationship between both variables (*i.e.*, larger ranges at higher latitudes). To consider only

the possibility of a monotonic, linear (instead of quadratic) relationship between our variables, we used the absolute latitude of the latitudinal bands' midpoints in all analyses.

### **Null model**

When studying species ranges and their overlap, methodological advances in macroecology in the last couple of decades have stressed the importance of considering appropriate null hypothesis to identify geographical patterns that can be explained by biological mechanisms (Gotelli *et al.* 2009). In this context, Colwell & Hurtt (1994) and Lyons & Willig (1997) showed that spatial restrictions (*i.e.*, geographic limits) influence the distribution of ranges and that this should be taken into account when testing for geographic patterns of diversity and distribution (Villalobos *et al.* 2014). In other words, it is important to consider the expected pattern under such restrictions. In our case, what is the expected relationship between species overlap and latitude? To consider such expected pattern and thus construct an appropriate null hypothesis, we developed a stochastic simulation model of species' range construction and placement.

We simulated cohesive ranges of species based on the spreading-dye algorithm (Jetz & Rahbek 2001) and keeping the observed species range sizes and spatial structure of the domain (*i.e.*, actual geography: North America for the rodents and the Americas for phyllostomids). This null model entertains the possibility of independent distributional patterns among species under geometric constraints and regardless of environmental gradients (essentially a Mid-Domain Effect model; Colwell *et al.* 2004, Villalobos & Arita 2010). First, we built a species presence-absence matrix (PAM) by overlaying an equal-area grid of ~2,500 Km<sup>2</sup> cells (roughly 0.5° x 0.5° longitude-latitude near the equator) to the range maps using the R package *letsR* (Vilela & Villalobos 2015). Then, we used the PAM for each genus to simulate the cohesive ranges with the R package *rangemodelR* (Marathe 2016) as follows: for each range, 1) select a random "seed" cell within the grid and 2) randomly adding spatially contiguous cells until reaching the observed range size (*i.e.*, number of cells occupied by the species in the PAM). One iteration of this process results in a single



**Figure 2.** Maps depicting the geographical distribution of the studied genera (rodent genera on the left-hand map and the combined distribution of the phyllostomid genera on the central map) and a graphic representation of Rapoport's constant overlap hypothesis (right-hand plot).

simulated scenario of  $N$  species randomly distributed across the geographic domain. We repeated this process 100 times and applied the protocol described above to estimate correlation and regression coefficients of the association between species overlap and latitude. From this, we obtained null distributions of such coefficients against which we contrasted our observed coefficients. We determined the statistical significance of observed coefficients if they fell outside the 95% confidence interval of the null distributions. All statistical analyses and simulations were conducted in R 3.3.3 (R Core Team 2017).

## RESULTS

Applying traditional statistical tests, we confirmed Rapoport's original results regarding the constant overlap for two (*Eutamias* [*Neotamias*] and *Sciurus*) of the three genera he studied as well as for seven out of 11 phyllostomid genera (those without \* in Table 1). Following a latitudinally constant pattern, these genera did not show a significant correlation or linear relationship between species proportional overlap within latitudinal bands and the latitudinal position of these bands. Conversely, the rodent genus *Microtus* and four phyllostomid genera (*Artibeus*, *Lophostoma*, *Micronycteris*, and *Sturnira*) did show significant and contrasting overlap patterns. *Microtus* showed a positive association and linear relationship whereas the four phyllostomid genera exhibited a negative association and linear relationship between proportional overlap and latitude, as evidenced by their Spearman's rank correlation coefficients

(Table 1). Observed within-genus overlaps across latitudinal bands for each studied genus can be found in the Supplementary Material 1. Regarding the range size-latitude relationship (Rapoport's rule), all three rodent genera and seven phyllostomid genera showed the expected positive relationship (*i.e.*, larger ranges at higher latitudes; Table 2).

