Is niche divergence more likely in parapatry? A test in *Sclerurus mexicanus* sensu lato (Aves: Furnariidae)

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ABSTRACT

Aim

While species' niches are understood to diverge through time, the mode of these divergences is not fully understood. The null hypothesis of niche divergence in the present is that of conservatism; that species are likely to occur in the same environment as their ancestors and, therefore, as allopatric sister species. Alternatively, species are expected to diverge when selective pressure, such as parapatry with a congener, occurs. Here, we analyse niche divergence in a mosaic of allo- and parapatric *Sclerurus mexicanus* sensu lato populations to determine if niche divergence is more likely in parapatry.

Location

Neotropics.

Methods

We created a dataset of 1,100 vetted localities for *S. mexicanus* sensu lato, and assigned each point to each of the seven described populations. We created individual dispersal areas for each species in Maxent following: 1) a broad approach in which training areas where allowed to overlap with parapatric congeners; and 2) a narrow approach in which species dispersal areas adhered to strict parapatry and there was no overlap in training areas. We complemented these ENMs with 'random' models drawn from points within each training area, thus creating 'null' ENMs against which we could test niche divergence using the metric Schoener's D.

Results

There was no significant difference in the performance of broad and narrow training areas. Few significant divergences were found, and all of those that were found consisted of allopatric populations. Partial divergences were frequently recovered when comparing parapatric taxa.

Main conclusions

In contrast to our expectation, we found no significant evidence for increased niche divergence in parapatric versus allopatric species. Possible explanations for these findings include true conservatism even among parapatric lineages (*e.g.*, additional environmental or biological factors may delimit distributions) or artefactual errors inherent to model creation. We discuss the implications of these findings, and discuss ways to improve upon tests of niche divergence in the future, especially when dealing with cases of parapatry.

Keywords

Allopatry, ecological niche modelling, Maxent, niche divergence, parapatry, Schoener's D, *Sclerurus mexicanus*.

INTRODUCTION

Since the conception of ecological niche theory, attempts have been made to quantify the differences between the occupied niche space of different taxa (Grinnell, 1917; Elton, 1927; Hutchinson, 1957; Colwell & Futuyma, 1971; Carnes & Slade, 1982; Austin et al., 1990; Glor & Warren, 2011). These differences have been hypothesized to be key or causal to species' diversification (Orr & Smith, 1998), especially in cases of related species' groups that inhabit spatially parapatric niches. In recent years, new methods have been put forth to test how species' niches differ in ecological space, all utilizing different approaches to Ecological Niche Modeling (ENM), and all with the overarching goal of testing whether or not species truly inhabit different multivariate environmental (*i.e.*, Hutchinsonian) niches (Hutchinson, 1957; Warren et al., 2008; Blonder et al., 2014; Nunes & Pearson, 2016).

As our knowledge of species' diversification has increased, it has become apparent that most species diverge in allopatry by means of genetic drift, differential selection, and a lack of genetic mixing (Price, 2008). Likewise, our expectation of niche divergence has approached the null; that is, when species become allopatric, we hypothesize that they are more likely retain their ancestral niche and therefore appear 'conserved' via ENM tests (Peterson et al., 1999; McCormack et al., 2009; Peterson, 2011; Ryan Shipley et al., 2013; Khaliq et al., 2015; Skeels & Cardillo, 2017). Furthermore, research has shown that competition and the re-establishment of contact can drive niche (and character) divergence, and thereby result in the para- and sympatric shifts we observe in the present (Jang & Gerhardt, 2006; Kirschel et al., 2009; Wooten & Gibbs, 2012; Freeman, 2015; Miller et al., 2016).

