UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
SISTEMÁTICA

ANÁLISIS INTEGRATIVOS DE LA ESPECIACIÓN EN EL COMPLEJO *Arremon brunneinucha*

(AVES: EMBERIZIDAE) EN MESOAMÉRICA

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

Brotherhood means not similar: Environmental overlap in the *Arremon brunneinucha*

complex (Aves: Passerellidae) in a Mesoamerican landscape

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO(A) EN CIENCIAS BIOLÓGICAS

PRESENTA:

ISRAEL MORENO CONTRERAS

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FACULTAD DE CIENCIAS, UNAM
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UNAM
Dra. María del Coro Arizmendi Arriaga
UNAM
CD. MX.   FEBRERO, 2019

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POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
DIVISIÓN ACADÉMICA DE INVESTIGACIÓN Y POSGRADO

OFICIO FCIE/DAIP/1169/2018

ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e.

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **1 de octubre de 2018** se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Sistemática** del alumno **MORENO CONTRERAS ISRAEL** con número de cuenta **517007590** por la modalidad de graduación de **tesis por artículo científico** titulado: "Brotherhood means not similar: Environmental overlap in the *Arremon brunneinucha* complex (Aves: Passerellidae) in a Mesoamerican landscape", el cual fue producto del proyecto realizado en la maestría que lleva por título "**Análisis integrativos de la especiación en el complejo** *Arremon brunneinucha* **(Aves: Emberizidae) en Mesoamérica**" realizado bajo la dirección del **DR. ADOLFO GERARDO NAVARRO SIGÜENZA** quedando integrado de la siguiente manera:

Presidente:	DR. OCTAVIO RAFAEL ROJAS SOTO
Vocal:	DRA. MERCEDES DEL PILAR RODRÍGUEZ MORENO
Secretario:	DR. LUIS ANTONIO SÁNCHEZ GONZÁLEZ
Suplente:	DRA. ÁNGELA PATRICIA CUERVO ROBAYO
Suplente:	DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA

Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 4 de diciembre de 2018

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

FACULTAD DE CIENCIAS
DIVISIÓN ACADÉMICA DE
INVESTIGACIÓN Y POSGRADO

AGNS/VMVA/ASR/grf*

ÍNDICE

Resumen

La identificación de los mecanismos que han generado la biodiversidad es una de las tareas principales en biogeografía y biología evolutiva. En este estudio, utilizando datos climáticos de alta resolución y registros de presencia obtenidos de especímenes de museos, evaluamos si los linajes alopátricos y parapátricos estrechamente relacionados dentro del complejo *Arremon brunneinucha* (Aves: Passerellidae) son ecológicamente más similares o diferentes respectivamente en su distribución en Mesoamérica. Esta información se utilizó para analizar (a través del enfoque PCA-env y las pruebas de similitud) la evolución de nicho en este complejo de especies y evaluar el papel relativo de los factores geográficos y ambientales en la configuración de la divergencia de linajes. Nuestros resultados sugieren que la mayoría de los linajes evolutivos alopátricos y parapátricos considerados en el complejo *A. brunneinucha* tienen un traslape de nichos climáticos de bajo a moderado (*D* de Schoener: 0.0 - 0.4). Del mismo modo, la hipótesis nula (es decir, el conservadurismo de nicho) se rechazó en ambas direcciones para el 60,71% de los casos de comparación. Encontramos que los linajes parapátricos muestran evidencia de que sus nichos ecológicos se han mantenido mediante gradientes climáticos marcados. Este patrón es indicativo de que los nichos de estas unidades evolutivas se han adaptado a diferentes condiciones ambientales en todo Mesoamérica. Es probable que estas diferencias reflejen el tiempo de divergencia de los linajes de este complejo, y sus respuestas a diferentes presiones selectivas y evolutivas.

Abstract

The identification of mechanisms that have generated biodiversity is one of the major tasks in biogeography and evolutionary biology. Here, using high-resolution climatic data and presence records obtained from museum specimens, we assessed whether closely related allopatric and parapatric lineages in the *Arremon brunneinucha* (Aves: Passerellidae) complex are either more ecologically similar or different respectively throughout their distribution in Mesoamerica. This information was used to analyse (through PCA-env approach and similarity tests) the niche evolution in this species complex and assess the relative role of geographic and environmental factors on shaping lineage divergence. Our results suggest that most allopatric and parapatric evolutionary lineages considered in the *A. brunneinucha* complex have a low to moderate climatic niche overlap (Schoener's D: 0.0 – 0.4). Likewise, the null hypothesis (i.e., niche conservatism) was rejected in both direction for 60.71% of comparison cases. We found that parapatric lineages show evidence that their ecological niches have been maintained by sharp climatic gradients. This pattern is an indicative that niches of these evolutionary units have been adapted to different environmental conditions throughout Mesoamerica. Such differences are likely to reflect the diversity of age and viability of different taxa, which are responding to different selective and evolutionary pressures.

I. INTRODUCCIÓN GENERAL

La identificación de los mecanismos que han generado la biodiversidad es una de las principales tareas en el estudio de la biogeografía y biología evolutiva. Una pregunta destacada en biología evolutiva es determinar si los procesos intrínsecamente genéticos o extrínsecos ecológicos generalmente impulsan la especiación (Coyne y Orr 2004; Schluter 2009). El primer modelo llamado mutación ordenada sugiere que el aislamiento reproductivo se debe a la ocurrencia aleatoria y fijación de diferentes mutaciones genéticas entre poblaciones adaptándose a presiones selectivas similares (Schluter 2009). Mientras que el modelo de especiación ecológica teoriza que la selección natural conduce al aislamiento reproductivo entre linajes debido a la adaptación a nichos ecológicos específicos (Van Valen 1976; Coyne & Orr 2004; Price 2008). Estos procesos pueden actuar en sinergia o de forma independiente y promover la especiación (Avise 2000). Sin embargo, a pesar de que la división entre linajes puede ser promovida principalmente por la alteración geográfica del nicho ecológico óptimo de las especies, también es posible que los linajes incipientes no logren adaptarse a las condiciones climáticas locales debido al conservadurismo de nicho (Hua y Wiens 2013). Por lo tanto, los cambios climáticos y ambientales pueden crear oportunidades ecológicas para que los organismos se adapten a entornos nuevos y, consecuentemente, pueden causar una diferenciación y evolución (Wiens y Graham 2005; Wiens 2008).