According to our stochastic simulation model, the null expectation under independent distributional patterns among species, geometric constraints and no environmental gradients was Rapoport's prediction itself: no significant trend between proportional species overlap and latitude. Indeed, the mean coefficients for all genera derived from the simulations were not statistically significant (Table S2, Supplementary Material 2). More interestingly, observed coefficients for all genera were not significantly different from the null distributions of simulated coefficients (Table 1). Tables and figures of the null distributions for linear regression and correlation coefficients for each studied genus can be found on the Supplementary Material 2 and 3.

## DISCUSSION

Eduardo H. Rapoport legacy to geographical ecology and macroecology has already been substantial for the development of both disciplines (Arita *et al.* 2005, Ruggiero & Hawkins 2006). Still, there is much to be learned by exploring his pioneering contributions. Here, we have tried to honor such legacy by revisiting one of his farsighted ideas. We found that range

**Table 1.** Results from linear regression and correlation analyses between species overlap and latitude across bands. Significance (p-value) was derived from null model comparisons. \* denote significant (s) results from traditional statistical analyses (*i.e.*, no support for constant overlap, see text for details).

Order/Genus	Species (n)	Linear regression			Spearman's rank correlation		s
		slope	R <sup>2</sup>	p-value	$\rho$	p-value	
<b>Rodentia</b>							
<i>Microtus</i>	19	1.723	0.538	0.396	0.774	0.297	*
<i>Neotamias</i>	23	0.296	0.000	0.535	0.153	0.634	
<i>Sciurus</i>	18	-0.263	0.000	0.832	-0.218	0.713	
<b>Chiroptera</b>							
<i>Anoura</i>	6	-0.519	0.000	0.832	-0.134	0.871	
<i>Artibeus</i>	11	-3.569	0.517	0.713	-0.744	0.653	*
<i>Carollia</i>	6	-2.363	0.265	0.930	-0.610	0.733	
<i>Dermanura</i>	9	-1.781	0.251	0.812	-0.560	0.574	
<i>Glossophaga</i>	5	0.149	0.000	0.832	-0.009	0.970	
<i>Lonchophylla</i>	10	-0.762	0.000	0.851	-0.559	0.436	
<i>Lonchorhina</i>	5	-3.199	0.298	0.554	-0.790	0.158	
<i>Lophostoma</i>	7	-4.314	0.797	0.119	-0.956	0.059	*
<i>Micronycteris</i>	9	-6.457	0.83	0.356	-0.899	0.436	*
<i>Platyrrhinus</i>	17	-2.132	0.318	0.792	-0.226	0.812	
<i>Sturnira</i>	16	-3.554	0.693	0.139	-0.805	0.119	*

range overlap among species of the same genus does not tend to differ with latitude. That is, there seems to be a latitudinally constant overlap among species regardless of the underlying species richness and range size gradients (Rapoport's rule) present in all of our studied genera. This finding could support Rapoport's idea of an optimum overlap among species and thus the potential existence of a general mechanism driving species partitioning of the physical space (Brown & Maurer 1989). Interestingly, we have also shown that the observed overlap pattern is actually the null expectation under random range construction and placement within a restricted, environmentally homogeneous domain. This was true for our phyllostomid genera as well as for Rapoport's original rodent genera.

What does it mean that an observed pattern does not differ from a null scenario of stochastic simulation? Can we infer something from this finding? Determining pattern significance and its association with underlying theory relies on contrasting observed patterns against theoretical or null expectations (Harte 2004). Accordingly, interpretation of results depends on the specified conditions of such expectations (Gotelli *et al.* 2009). Our null model envisioned a scenario in

which species ranges are independent of each other and of the environmental gradient within the geographic domain. Thus, important biological processes such as species interactions, history, and their relationship with climate were not considered in our model. On the one hand, and taken at face value, this would mean that such processes are not important in determining our observed patterns of species overlap across latitude. Hence, contradicting Rapoport's implicit assumption of ecological differentiation among species of the same genus as a driver of their geographic overlap. In other words, such drivers are not necessary to produce the observed pattern. On the other hand, it would mean that the observed range cohesion and size variation, which is already considered in our simulation, suffices to explain the overlap among species regardless of the processes driving their spatial arrangement.