While ecological niche divergence has been examined in allopatric complexes (e.g., McCormack et al., 2009), it has been less studied in parapatric species complexes. Given the expectation in allopatric speciation that niches remain conserved until secondary contact with a competitor occurs, it is therefore logical to hypothesize that the magnitude of niche divergence will be greater when species have a contact zone during their speciation cycle (Nunes & Pearson, 2016). This hypothesis is reinforced by our understanding of niche shifts that accompany speciation events involving species moving into parapatric habitats or geographic realms (Benkman et al., 2009; Fjeldså et al., 2011; Knowles & Massatto, 2016), and has provided the basis of a novel methodology for testing ecological niche divergence (Nunes & Pearson, 2016). There are few tests of the assumption of niche divergence within monophyletic parapatric groups (Reino et al., 2016), and it is difficult to fully assess the other factors that may be influencing species' realized niches in ENMs.

Soberón & Peterson (2005) elucidate ways to address additional factors in their **BAM** framework, highlighting three factors that are responsible for limiting species' distributions: (**B**) biotic interactions; (**A**) abiotic environmental conditions (*i.e.*, scenopoetic variables *sensu* Soberón, 2007); and (**M**) motility restrictions, such as geographic barriers (*i.e.*, an invasible area). Biotic interactions, collectively known as a species' Eltonian niche (Soberón, 2007), are often assumed to be implicitly accounted for in ENMs by a study species' absence from areas with a biotic amensal or without a biotic commensal. Linking these factors directly into an ENM is often done by restricting a species' explorable area in the initial steps of ENM creation, thereby removing regions of potential sympatry from model training (Saupe et al., 2012; de Araújo et al., 2014; Cooper & Soberón, 2018). ENMs can also opt to ignore these biotic factors, as many of the localized competitors and commensals a species encounters may not be as important as abiotic factors in large-scale spatial analyses (*i.e.*, the Eltonian Noise Hypothesis; Soberón, 2007; Soberón & Nakamura, 2009).

In order to better understand niche divergence in parapatry, we performed a multi-directional niche-difference test of a widespread species group, *Sclerurus mexicanus* sensu lato (Cooper & Barragán, 2016). Now known to comprise of at least five major groups of taxa (d'Horta et al., 2013; Cooper & Cuervo, 2017), populations of *S. mexicanus* occur in allo- and parapatric populations from central Mexico to southern Brazil, and exhibit remarkable levels of ecomorphic and phenotypic conservatism, with field reports of species' responding to unrelated, allopatric population's songs (Remsen, 2003; Cooper & Barragán, 2016). Given their lack of known sympatry, it is likely that parapatric populations are competitors with other members of the super species, and therefore provide an excellent mosaic of parapatric and allopatric

populations in which to test the magnitude of niche divergence in the presence and absence of amensals.

Here, we perform two sets of niche divergence analyses on this species complex under two alternative hypotheses: 1) that species can freely disperse into regions occupied by parapatric congeners, and 2) that species are prohibited from dispersal into regions where congeners are known occur. While both of these methods will model a species' absence in areas with direct competitors, their mechanisms in reaching these conclusions differ. The first hypothesis excludes environments that are more optimal for competitive congeners by accounting for these as "absent" environments for the species of interest, while the second hypothesis manually thresholds environments and excludes these areas from analyses altogether. The first hypothesis also assumes that species have differential competitive abilities in different parts of their shared niche space or differ to at least some extent in their fundamental niches, while the second hypothesis assumes that competitive exclusion is masking the limits of a species' ecological niche. While there is no way to get around these errors for attempting to assess a species' complete fundamental niche, it is still possible to analyze a species' realized niche and determine whether or not species are significantly differing in their occupied ecological space. Furthermore, a test of both methods will help reveal whether biotic exclusion is significantly affecting our interpretations of ecological niche divergence.