En los últimos años, la modelación de nichos ecológicos (MNE) han recibido una atención cada vez mayor en diferentes campos de la biología, como una metodología que permite probar diferentes escenarios de especiación y evolución de los nichos grinellianos (McCormack et al. 2010). Además, la disponibilidad de datos ambientales ha influido en la investigación de la especiación (Kozak et al. 2008; Peterson et al. 2011). Los MNE ha permitido probar el papel de la ecología y las barreras geográficas para la especiación en el espacio y el tiempo a través de la comparación de nichos grinnellianos (Kozak y Wiens 2006; Rödder y Engler 2011).

Los rascadores del complejo *Arremon brunneinucha* (Aves: Passerellidae) habitan en los bosques montanos de pino y encino de los neotrópicos, mostrando patrones dramáticos de diferenciaciones poblacionales, pero han sido reconocidos como un taxón cuyas relaciones filogenéticas y evolución han demostrado ser difíciles de comprender (Parkes 1954; Parkes 1957; Remsen & Graves 1995). El grupo, anteriormente considerado dentro del género *Buarremon* (Dicknson 2003), se ha clasificado

tradicionalmente en tres especies: *A. virenticeps* ("cejas verdes") endémica del centro de México, y dos complejos de especies politípicas y de amplia distribución, es decir, *A. torquatus* ("ceja blanca") que va desde el sur de América Central hasta los Andes del noroeste de Argentina y *A. brunneinucha* ("gorra castaña"), distribuida desde el este de México hasta los Andes del sur de Perú (Dicknson 2003).

Los estudios moleculares en este taxón han sugerido una considerable estructura poblacional a escalas espaciales pequeñas (Peterson et al. 1992), así como a escalas espaciales grandes, lo que ha permitido la detección de aparentes discordancias entre la morfología y los análisis moleculares basados en secuencias (Cadena et al. 2007; Navarro-Sigüenza et al. 2008; Navarro-Sigüenza et al. 2013). Los resultados en estos estudios coinciden, desde una perspectiva biogeográfica, en que cada linaje está restringido a una sola cadena montañosa. Este patrón de distribución geográfico para el complejo *A. brunneinucha*, se relaciona también con la historia compleja de las cadenas montañosas mesoamericanas, que han aislado y promovido el contacto en varios ciclos de tiempo de muchos grupos biológicos en tiempos evolutivos y ecológicos (Sánchez-González et al. 2008).

Teniendo en cuenta que los linajes evolutivos dentro del complejo *A. brunneinucha* son en gran parte alopátricos, pero que en Mesoamérica algunos de ellos aparentemente coexisten en parapatría (por ejemplo, *A. b. suttoni-A. kuehnerii*; Fig. I) (Navarro-Sigüenza et al. 2013), este complejo de especies representa un modelo adecuado para analizar el conservadurismo de nicho y el traslape ambiental en la divergencia de las poblaciones. Los estudios recientes sugieren divergencia genética entre las poblaciones de *A. brunneinucha*, por lo que es importante evaluar si esta diferenciación evolutiva es acompañada también de divergencia de nicho. Esta información es relevante no sólo para identificar los patrones de variación genética y morfológica en toda la distribución de las especies, sino también para comprender los factores (e.g. selección natural, deriva genética) que podrían haber influido en la divergencia (Peterson et al. 2011; Rödder & Engler 2011; Navarro-Sigüenza et al. 2013).

En el presente estudio, utilizando datos climáticos de alta resolución (aproximadamente 1 km^2) junto con registros de presencia obtenidos de especímenes de museos, estudiamos la evolución de nicho en el clado mesoamericano del complejo *A. brunneinucha* para evaluar el papel relativo de los factores geográficos y ambientales en la configuración de la divergencia dentro del complejo (Navarro-Sigüenza et al. 2008). Específicamente, examinamos si: (1) los linajes alopátricos y parapátricos estrechamente relacionados son ecológicamente más similares o diferentes, respectivamente en el