The first possibility above, that no biological processes are necessary for explaining observed overlap patterns, would seem to suggest that these patterns are random. However, null models such as ours are not entirely random as they retained biological information (in our case, genus species richness and their range sizes). The meaning of "randomness" in these models is related to the

**Table 2.** Results from linear regression and correlation analyses between species range size (latitudinal extents) and latitude (*i.e.*, Rapoport's rule *sensu* Stevens [1989]). Bold figures denote significant results from statistical analyses.

Order/Genus	Species (n)	Bands (n)	Linear regression			Spearman's rank correlation	
			slope	R <sup>2</sup>	p-value	ρ	p-value
<b>Rodentia</b>							
<i>Microtus</i>	19	15	0.303	<b>0.533</b>	<b>0.001</b>	<b>0.839</b>	<b>&lt;0.001</b>
<i>Neotamias</i>	23	12	0.689	<b>0.840</b>	<b>&lt;0.001</b>	<b>0.929</b>	<b>&lt;0.001</b>
<i>Sciurus</i>	18	12	0.454	<b>0.925</b>	<b>&lt;0.001</b>	<b>0.954</b>	<b>&lt;0.001</b>
<b>Chiroptera</b>							
<i>Anoura</i>	6	15	0.666	<b>0.556</b>	<b>0.001</b>	<b>0.812</b>	<b>&lt;0.001</b>
<i>Artibeus</i>	11	16	-0.606	0.140	0.085	-0.155	0.566
<i>Carollia</i>	6	14	0.098	0.000	0.776	0.002	0.994
<i>Dermanura</i>	9	14	-0.090	0.000	0.546	-0.159	0.587
<i>Glossophaga</i>	5	16	0.744	<b>0.279</b>	<b>0.021</b>	<b>0.589</b>	<b>0.016</b>
<i>Lonchophylla</i>	10	9	-0.472	0.000	0.386	-0.229	0.554
<i>Lonchorhina</i>	5	12	1.518	<b>0.703</b>	<b>&lt;0.001</b>	<b>0.842</b>	<b>0.001</b>
<i>Lophostoma</i>	7	12	0.633	<b>0.304</b>	<b>0.037</b>	0.537	0.072
<i>Micronycteris</i>	9	14	0.417	<b>0.652</b>	<b>&lt;0.001</b>	<b>0.824</b>	<b>&lt;0.001</b>
<i>Platyrrhinus</i>	17	14	0.747	<b>0.356</b>	<b>0.014</b>	<b>0.548</b>	<b>0.043</b>
<i>Sturnira</i>	16	16	1.195	<b>0.370</b>	<b>0.007</b>	<b>0.781</b>	<b>0.000</b>

species' ranges placement relative to each other (Colwell *et al.* 2004). So, this possibility does not support Rapoport's implicit idea of ecological similarity among congeneric species as determining their overlap. Indeed, current understanding of biogeographic patterns suggest that biotic interactions become less relevant at large spatial scales (Soberón 2010, Araújo & Rozenfeld 2014) such that their potential effect is either small or not discernable at the level of species ranges and their overlap (but see Wisz *et al.* 2013, Godsoe *et al.* 2015). Alternatively, the second possibility above, that biological information included in the model could explain observed patterns, suggests that biological characteristics that determine species range size variation may be responsible for the observed latitudinal pattern of species range overlap. Such characteristics comprise a complex array of traits from body size and dispersal capacity to speciation and extinction dynamics (Gaston 2003). Of course, evaluating the influence of these biological characteristics would require more information and different approaches than the ones used here (*e.g.*, mechanistic simulation models; Cabral *et al.* 2017).