METHODS

We downloaded occurrence data for *Sclerurus mexicanus* sensu lato from the Global Biodiversity Informatics Facility (GBIF; 20 February 2015; Global Biodiversity Informatics Facility, 2016) and from eBird (EBD_relMay-2015; Sullivan et al., 2009; eBird, 2012) . These data were combined with a set of georeferenced recordings from Cooper & Cuervo (2017), and

were subsequently separated into species groups corroborated by the recordings. We recognized five species within the complex sensu Cooper & Cuervo (2017), but separated subspecies of *S. macconnelli* for niche analyses in light of the genetic monophyly of *peruvianus* with respect to *macconnelli* and the uncertain relationships of *bahiae* (d'Horta et al., 2013). We thus modeled seven recognized populations from *S. mexicanus* sensu lato, ordered in this manuscript from north to south and listed here with the number of vetted occurrences used for each: *Sclerurus mexicanus* (*n* = 532); *S. pullus* (*n* = 358); *S. obscurior* (*n* = 19); *S. andinus* (*n* = 24); *S. macconnelli peruvianus* (*n* = 77); *S. macconnelli macconnelli* (*n* = 41); and *S. macconnelli bahiae* (*n* = 49; Fig. 1). Localities were cross-referenced with the literature, and we omitted records that were unidentifiable by range or lacked physical documentation, most notably: intermediate elevations (*c.* 1200-1800 m) in the western Andes of Colombia and Ecuador where *S. obscurior* and *S. andinus* potentially overlap; an unidentified population from intermediate elevations from southern Ecuador; and an unidentified population from Ceará, Brazil (Cooper & Barragán, 2016).

Based on these occurrence data, we created accessible areas in which to train the models (hereafter, **M**s, sensu Soberón & Peterson, 2005 and Cooper & Soberón, 2018) using QGIS 2.8.2 (QGIS Development Team, 2016). **M**s were bounded by major biogeographic barriers (*e.g.*, mountain ridgelines, major rivers, ecoregion boundaries [World Wildlife Fund, 2010], etc.) and incorporated what is hypothesized to be the entire accessible area for the species (Soberón & Peterson, 2005; Guisan et al., 2006). We created two types of **M**: broad **M**s that encompassed the geographic distribution of a species and included regions of potential dispersal, including areas in which a parapatric species occurs (*i.e.*, hypothesis 1); and narrow **M**s that excluded the entirety of the distribution of a parapatric species from the training area (and are thus a subset of

the broad **M**s), with divisions approximated halfway between known populations (*i.e.*, hypothesis 2; Fig. 2).

Analyses were performed in R 3.2.5 (R Core Team, 2016), with our study following the methodology of Warren et al. (2008). Bioclimatic data were downloaded at a resolution of 2.5 arcminutes (*c.* 5 km at the equator) for four bioclimatic variables: mean temperature of the warmest quarter, mean temperature of the coldest quarter, mean precipitation of the wettest quarter, and mean precipitation of the driest quarter (Hijmans et al., 2005). Suitability models were created using the average of five raw, unclamped outputs of MaxEnt 3.3.3k (Phillips et al., 2004), using the packages 'dismo' (Hijmans et al., 2015), 'raster' (Hijmans, 2015), and 'rJava' (Urbanek, 2013). Suitability models were projected into a larger 'clade' area (an **M** encompassing the entire super species) so that all populations could be modeled within each others' distributions and suitability comparisons could be made in identical spatial and environmental extents.

Sets of random points were drawn from each population's appropriate **M** to create environmentally 'null' suitability predictions in MaxEnt for contrast against actual population comparisons using the R package 'maptools' (Bivand & Lewin-Koh, 2015). These random point sets are equal in number to the known occurrences and exclude exact coordinates of known occurrences. We used these points to create null ENMs within the **M** of each species for each hypothesis using the same methodology outlined for individual species' models. Following Warren et al. (2008), we used the metric of Schoener's D to assess niche similarity, where the metric *D* is an indicator of the similarity between MaxEnt outputs, with total dissimilarity being 0 and identical outputs being 1. We replicated these analyses 100 times bi-directionally for each of the 21 pairwise comparisons for each hypothesis to create two independent random

distributions of Schoener's D using the R package 'dismo' (Warren et al., 2008; Glor & Warren, 2011; Peterson et al., 2011; Hijmans et al., 2015). If the Schoener's D value of the direct comparison was less than the critical value (i.e. within the lower 5%) of both pseudoreplicate distributions, the comparison was scored as a "2" for being significantly divergent; if the value was significant with regard to only one distribution, the comparison was ranked as "1" for being partially divergent; no significance was ranked as "0". Plots for all comparisons were visually inspected using the R package 'ggplot2' (Wickham, 2009). We did not assess extreme conservatism, as this is indistinguishable from the null hypothesis for ecological niches between allopatric populations. Differences in performance between the two methods was assessed via a Fisher's Exact Test on the number of successes in allopatry and parapatry for broad and narrow **M**s and on the sum of the net amount of divergence for these categories.