espacio ambiental ("E-space"), a lo largo de su distribución en el norte de Mesoamérica. Los resultados y análisis se ven reflejados en el manuscrito anexo que fue enviado para su evaluación a la revista Nature Scientific Reports.
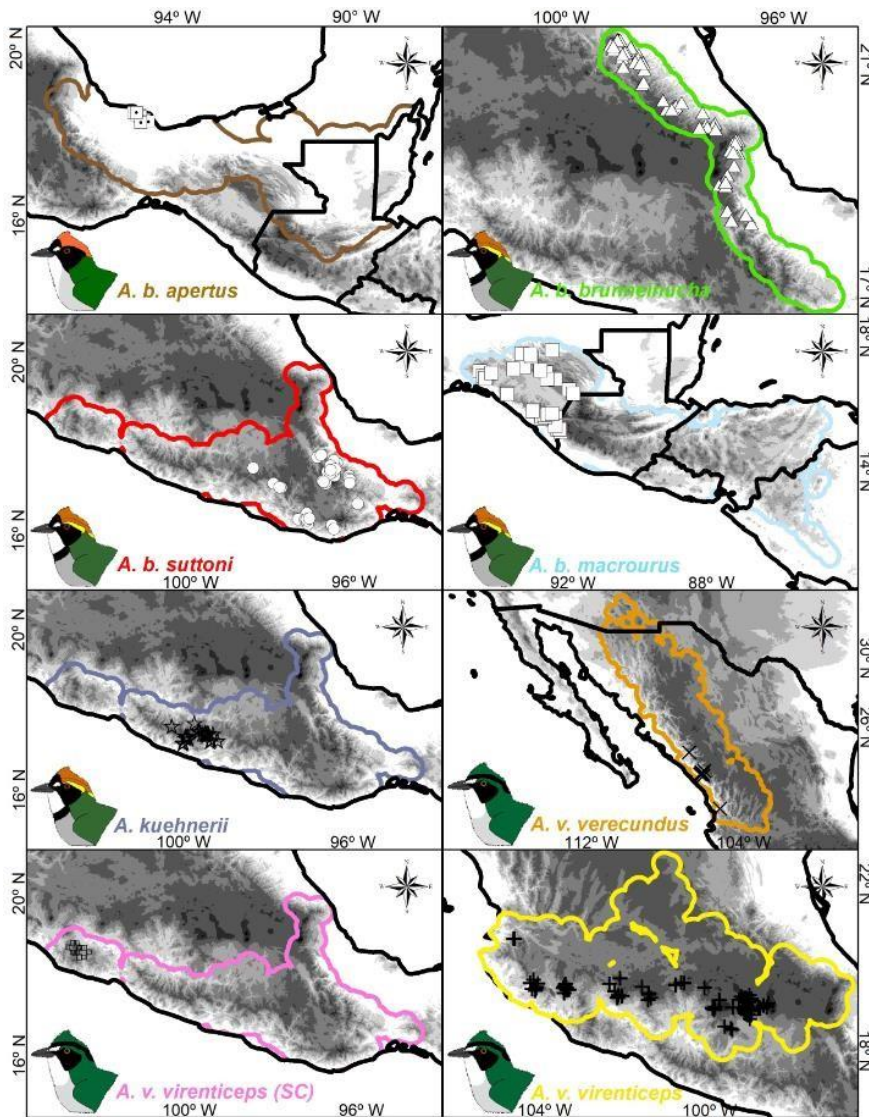
Figura I. Áreas accesibles y registros de presencia de cada linaje evolutivo dentro del complejo *Arremon brunneinucha*. Las aves que se encuentran dentro de cada mapa representan el morfo (con cejas verdes y gorra castaña) que caracteriza a cada linaje.
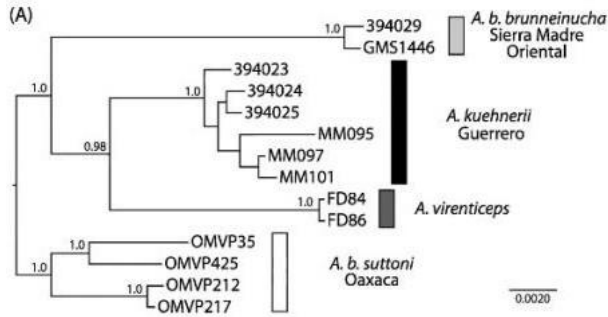
Figura II. Árbol de consenso bayesiano mostrando las relaciones filogenéticas de *Arremon* basado en datos mitocondriales y nucleares de cinco genes concatenados (Navarro-Sigüenza et al. 2013). Los números sobre las ramas indican probabilidades posteriores bayesianas por encima de 0.95.
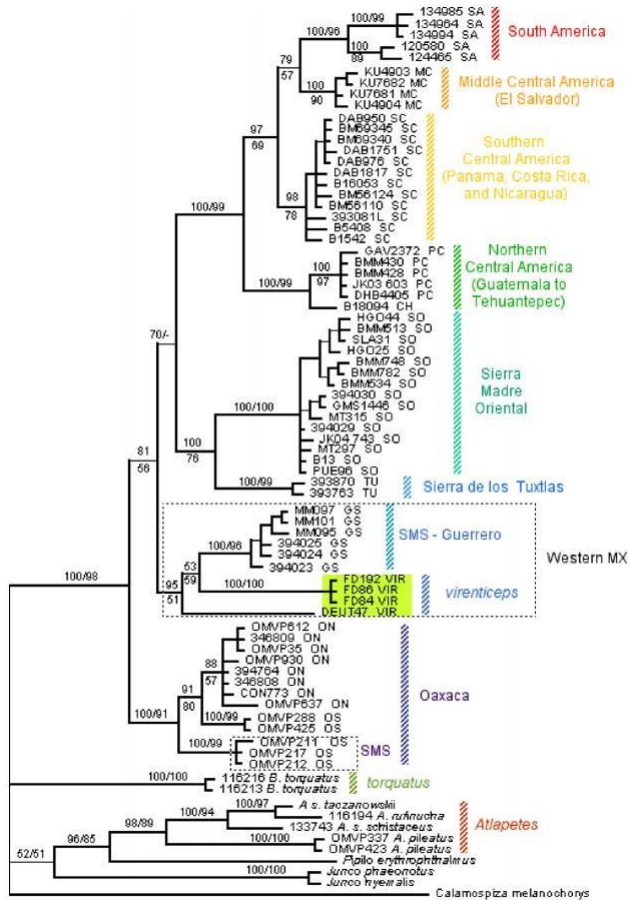
Figura III. Árbol bayesiano mostrando las relaciones filogenéticas del complejo *Arremon brunneinucha* basado en datos mitocondriales (Navarro-Siguenza et al. 2008). Los valores en los nodos indican las probabilidades posteriores (arriba) y el soporte de bootstrap (abajo).

III. MANUSCRITO

Moreno-Contreras, I., L. A. Sánchez-González, M. C. Arizmendi, D. A. Prieto-Torres & A. G. Navarro-Sigüenza. 2018. Brotherhood means not similar: Environmental overlap in the *Arremon brunneinucha* complex (Aves: Passerellidae) in a Mesoamerican landscape. *Nature: Scientific Reports* (En revisión).

Brotherhood means not similar: Environmental overlap in the *Arremon brunneinucha* complex (Aves: Passerellidae) in a Mesoamerican landscape

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The identification of mechanisms that have generated biodiversity is one of the major tasks in biogeography and evolutionary biology. Here, using high-resolution climatic data and presence records obtained from museum specimens, we assessed whether closely related allopatric and parapatric lineages in the *Arremon brunneinucha* (Aves: Passerellidae) complex are either more ecologically similar or different respectively throughout their distribution in Mesoamerica. This information was used to analyse (through PCA-env approach and similarity tests) the niche evolution in this species complex and assess the relative role of geographic and environmental factors on shaping lineage divergence. Our results suggest that most allopatric and parapatric evolutionary lineages considered in the *A. brunneinucha* complex have a low to moderate climatic niche overlap (*Schoener*'s D: 0.0 – 0.4). Likewise, the null hypothesis (i.e., niche conservatism) was rejected in both direction for 60.71% of comparison cases. We found that parapatric lineages show evidence that their ecological niches have been maintained by sharp climatic gradients. This pattern is an indicative that niches of these evolutionary units have been adapted to different environmental conditions throughout Mesoamerica. Such differences are likely to reflect the diversity of age and viability of different taxa, which are responding to different selective and evolutionary pressures.

Introduction

The identification of mechanisms that have generated biodiversity is one of the major tasks in biogeography and evolutionary biology. An outstanding question in evolutionary biology is whether intrinsic genetically-based or extrinsic ecologically-based processes generally drive speciation[1-2]. The first model suggests fixation of different genetic mutations when adapting to similar selective pressures[1], while the ecological speciation model theorizes that natural selection leads to reproductive isolation between lineages because adaptation to distinctive ecological niches[2-4]. By acting together or separately, these different factors could promote speciation[5]. However, despite the split between lineages may be mostly promoted by the geographic disruption of the optimal ecological niche for the species, these incipient lineages may fail to adapt to climatic conditions there because they maintain similar niche over time (i.e., niche conservatism)[6]. Therefore, niche differentiation could occur only when there is a significant accumulation of ecological divergence after split of lineages over space[7-9].