Nevertheless, focusing only on range cohesion and size, it has been shown through simulations that these properties alone generate positive co-occurrence (*i.e.*, more overlap than expected by chance) among phyllostomid species (Villalobos *et al.* 2014). Such positive co-occurrence, in turn, may in part determine the observed degree of overlap among species of the same genus.

Positive co-occurrence among species can arise simply under geometric constraints and range cohesion (Villalobos & Arita 2010) and exacerbated by ample variation in species ranges sizes, with larger ranges contributing disproportionately to the composition of different regions (Borregaard & Rahbek 2010). This effect may, in turn, generate similar levels of overlap across regions such as the latitudinal bands we used here. Indeed, phyllostomid bats do have relatively large ranges within mammals (Lyons & Willig 1997). Thus, a species or a few of them within each genus may distribute over most of the latitudinal gradient and overlap substantially with their congeneric species. Although rodents have comparatively smaller ranges than other mammalian orders (Patton *et al.* 2015), the stated large-range effect may still be



acting given that it is relative only to the species being considered (*i.e.*, those within the same genus) and thus their geographic extent. For example, considering North America, each of the three rodent genera occupy a large proportion of the continent (Figure 2) and some species may distribute over most of those extents. In fact, for each of these rodent genera, there were at least two species that occupied around half or more of the complete latitudinal extent of their genus (Supplementary Material 4). Accordingly, these relatively large-ranged species could overlap with most of their congenics and thus contribute to the observed within-genus overlaps across most latitudinal bands.

Methods applied to evaluate the latitudinal variation in species properties can also influence the outcome of analyses (Ruggiero & Werenkraut 2007, Gaston *et al.* 2008). In particular, “band methods” have been criticized for reducing the number of observations and thus the power of statistical tests (Ruggiero & Werenkraut 2007). Our application of Stevens’ method using latitudinal bands obeyed Rapoport’s original approach, but it may have biased our findings toward non-significant results, thus supporting a constant species overlap across latitude. However, the same study that highlighted the effects of methods on ecogeographical rules showed that band methods would indeed bias results but towards significant findings (*e.g.*, positive trends) instead of non-significant ones. Thus, such potential bias may not be particularly important in our study. Also, the consistency of results from evaluating distinct genera and clades (rodents and bats) with different species numbers reduces the effect of biases related to statistical power. Furthermore, recent studies applying a suite of methods for testing Rapoport’s rule (Ribas & Schoereder 2006, McCain & Bracy Knight 2013) found consistent results among these methods with no clear differences in their degree of support for the studied pattern.

Another potential methodological issue relates to Rapoport’s overlap metric itself ( $O^*$ , “intrinsic percentage overlap”). In proposing it, Rapoport highlighted the metric advantages over other metrics and its applicability under different requirements (Rapoport 1982, Fig. 5.12, p. 193). Several metrics have been proposed to measure

the association (or segregation) of species in terms of range overlap, with recent methods advocating those that consider complete sets of species within their entire domain (*i.e.*, full presence-absence matrices of species within a region; Soberón 2015, Arita 2017). The reasoning behind such recent methods is that the factors responsible for species range overlap act jointly on entire sets of species within the entire domain (Soberón 2015), thus requiring the consideration of complete species ranges and regions under study without recurring to the arbitrary division of such regions (*e.g.*, latitudinal bands) and the description of patterns within such divisions (Villalobos *et al.* 2014). Accordingly, evaluating species range overlap within latitudinal bands may thus bias the description and interpretation of the overlap pattern. Of course, all of these potential methodological issues warrant a more detailed investigation of species range overlap metrics that is beyond the scope of our study but that has already been presented in the macroecological literature (*e.g.*, Arita 2017).