RESULTS

A total of 21 pair-wise comparisons of *Sclerurus mexicanus* sensu lato populations for both the broad and the narrow **M**s were completed (Table 1). Using broad training areas, three of these comparisons showed significant divergence (i.e. a "2") among the populations compared, with all three of these involving comparisons with *S. macconnelli bahiae.* Twelve comparisons showed slight divergence (i.e. a "1") while the remaining six comparisons showed no evidence for ecological divergence. In almost every case of slight divergence, the critical value fell within the range of the values derived from a montane population's model compared to pseudoreplicates of its lowland congener, and not vice versa (Fig 3).

When species were modeled in narrow regions, the number of highly significant tests dropped, with only one "2" result obtained (*S. mexicanus* vs. *S. macconnelli bahiae*). In total, five comparisons lost significance (e.g., decreased from 1 to 0), eleven remained the same, and

three gained significance (always from 0 to 1), with no significant difference in **M** performance. There was no observable trend as to whether allo- or parapatry increased the likelihood of obtaining a significant result, nor was there any evidence that particular combination of habitat increased the probability of significance decreasing.

DISCUSSION

Evidence for niche divergence was strongest (i.e., a 2) only in comparisons of the Atlantic forest *S. macconnelli bahiae* to the montane and semi-montane *S. mexicanus*, *S. pullus*, and *S. andinus*. Both **M** scenarios appeared to perform equally well, with the greatest divergences restricted to broad models between aforementioned allopatric populations. These results confirm the null hypothesis that niches will remain largely conserved through time, and that niche divergence in allopatric populations only occurs when coupled with differential selective pressures. In our tests, we failed to find strong support for increased niche divergence in parapatric versus allopatric taxa, despite the expectation that secondary contact drives species into different environments.

Despite a lack of evidence of increased divergence in parapatric taxa, it is worth noting that almost every instance of partial divergence (or potentially diverging niches) was the result of a direct comparison falling within the Schoener's D distribution derived from comparing the montane population to random points from a lowland population. Given that *Sclerurus* as a whole is predominately a lowland genus, these results may indicate competitive exclusion of highland taxa from lowland areas. Alternatively, these results may indicate elevational stacking of species upon secondary contact where species segregate based on the elevations at which they out-compete one another. Such a scenario would result in different realized niches, but we would be unable to recover significant differences via ENM tests as the environmental niches would be

222abutting and potentially overlapping. Field tests of populations' physiological tolerances and 223habitat preferences will be needed to determine whether there are uni- or bidirectional amensal 224relationships dictating elevational turnover within *Sclerurus mexicanus* sensu lato.

225 Conversely, these skewed divergences may be an artefact of model design, wherein 226montane habitats are usually proportionately smaller than adjacent lowland habitats and the 227probability of selecting montane points for a null model is thus lower. Thus, lowland taxa whose 228**M**s abut mountain ranges are more likely to have random points drawn from lowlands, whereas 229montane taxa are also more likely to have lower elevational limits drawn in a random process. 230Narrow models, while limiting the amount of habitat at different elevations that can be drawn, 231fail to account for potential biotic interactions between related taxa and assume *a priori* that taxa 232that are not explicitly sympatric are amensal. Further studies into the best ways to mitigate 233inherently unequal areas of habitat between species with different elevational ranges are needed 234to understand the best way to compensate for these inequalities, and the usage of presence-only 235techniques may be warranted (*e.g.*, minimum volume ellipsoids; Van Aelst & Rousseeuw, 2009).