In recent years, ecological niche models (ENMs) have received increasing attention in different biological fields as a methodology that allows testing of different speciation scenarios, and on the evolution of environmental niches[10]. Moreover, the recent availability of high amounts of environmental data from satellites and weather stations worldwide has infused speciation research with large-scale ecological data for the first time[11,12]. This methodological approach have allowed the testing of the role of the ecology and geographic barriers for speciation in space and time thorugh the comparison of Grinnellian niches[13,14], in both geographical (through species distribution models [SDM] outputs) and ecological (using multivariate statistics such as principal components analyses [PCAs]) spaces[15,16].

Brushfinches of the *Arremon brunneinucha* complex inhabit montane pine-oak and cloud forests of the Neotropics, show dramatic patterns of population differentiation, but have been long recognized as a taxon whose phylogenetic relationships and evolution have proved to be difficult to understand[17-19]. The group, formerly considered within the separate genus *Buarremon*[20], has traditionally been classified into three species: *A. virenticeps* ('green-striped') endemic to central Mexico, and two polytypic and broadly distributed species complexes, namely *A. torquatus* ('stripe-headed') ranging from southern Central America to the Andes of northwestern Argentina and *A. brunneinucha* ('chestnut-capped')*,* distributed from eastern Mexico to the southern Andes of Perú[20]. Molecular studies in this latter, have indicated considerable population structuring at small spatial scales[21], as well as at large spatial scales, which allowed the detection of apparent mismatches between morphology and sequence-based analyses[22-24]. Results in these studies coincide, from a biogeographic perspective, in that each lineage is restricted to a single mountain range. This geographical pattern of distribution for *A. brunneinucha* complex is related also to the complex history of Mesoamerican mountain chains, that have isolated and promoted contact in several time cycles of many biological groups in evolutionary and ecological times[25].

Considering that evolutionary lineages within the *A. brunneinucha* complex are largely allopatric throughout, but that in Mesoamerica some of them apparently coexist in parapatry (e.g., *A. b. suttoni-A. kuehnerii*; Fig. 1)[24], this species complex represent a suitable model to analyse niche conservatism and environmental overlap on populations divergence. Because all recent information suggests divergence among *A. brunneinucha* populations, it is important to conduct a study that allows identifying whether niche divergence accompanies this evolutionary differentiation. In fact, as niche divergence and/or environmental variation could promote

population differentiation and/or cryptic speciation between closely related lineages[26], this information is relevant to not only identifying the patterns of genetic and morphologic variation throughout the species distribution, but also understand the factors that could have influenced the divergence[12,14,24].

Here, using high-resolution climatic data in conjunction with presence records obtained from museum specimens, we studied niche evolution in the Mesoamerican clade of the *A. brunneinucha* complex[23] to assess the relative role of geographic and environmental factors on shaping divergence within the species. Specifically, we examine whether: (1) closely related allopatric and parapatric lineages are either more ecologically similar or different respectively throughout their distribution in Mesoamerican environments (environmental space; E-space); and (2) the mismatch observed for the ecological variation among lineages corresponds to the presence of barriers to gene flow and/or the spatial structure of the ecosystems.

Results

Environmental data. According to our PCA analysis, the first two components explained 50.1% and 29.9% of variation respectively, and were used to represent in a bidimensional gradient the environmental conditions (Fig. 2), as well as the niches for each lineage (Fig. 3a), throughout Mesoamerica. PC1 was mainly represented by the variables bio 2, bio 12, and bio 4; while the PC2 was explained mainly the bio 3, bio 15, and bio 14 (Fig. 2). This ordination approach using PCA-env, revealed niche patterns for each lineage pair in E-space under the background defined. Overall, the green-striped group (*A. virenticeps*) but including the chestnut-capped form *A. kuehnerii*, were associated to more seasonal temperature gradients and less rainfall than the remaining chestnut-capped populations (Fig. 3a). Nevertheless, chestnut-capped populations (excluding *A. kuehnerii*) have a wider isothermality than their nearly morphologically similar *A.*

b. apertus (distributed in Sierra de Los Tuxtlas, Veracruz, Mexico) and *A. b. macrourus* (distributed in Central American, Chiapas and Chimalapas montane forests). On the other hand, four 'eastern' chestnut-capped brushfinch lineages (*A. b. apertus*, *A. b. brunneinucha*, *A. b. suttoni*, and *A. b. macrourus*) tended to be present in areas that show an increase of humidity, such as total precipitation of driest month.

Niche overlap in E-space and similarity test. According to the niche overlap values observed, we found 17 paired comparisons (60.7% of cases) with a null overlapping, including allopatric and parapatric lineages (Fig. 3b). Only two comparisons showed niche overlap categorized as a low overlap (i.e., 0.2–0.4). These latter correspond to comparisons between the allopatric *A. v. verecundus* and *A. v. virenticeps*, and between *A. kuehnerii* and *A. v. virenticeps*. On the other hand, the background similarity tests, which take into account the availability of conditions across accessible areas by lineages, indicated generally little similarity among the eight lineages (Fig. 3b). In this sense, the null hypothesis was rejected ($P > 0.5$) for 17 cases (60.71%) in both directions, while 9 (32.14%) comparisons were significant in only one direction. We do not reject the null hypothesis (i.e., niche conservatism) only in two cases (7.14%), considering both directions (Fig. 3b).

As predicted, allopatric chestnut-capped lineages and almost all allopatric green-striped lineages from Mesoamerican cloud forests (including populations of *A. virenticeps* in the Sierra de Coalcomán) have a low niche overlap (*Schoener*'s D < 0.5; Fig. 3b). For example, in the most extreme cases of allopatry between chestnut-capped lineages, *A. b. apertus* was significantly different in three out of four comparisons, being the exception when compared to *A. b. suttoni* background (Fig. 3b). Niche overlap between the parapatric chestnut-capped lineages was significantly different in both directions for *A. b. brunneinucha–A. b. suttoni*, while that the

comparison including the morphologically similar *A. b. suttoni–A. kuehnerii* was significative only in one direction. The null hypothesis was rejected ($P > 0.05$) in both directions for five comparisons (10 in total) involving only chestnut-capped lineages. Conversely, allopatric green-striped lineages have a moderate niche overlap, except *A. v. virenticeps* populations from Sierra de Coalcomán (Michoacán). The null hypothesis was rejected ($P > 0.05$) in two comparisons (3 in total) involving only green-striped lineages in both directions. When the morphologically different *A. kuehnerii* is compared with its sister lineage (the 'green-striped' *virenticeps* group), the null hypothesis was rejected twice (i.e., *A. v. verecundus* and *A. v. virenticeps*).