To answer our original questions, we have shown that a constant overlap among species of the same genus is indeed present in mammalian genera other than Rodentia, particularly the highly diverse mammalian family Phyllostomidae. This range overlap pattern is consistent across the distribution of this bat family, which comprises most of the Neotropics. Finally, we showed that such latitudinal constant species’ ranges overlap pattern is the expected pattern given the observed variation in species range sizes and their cohesion (*i.e.*, null expectation). In exploring this forgotten idea of E. H Rapoport we have gained several insights. For instance, we have reinforced the necessity of contrasting observed patterns against appropriate null hypothesis and learned that within-genus species’ ranges overlap may be a different phenomenon from other distributional patterns among species such as overall co-occurrence within families, given that this latter pattern cannot be explained solely by range cohesion and size variation (Villalobos & Arita 2010, Villalobos *et al.* 2014). Rapoport’s ideas will continue to be influential for geographical ecology and macroecology and will still guide us on how to approach the study of one of the most interesting phenomena of life on earth: its uneven distribu-

tion across the globe. For these and for being a constant source of inspiration, we are forever indebted to E. H. Rapoport. Rest in peace.

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## REFERENCES

- Araújo, M. B., & Rozenfeld, A. 2014. The geographic scaling of biotic interactions. *Ecography*, 37(5), 406–441. DOI: 10.1111/j.1600-0587.2013.00643.x
- Arita, H. T. 2017. Multisite and multispecies measures of overlap, co-occurrence, and co-diversity. *Ecography*, 40(6), 709–718. DOI: 10.1111/ecog.01942
- Arita, H. T., Rodríguez, P., & Vázquez-Domínguez, E. 2005. Continental and regional ranges of North American mammals: Rapoport's rule in real and null worlds. *Journal of Biogeography*, 32(6), 1–11. DOI: 10.1111/j.1365-2699.2005.01276.x
- Arita, H. T., Christen, J. A., Rodríguez, P., & Soberón, J. 2008. Species diversity and distribution in presence-absence matrices: mathematical relationships and biological implications. *The American Naturalist*, 172(4), 519–532. DOI: 10.1086/590954
- Bivand, R., Keitt, T., & Rowlingson, B. 2014. rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 0.9-1. <http://CRAN.R-project.org/package=rgdal>.
- Bivand, R., & Lewin-Koh, N. 2015. maptools: Tools for Reading and Handling Spatial Objects. R package version 0.8-34. <http://CRAN.R-project.org/package=maptools>.
- Bivand, R., & Piras, G. 2015. spdep: Spatial Dependence: Weighting Schemes, Statistics and Models. R package version 0.6-8. <http://CRAN.R-project.org/package=spdep>.
- Bivand, R., & Rundel, C. 2015. rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-11. <https://CRAN.R-project.org/package=rgeos>
- Borregaard, M. K., & Rahbek, C. 2010. Dispersion fields, diversity fields and null models: Uniting range sizes and species richness. *Ecography*, 33(2), 402–407. DOI: 10.1111/j.1600-0587.2010.06323.x
- Brown, J. H. 1995. *Macroecology*. Chicago: University of Chicago Press: p. 284.
- Brown, J. H., & Maurer, B. A. 1989. Macroecology: the division of food and space among species on continents. *Science*, 243(4895), 1145–1150. DOI: 10.1126/science.243.4895.1145
- Buckley, L. B., Davies, T. J., Ackerly, D. D., Kraft, N. J., Harrison, S. P., Anacker, B. L., Cornell, H. V., Damschen, E. I., Grytnes, J.-A., Hawkins, B. A., McCain, C. M., Stephens, P. R., & Wiens, J. J. 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society of London B: Biological Sciences*, 277, 2131–2138. DOI: 10.1098/rspb.2010.0179
- Cabral, J. S., Valente, L., & Hartig, F. 2017. Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. *Ecography*, 40(2), 267–280. DOI: 10.1111/ecog.02480
- Colwell, R. K., & Hurtt, G. C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *The American Naturalist*, 144(4), 570–595. DOI: 10.1086/285695
- Colwell, R. K., Rahbek, C., & Gotelli, N. J. 2004. The mid-domain effect and species richness patterns: what we have learned so far? *The American Naturalist*, 163(3), E1– E23. DOI: 10.1086/382056
- Darwin, C. 1859. *The origin of species by means of natural selection*. London: Murray: p. 502.
- Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press: p. 280.
- Gaston, K. J., Blackburn, T. M., & Spicer, J. I. 1998.

- Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution*, 13(2), 70–74. DOI: 10.1016/S0169-5347(97)01236-6
- Gaston, K. J., Chown, S. L., & Evans, K. L. 2008. Ecogeographical rules: elements of a synthesis. *Journal of Biogeography*, 35(3), 483–500. DOI: 10.1111/j.1365-2699.2007.01772.x
- Godsoe, W., Murray, R., & Plank, M. J. 2015. The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography*, 38(11), 1071–1079. DOI: 10.1111/ecog.01134
- Gotelli, N. J., Anderson, M. J., Arita, H. T., Chao, A., Colwell, R. K., Connolly, S. R., Currie, D. J., Dunn, R. R., Graves, G. R., Green, J. L., Grytnes, J.-A., Jiang, Y.-H., Jetz, W., Lyons, S. K., McCain, C. M., Magurran, A. E., Rahbek, C., Rangel, T. F. L. V. B., Soberón, J. Webb, C. O., & Willig, M. R. 2009. Patterns and causes of species richness: A general simulation model for macroecology. *Ecology Letters*, 12(9), 873–886. DOI: 10.1111/j.1461-0248.2009.01353.x
- Guisan, A., & Rahbek, C. 2011. SESAM—a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*, 38(8), 1433–1444. DOI: 10.1111/j.1365-2699.2011.02550.x
- Harte, J. 2004. The value of null theories in ecology. *Ecology*, 85(7), 1792–1794.
- Hijmans, R. 2015. raster: Geographic data analysis and modeling. R package version 2.3-24. <http://CRAN.R-project.org/package=raster>.
- IUCN. 2015. International Union for Conservation Nature Diversity - IUCN red list of threatened species version 5.1. Retrieved on April 14, 2017, from <http://www.iucnredlist.org>.
- Jetz, W., & Rahbek, C. 2001. Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Sciences of the USA*. 98(10), 5661–5666. DOI: 10.1073/pnas.091100998
- Kaufman, D. M. 1995. Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. *Journal of Mammalogy*, 76(2), 322–334. DOI: 10.2307/1382344
- Lyons, S. K., & Willig, M. R. 1997. Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos*, 79(3), 568–580.
- MacArthur, R. H. 1972. *Geographical ecology*. Princeton: Princeton University Press: p. 269.
- Marathe, A. 2016. rangemodelR: Mid-Domain Effect and Species Richness Patterns. R package version 1.0.1. <https://CRAN.R-project.org/package=rangemodelR>
- McCain, C. M., & Bracy Knight, K. 2013. Elevational Rapoport's rule is not pervasive on mountains. *Global Ecology and Biogeography*, 22(6), 750–759. DOI: 10.1111/geb.12014
- Patton, J. L., Pardiñas, U. F. J., & D'Elia, G. 2015. *Mammals of South America, Vol. 2: Rodents*. Chicago: University of Chicago Press: p. 1336.
- Pebesma, E., & Bivand, R. 2005. sp: Classes and methods for spatial data in R. R package version 1.2-6. <https://CRAN.R-project.org/package=sp>
- Pintor, A. F., Schwarzkopf, L., & Krockenberger, A. K. 2015. Rapoport's Rule: Do climatic variability gradients shape range extent? *Ecological Monographs*, 85(4), 643–659. DOI: 10.1890/14-1510.1
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rapoport, E. H. 1975. *Areografía: Estrategias geográficas de las especies*. Mexico City: Fondo de Cultura Económica: p. 214.
- Rapoport, E. H. 1982. *Areography: geographical strategies of species*. New York: Pergamon: p. 286.
- Ribas, C. R., & Schoereder, J. H. 2006. Is the Rapoport effect widespread? Null models revisited. *Global Ecology and Biogeography*, 15(6), 614–624. DOI: 10.1111/j.1466-8238.2006.00265.x
- Ruggiero, A. 1994. Latitudinal correlates of the sizes of mammalian geographical ranges in South America. *Journal of Biogeography*, 21(5), 545–559. DOI: 10.2307/2845657
- Ruggiero, A. 1999. Búsqueda de patrones en macroecología: la regla de Rapoport. *Ecología Austral*, 9, 45–63.
- Ruggiero, A., & Hawkins, B. A. 2006. Mapping macroecology. *Global Ecology and Biogeography*, 15(5), 433–437. DOI: 10.1111/j.1466-822X.2006.00238.x