236 We are aware of one other study that assessed multiple related taxa in a mosaic of allo- 237and parapatric distributions: McCormack et al. (2009). They likewise failed to find strong 238support for niche divergence in allopatric populations, and noted the apparent conservatism of 239niches within their study genus, *Aphelocoma* (Aves: Corvidae). McCormack et al. (2009) used 240defined distributions to determine areas for drawing random points and filtering occurrence data, 241but apparently did not use **M**s to constrain taxa-specific ENMs. Similar to this study, many of the 242taxa in question are restricted to montane habitats and thus have a predilection for random points 243being drawn from lowland habitats, especially when dispersal limitations are not enforced for 244individual ENMs. Coincidentally, McCormack et al.'s (2009) sympatric species pair possessed

Schoener's D distributions closely resembling our parapatric comparisons, wherein the test indicates unidirectional, potentially ongoing niche divergence.

Implications

Given the results of this and other studies using Warren et al.'s (2008) methodology for determining niche divergence, it is possible that parapatric species may not be recoverable as possessing different ecological niches using this framework. We know from specimen and vocal data that members of *Sclerurus mexicanus* sensu lato occupy elevational gradients in the Andes, and thus infer that these species must possess some differences in their ecological niches. However, the topography of these regions and the nature of the modeling programs used may make quantifying full niche divergence impossible. Furthermore, the potential biotic element of these scenarios – amensal relationships with congeners – implies that species' distributions may be extremely proximate in nature and thus difficult to fully distinguish using broad-scale ENM procedures. The absence of a competitor in part of a species' distribution may also influence the recovered environmental niche breadth; *i.e.*, species may overlap environmentally with competitors in models due to records from areas where competitors are not present and thus not limiting a species' niche or distribution (Connell, 1961).

Investigations into presence-only methods for determining niche divergence are needed, as well as continued explorations of lesser-used variables such as elevation and tree cover (Cord et al., 2014; Title & Bemmels, 2017). While differences in fundamental niche will necessitate field research into species' physiological tolerances, presence-only methods will serve to circumvent topographical and areal biases that are introduced from pseudoabsence data. Further examinations of niche difference tests are also needed to determine if unidirectional shifts are typical for proximate species that differ in their realized ecological niches. While the results we

present are not as significant as we expected, it is entirely plausible that they still exhibit evidence of realized niche divergence, and should be investigated as such.

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Figures

Figure 1. The estimated geographic distribution of different *Sclerurus mexicanus* sensu lato populations from and basemap from Cooper & Cuervo (2017) with an overlay of training points from this study. Question marks indicate areas in which the population's identity has not been corroborated with vocal data or genetic data.

Figure 2. Narrow (left) and broad (right) training areas for three study taxa, listed from north to south: *S. pullus, S. obscurior,* and *S. andinus*. In the narrow training areas, strict parapatry (*i.e.*, no sympatry) is enforced.

Figure 3. A comparison of broad models for *Sclerurus andinus* and *Sclerurus m. macconnelli*. The red (left) distribution is the random iterations of *S. andinus* compared to the true *S. m. macconnelli*, while the blue-green (right) distribution is the random iterations of *S. m. macconnelli* compared to *S. andinus*. Vertical dashed lines represent the critical values for this test (i.e. the point at which any test to the left has a *P* value of 0.05 or lower), while the solid vertical is the test statistic of the true ENM of *S. andinus* compared to the true ENM of *S. m. macconnelli*. As with many tests of montane vs. lowland taxa, the test was significant for the distribution of random lowland derived models, but not for random montane models.

mexicanus
andinus
pullus
obscurior
?
?
macconnelli
?
peruvianus
bahiae

Figure 1.