Discussion

Ecological niche overlap studies have been conducted under different conditions (using species distribution models or raw environmental data) and in several taxa[10,13,14,27]. This approach is a subject of central interest in biology, because it allows a better understanding on the relationships between evolution and ecology in changing landscapes[7-9]. Pioneering studies in different taxonomic groups have generally suggested niche conservatism as one of the main drivers of allopatric and parapatric speciation[13,28,29]. Therefore, it has become increasingly common to combine genetic and morphologic data along with ecological niche modelling to determine the relative contribution of geographic and environmental factors on population divergence, which in turn is important for species delimitation[9,30].

Our results using PCA-env[16], suggest that most allopatric and parapatric evolutionary lineages considered in the *A. brunneinucha* complex have a low to moderate climatic niche overlap. This pattern is an indicative that niches of these evolutionary units have been adapted to different environmental conditions throughout Mesoamerica. Such differences are likely to reflect the diversity of evolutionary processes that promote the formation of new lineages in each

15

case. In fact, the genetic isolation between lineages for significant periods of time[21,23], the phylogenetic distinctiveness[22,24], and the incidence of climatic historical events such as establishment of warm and dry conditions in the lowland valleys[25,31], represent important evidences on the separation of montane sister lineages, as well as on promoting niche differentiation before or during habitat fragmentation throughout the different Mesoamerican mountain ranges.

We found that parapatric lineages (*A. kuehnerii* and *A. b. suttoni*) show evidence that their ecological niches were generated or have been maintained by sharp climatic gradients (Fig. 3). For this case, we observed that *A. kuehnerii* maintained a similar niche when randomized in the environmental background of *A. b. suttoni*, but not the opposite. One potential interpretation for this pattern is that the range limits for both lineages may have been settled by ecological interactions to sister lineages rather than by climatic tolerances[19], as well as by physical barriers, such as major lowland rivers limiting the distribution of both lineages along central Sierra Madre del Sur preventing gene flow[13]. Parapatric sister species may have been originated in allopatry, and later came into secondary contact along a sharp environmental gradient[6] in the easternmost region of the Sierra Madre del Sur, as in of *A. b. suttoni*. Both lineages from Sierra Madre del Sur not only share somewhat similar Grinnellian niches, but also similar plumages patterns. From this perspective, we assumed that plasticity of plumage features among lineages of *A. brunneinucha* complex is outstanding[17,18] due to adaptations for foraging and flight efficiency, camouflage, and thermoregulation[32].

On the other hand, we observed that green-striped lineages do not occur in more humid environments than the more reddish coloured chestnut-capped ones. Considering that parapatric range boundaries are generally associated with environmental gradients[11], it is important to note

that in the case of closely-related species in montane regions, northern Mesoamerica (from southern Mexico to northern Nicaragua) is characterized by a greater seasonality in both temperature and precipitation in comparison to southern of region[33]; therefore, differentiation of these populations may be attributed to the presence of important topographic-ecological barriers to dispersal (e.g., Tehuantepec Isthmus and the Balsas Depression)[25,31]. In fact, a recent study evaluating the environmental overlap with the *Desmopsis-Stenanona* clade (Annonaceae), supports the idea that conservatism in climatic tolerances has been one of the main diversity drivers in tropical rainforests of Mesoamerica[33].

We found that both the green-striped lineages and the chestnut-capped *A. kuehnerii* had more restricted ecological niches, which is likely the reflection of specific climatic requirements that may limit their respective geographic ranges. Many genera and families of vertebrates are geographically restricted and so experience a limited range of environmental variation, making climatic niche conservatism harder to detect[9]. A more refined characterization of the niches of the lineages we have examined would require detailed and spatially extensive field studies and doubtless include variables beyond the climatic and vegetation variables[10,34]. Considering branch lengths in the phylogeny, in those evolutionary lineages with more restricted niches (i.e., *A. kuehnerii* and *A. virenticeps* group), the divergence processes are still very recent and therefore the prediction is kept at least in one direction within the similarity test. This propensity to conserve the main components of their ancestral niche is observed, because most of them partially share the environmental space of the first diverging lineage (*A. b. suttoni*) in the phylogeny (Fig. 3)[23,24].

Finally, despite previous studies showing mixed plumage patterns across bird populations[35], the geographical and ecological analyses trace an evolutionary history for

Arremon brunneinucha complex shaped by isolation of populations across topographic-ecological barriers that may favour genetic divergence among lineages. However, the degree in which such divergence is coupled with changes in the ecological variation among lineages is not similar among those closely related allopatric and parapatric populations. Therefore, it would be valuable to test whether isolated populations may be responding to different selective pressures that promote or constrain evolution. This study may also be useful in guiding research with regard to lineage diversification and niche evolution in global threatened ecosystems under a systematic conservation planning[12,31].

Methods

Presence data gathering. Records were obtained from the 'Atlas of distributions of Mexican birds'[36], a database that has focused on comprehensive capture of distributional data from Mexican bird specimens housed in 70 scientific collections (accession date: 26 July 2018, see Acknowledgements). These raw data consisted of 954 records including all of the different evolutionary lineages within the *A. brunneinucha* complex. Geographic coordinates were transformed to decimal degrees, based on the WGS84 datum.

Most museum records are collected opportunistically. Historically, researchers and bird collectors mostly sample easily accessible areas (i.e., near roads or towns and cities), leading to geographic clusters of unique but spatially auto-correlated records[37,38] that may lead to potentially large biases in measures of niche overlap[16]. Although dealing with this kind of "accessibility bias" is challenging, we partially controlled for these geographic clusters by using the "*spThin*" R-package[39], which through the estimation of nearest neighbour distances thins data to retain presence records at a given distance. We empirically explored several distances and found that retaining points separated by a minimum distance of 2 km was appropriate, which

allowed the retention of an adequate number of records for each evolutionary lineage. After

eliminating non-reliable locations and records without precise date collection for subsequent

analysis, the final dataset consisted of 273 spatially rarefied records for the following lineages

within the complex (*sensu* Gill & Donsker, 2018; Navarro-Sigüenza et al., 2008; Navarro-

Sigüenza, García-Hernández & Peterson, 2013) (mean = 34, SD = 26): *A. b. apertus* (*n* = 10), *A.

b. brunneinucha* (*n* = 64), *A. b. suttoni* (*n* = 44), *A. b. macrourus* (*n* = 36), *A. kuehnerii* (*n* = 24),

A. v. verecundus (*n* = 11), *A. v. virenticeps* (*n* = 79), and *A. v. virenticeps* populations from Sierra

de Coalcomán (*n* = 5).