- Ruggiero, A., & Wrenkraud, V. 2007. One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. *Global Ecology and Biogeography*, 16(4), 401–414. DOI: 10.1111/j.1466-8238.2006.00303.x
- Simmons, N. B., & Conway, T. M. 2003. Patterns of range size, richness, and body size in the Chiroptera. In: T. H. Kunz & M. B. Fenton (Eds.), *Bat ecology*. pp. 493–535. Chicago: Chicago University Press.
- Šizling, A. L., Storch, D., & Keil, P. 2009. Rapoport's rule, species tolerances, and the latitudinal diversity gradient: geometric considerations. *Ecology*, 90(12), 3575–3586. DOI: 10.1890/08-1129.1
- Soberón, J. 2010. Niche and area of distribution modeling: a population ecology perspective. *Ecography*, 33(1), 159–167. DOI: 10.1111/j.1600-0587.2009.06074.x
- Soberón, J. 2015. Pairwise versus presence–absence approaches for analysing biodiversity patterns. *Journal of Biogeography*, 42(4), 807–808. DOI: 10.1111/jbi.12475
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, 133(2), 240–256. DOI: 10.1086/284913
- Stevens, R. D. 2004. Untangling latitudinal richness gradients at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. *Journal of Biogeography*, 31(4), 665–674. DOI: 10.1111/j.1365-2699.2003.01042.x
- Vilela, B., & Villalobos, F. 2015. letsR: a new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution*, 6(10), 1229–1234. DOI: 10.1111/2041-210X.12401
- Villalobos, F., & Arita, H. T. 2010. The diversity field of New World leaf-nosed bats (Phyllostomidae). *Global Ecology and Biogeography*, 19(2), 200–211. DOI: 10.1111/j.1466-8238.2009.00503.x
- Villalobos, F., Rangel, T. F., & Diniz-Filho, J. A. F. 2013. Phylogenetic fields of species: Cross-species patterns of phylogenetic structure and geographic coexistence. *Proceedings of the Royal Society B: Biological Sciences*, 280(1756), 20122570. DOI: 10.1098/rspb.2012.2570
- Villalobos, F., Lira-Noriega, A., Soberón, J., & Arita, H. T. 2014. Co-diversity and co-distribution in phyllostomid bats: Evaluating the relative roles of climate and niche conservatism. *Basic and Applied Ecology*, 15(1), 85–91. DOI: 10.1016/j.baae.2013.11.001
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505. DOI: 10.1146/annurev.ecolsys.33.010802.150448
- Wisn, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., Dormann, C. F., Forchhammer, M. C., Grytnes, J.-A., Guisan, A., Heikkinen, R. K., Høye, T. T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N. M., Termansen, M., Timmermann, A., Wardle, D. A., Aastrup, P., & Svenning, J.-C. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, 88, 15–30. DOI: 10.1111/j.1469-185X.2012.00235.x
- Supplementary Material 1.** Description of the overlap pattern among species across latitudinal bands within each studied genus and scatterplots depicting such patterns.
- Supplementary Material 2.** Simulated linear regression and correlation coefficients ( $R^2$  and  $\rho$ ) for each studied genus.
- Supplementary Material 3.** Density plots depicting the distribution of simulated coefficients for each studied genus.
- Supplementary Material 4.** Latitudinal extent of rodent species and its proportional value relative to the total extent of their respective genus.

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