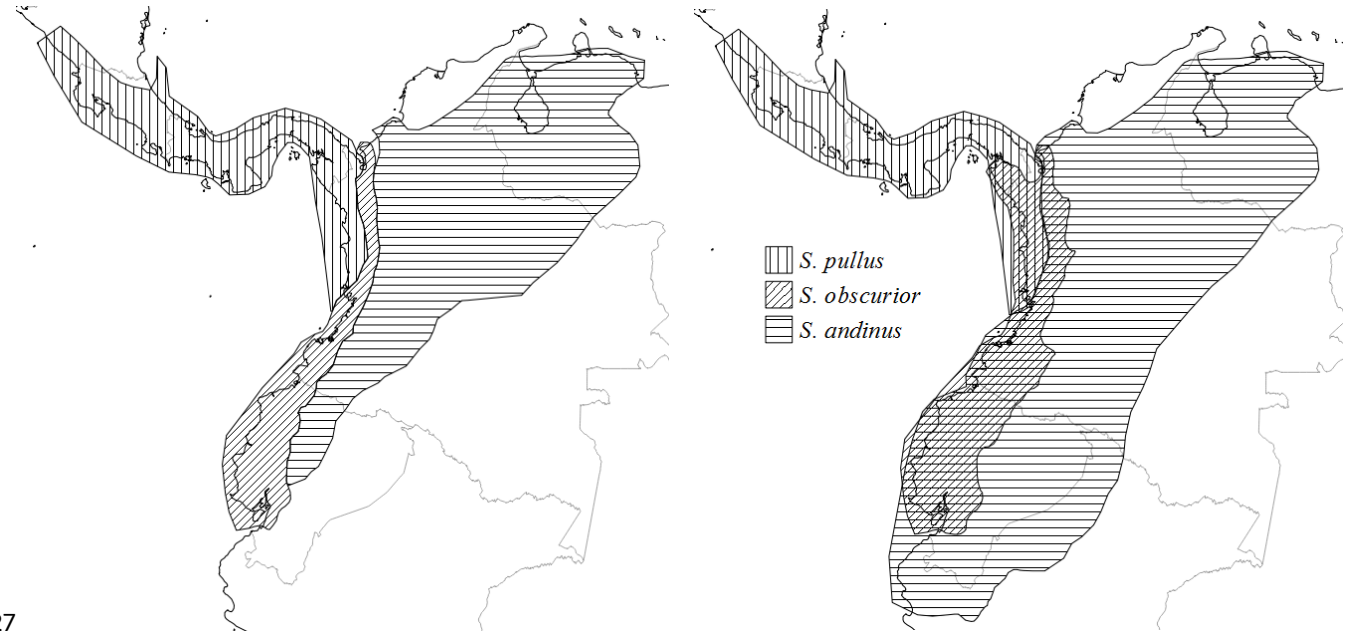
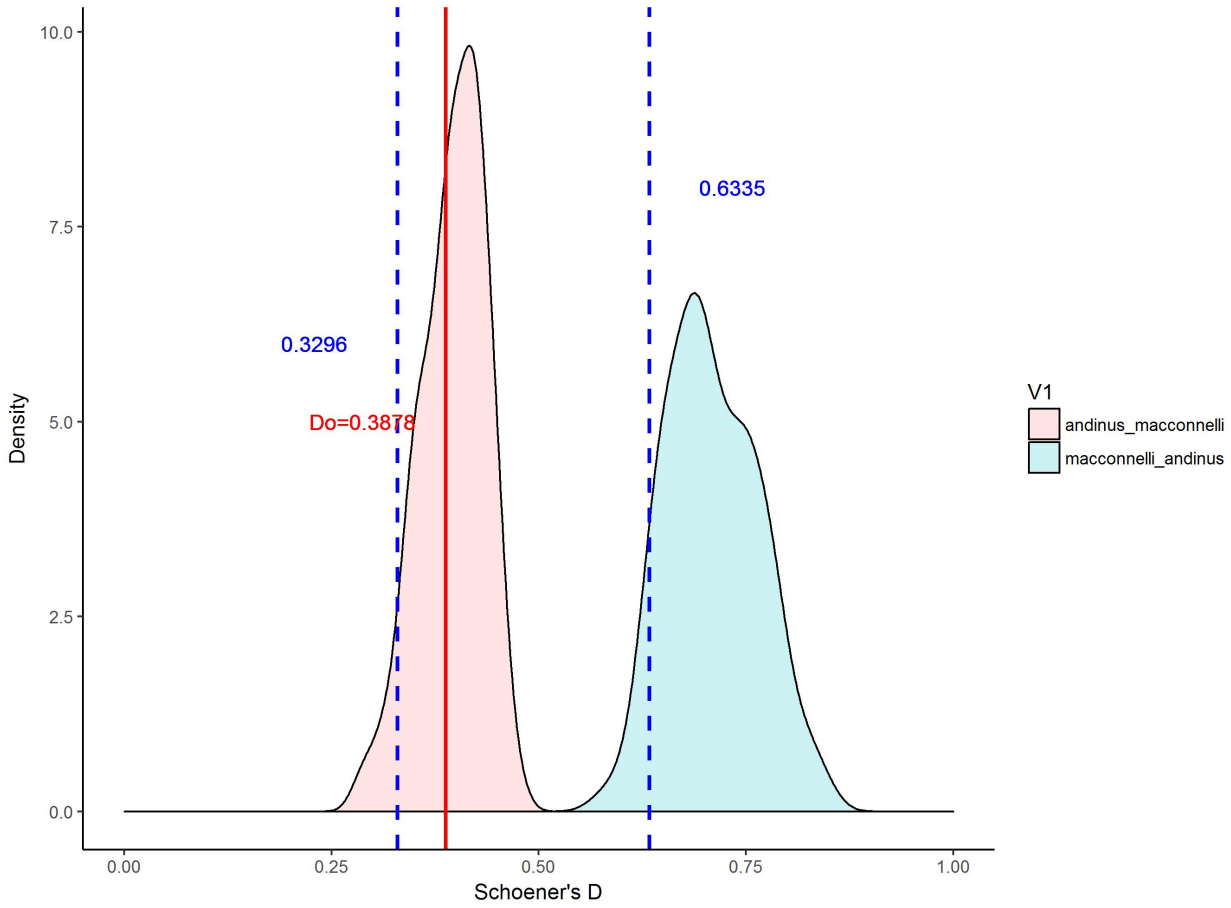