Environmental data. Establishing appropriate areas for niche overlap comparisons is a critical

step when ecological niches are projected on environmental space (E-space)[12,27,29]. These areas

and their extent (the accessibility area **M**), must be customized for each species involved based

on biogeographic and ecological features on relevant period times[27,40]. To delimit the accessible

areas for each lineage in the *A. brunneinucha* complex (Fig. 1), we intercepted the occurrence

records with the terrestrial ecoregions[41], to which we added a buffer of 25 km around each in

ArcGIS 10.3 (ESRI, Redlands, CA) to serve as the environmental background available for the

ecological niche overlap analysis[10,27,29]. Such consideration was based on the assumption that

these regions may define the ecological accessible areas for each species in geographical space

for each species. In sum, the study area here was defined according to the distribution range of *A.

brunneinucha* complex in northern Mesoamerica (84–111°W and 11–33°N; Fig. 1)[42].

In order to quantify the climate niches for the different evolutionary lineages, we obtained

bioclimatic data from WorldClim 2.0[43], which includes 19 bioclimatic variables summarizing

aspects of precipitation and temperature with 30" of resolution (~1 km^2 cell size) and spanning a

30-year period (1970–2000). An initial exploratory visualization of bioclimatic variables allowed

the detection of a number of apparent spatial biases in four environmental variables[44]: mean temperature of wettest quarter, mean temperature of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter. Therefore, in order to avoid inconsistencies in niche overlap analyses these variables were eliminated from the analyses.

In addition, because numerous studies have documented that including redundant variables with high collinearity leads to a complex model that is difficult to interpret in an ecological context[12,45], all environmental variables were examined for cross-correlation using a Pearson's correlation coefficient in R software[46]. This last step, implemented in the "*corrplot*" library[47], allowed us to minimize collinearity and redundancy among environmental layers[45]. To visualize correlation between variables, we performed a cluster analysis (see Supplementary material) following a published protocol[48]. In this sense, we first extracted pixel values from the bioclimatic layers using our spatially rarefied dataset of presence records. Then, we plotted an UPGMA cluster of the selected 15 variables, and performed a bootstrap analysis (1,000 randomizations) to obtain statistical support for each cluster detected using the "*pvclust*" library[49] for R[46]. The decision to drop or retain a variable was based on its biological relevance to physiological importance and natural history data for our study species[17-19], as these environmental predictors include limiting factors which control ecophysiology and distribution in birds[50,51]. Finally, we retained the following uncorrelated seven bioclimatic variables ($r <$ 0.7)[45] for subsequent niche overlap analysis, including: the annual mean temperature (bio 1), the mean diurnal range (bio 2), the isothermality (bio 3), the temperature seasonality (bio 4), the annual precipitation (bio 12), the precipitation of driest month (bio 14), and the precipitation seasonality (bio 15).

Niche overlap in E-space and similarity test. To understand the role of ecological conditions in niche divergence or conservatism, we analysed ecological niche overlap among the eight evolutionary lineages of the *A. brunneinucha* complex by estimating the niche similarity among groups as suggested by Broennimann *et al.*[16]. E-space was represented through a Principal Component Analysis (PCA) as implemented in the R package "*ecospat*"[52]. From this perspective, niche overlap between evolutionary lineages was represented by plotting together the E-space for each pair of lineages, calculating the density of the background environments and species records across the first two PCs by a kernel density smoother and divided by the maximum number of occurrences in any one cell of the environmental space and by the number of sites with the most common environment, respectively[16,29]. The resulting density grids of $r \times r$ cells ($r = 100$) in the environmental space were used to compute niche overlaps between each pair of species in terms of *Schoener*'s D[15,53], a metric ranging from 0 (no overlap) to 1 (complete overlap). We used the terminology for the description of niche overlap following Rödder & Engler'[14]: 0–0.2 = no or very limited overlap, 0.2–0.4 = low overlap, 0.4–0.6 = moderate overlap, 0.6–0.8 = high overlap, 0.8–1.0 = very high overlap.

We also assessed, using the niche similarity test, the hypothesis of niche conservatism among the evolutionary lineages by comparing the observed niche overlap to a simulated overlap obtained using random subsets of samples[15,16]. In this sense, the niche similarity test checks whether the overlap between two niches is more similar than the simulated overlap (for this case based on 100 iterations) if random shifts within each environmental space are allowed (rand.type = 1, "greater" option). The null hypothesis is rejected when the value of the observed overlap is significantly lower ($P > 0.05$) than the simulated one[15,16]. Visualizations of niche overlap were obtained with the *niceOverPlot* function for R, which was developed *ad hoc* by J. Fernández-

López (Real Jardín Botánico, Madrid, Spain), but modifying the original script to increase the number of lineages to eight for adapting it to our study. all of the analysed datasets and R-scripts generated in our study are available from the corresponding author upon request.

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Author contributions

IM-C, AGN-S, LAS-G designed the study. IM-C developed the analyses. All authors contributed in the analysis and interpretation of results, and in the writing of the manuscript.

Additional Information

Supplementary Information accompanies this paper at:

Competing interests: The authors declare no conflicts of interest.

Figure Legends

Figure 1. Accessible areas and presence records of each evolutionary lineage within the *Arremon brunneinucha* complex. Birds within each map depict the morph (green-striped vs. chestnut-capped) characterizing each lineage.

Figure 2. Explained variance of the correlation circle plot for the PCA-env.

Figure 3. Niche overlap in E-space (PCA-env) for the eight evolutionary lineages of the *A. brunneinucha* complex. Letters correspond to: Principal Components Analysis (a) and Niche similarities values obtained based on the *Schoener*'s D (b). In all cases for (b) graph the number represents the observed values of the overlap between the lineages' niches: the 'chestnut-capped' *brunneinucha* group (reddish brown color) and the 'green-striped' *virenticeps* group (green color). Higher indexes indicate more similarity as shown by the red intensity. For similarity test the null hypothesis was rejected when the value of observed overlap is significantly ($P > 0.05$) lower than the simulated one. Significant values correspond: ns= non-significant; * significant in only one direction; and ** significant in both directions. Individual results for the paired comparisons among lineages are shown in the Supplementary material.

Figure 4. Niche similarities of the evolutionary lineages overlaps based on the *Schoener*'s D on the E-space.