Figure 2.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7.5
5.0
2.5
0.0
Density
0.3296
Do=0.3878
0.6335
0.00
0.25
0.50
0.75
1.00
Schoener's D
V1
andinus_macconnelli
macconnelli_andinus

Figure 3.

Tables

Table 1. Pairwise comparisons of Schoener's D for all combinations of *S. mexicanus* populations. Significance is ranked thusly: 2 = comparison was significant for the tails of both bidirectional comparisons; 1 = test was significant for one of the bidirectional comparisons; 0 = test was not significant.

Populations	**Broad *M* Results**	**Narrow *M* Results**	**Allopatric ?**	**Parapatric?**
andinus-bahiae	2	1	Yes	
andinus-macconnelli	1	1	Yes	
andinus-mexicanus	0	0	Yes	
andinus-obscurior	1	1		Yes
andinus-peruvianus	0	0		Yes
andinus-pullus	1	0	Yes	
bahiae-macconnelli	0	1	Yes	
bahiae-mexicanus	2	2	Yes	
bahiae-obscurior	1	1	Yes	
bahiae-peruvianus	1	0	Yes	
bahiae-pullus	2	0	Yes	
macconnelli-mexicanus	1	1	Yes	
macconnelli-obscurior	1	0	Yes	
macconnelli-peruvianus	1	1		Yes
macconnelli-pullus	1	1	Yes	
mexicanus-obscurior	1	1	Yes	
mexicanus-peruvianus	0	0	Yes	
mexicanus-pullus	0	1	Yes	
obscurior-peruvianus	1	1	Yes	
obscurior-pullus	1	1		Yes
peruvianus-pullus	0	1	Yes	

Table 1.