Fig. 1

A. b. apertus
A. b. brunneinucha
A. b. suttoni
A. b. macrourus
A. kuehnerii
A. v. verecundus
A. v. virenticeps (SC)
A. v. virenticeps
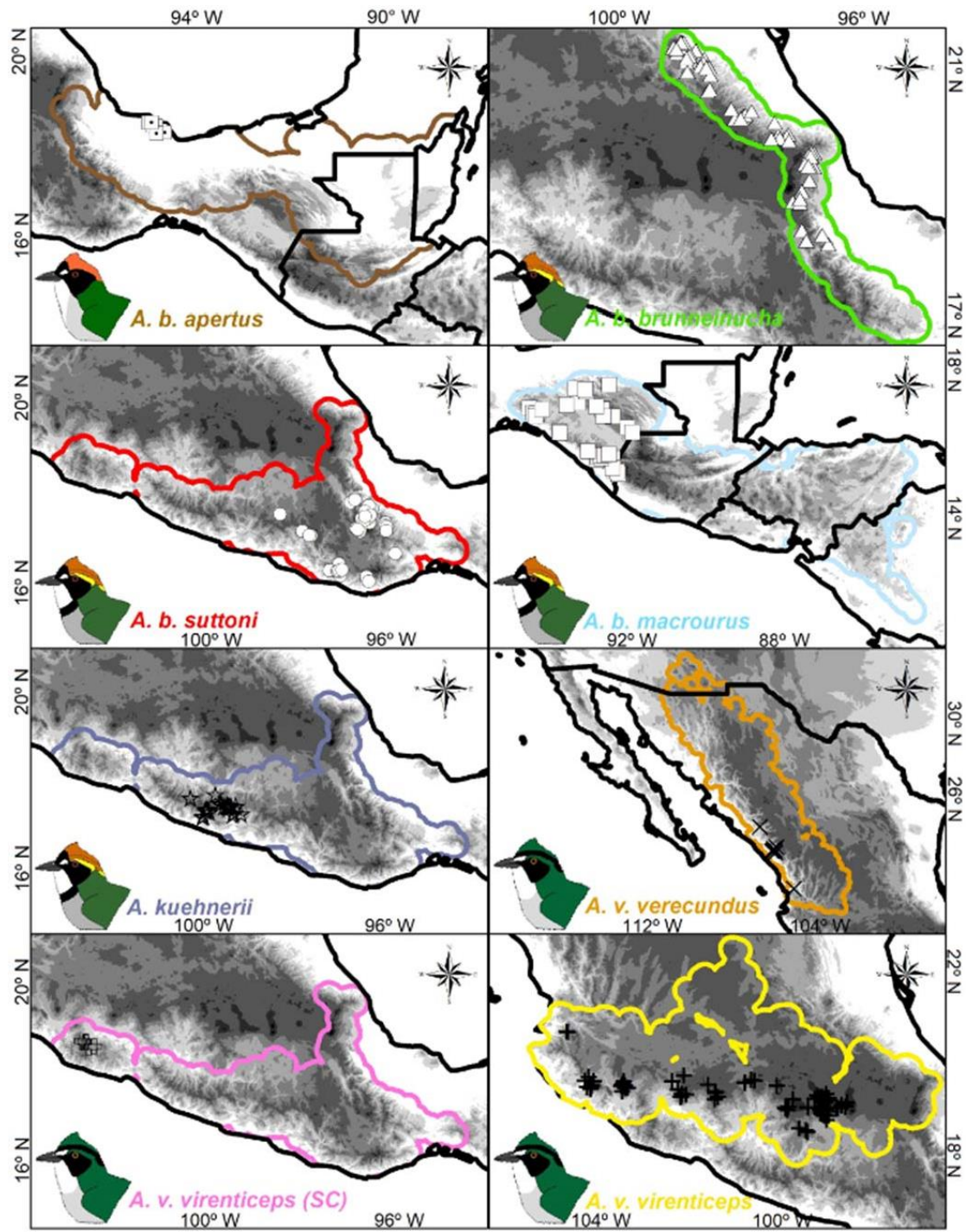
Fig. 2
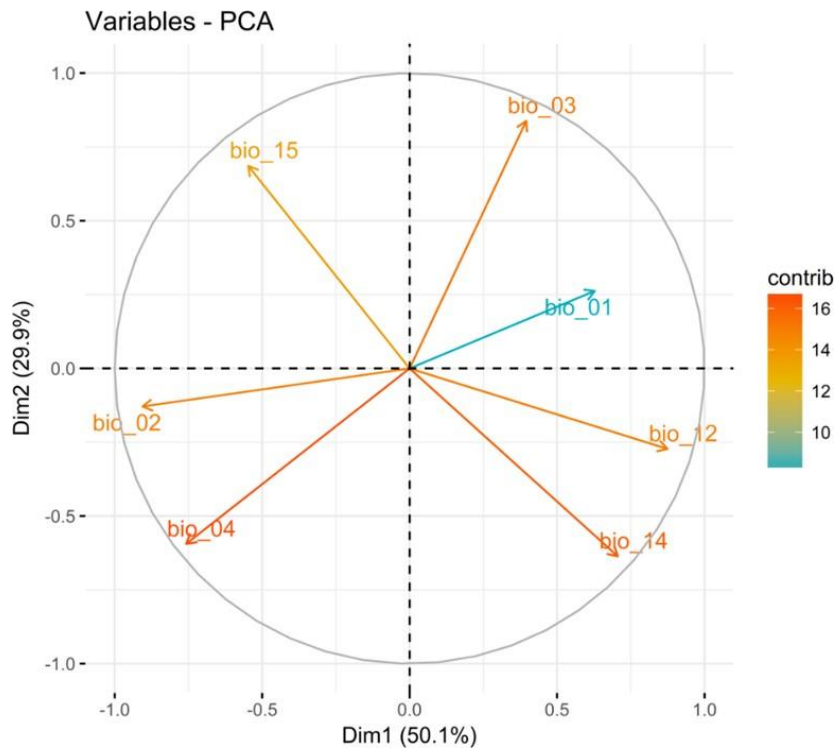
Fig. 3

Supplementary Figure A. Cluster analysis showing correlation between 15 bioclimatic layers

supported by AU (approximately unbiased) P-value (left) and bootstrap values (right).
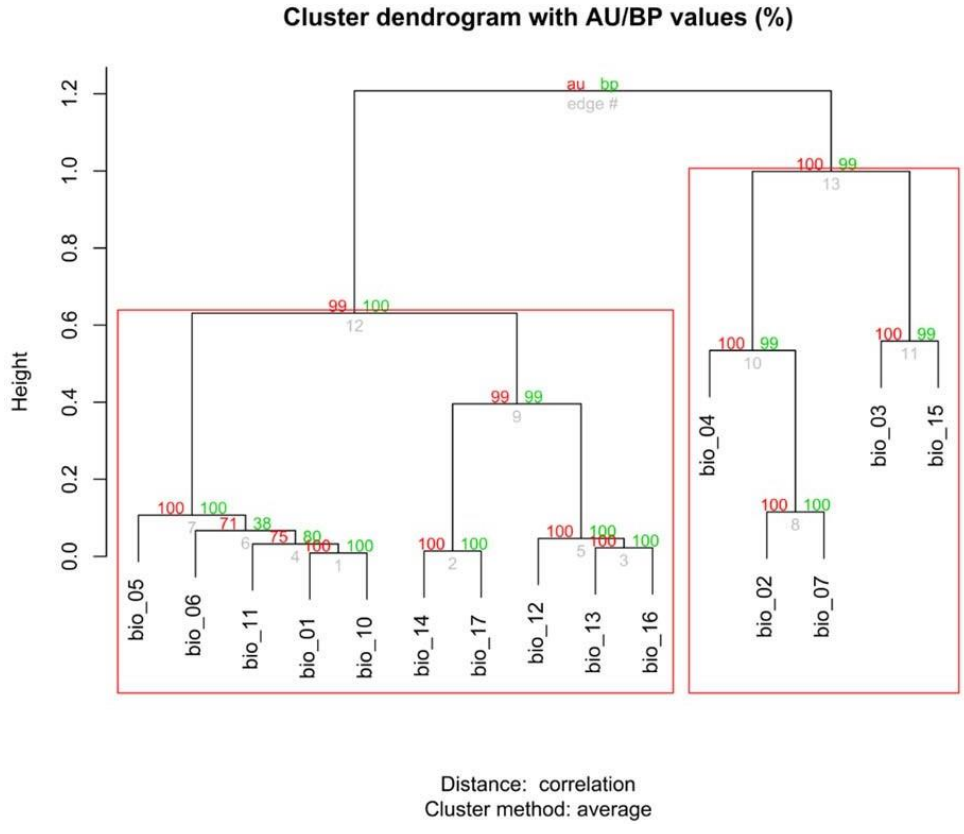
Supplementary Figure B. Correlation plot between 15 bioclimatic layers. We retained the following uncorrelated seven bioclimatic variables ($r < 0.7$) as suggested by Dormann *et al.*[45] to subsequent niche overlap analysis: the annual mean temperature (bio 1), the mean diurnal range (bio 2), the isotherm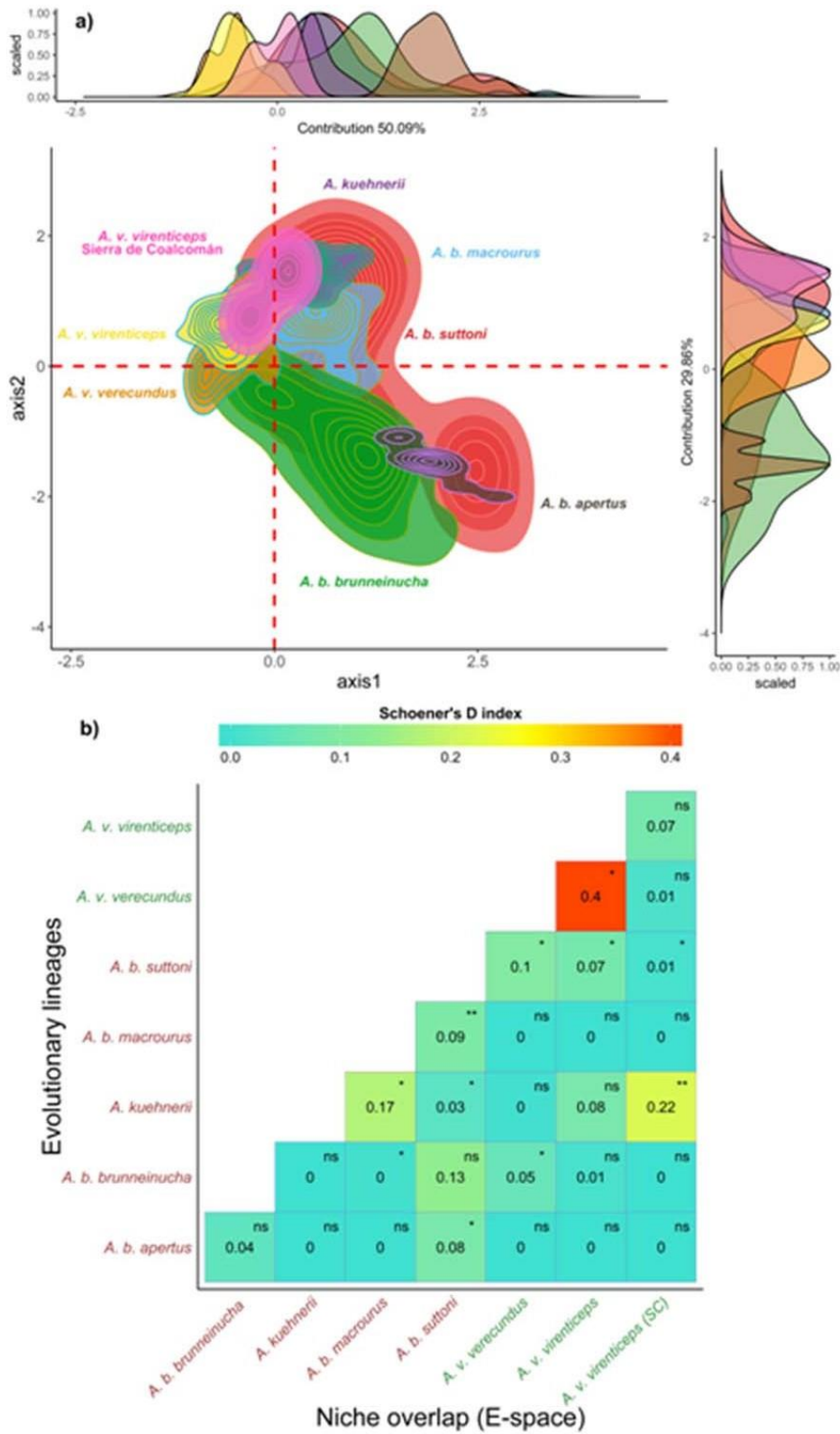ality (bio 3), the temperature seasonality (bio 4), the annual precipitation (bio 12), the precipitation of driest month (bio 14), and the precipitation seasonality (bio 15).
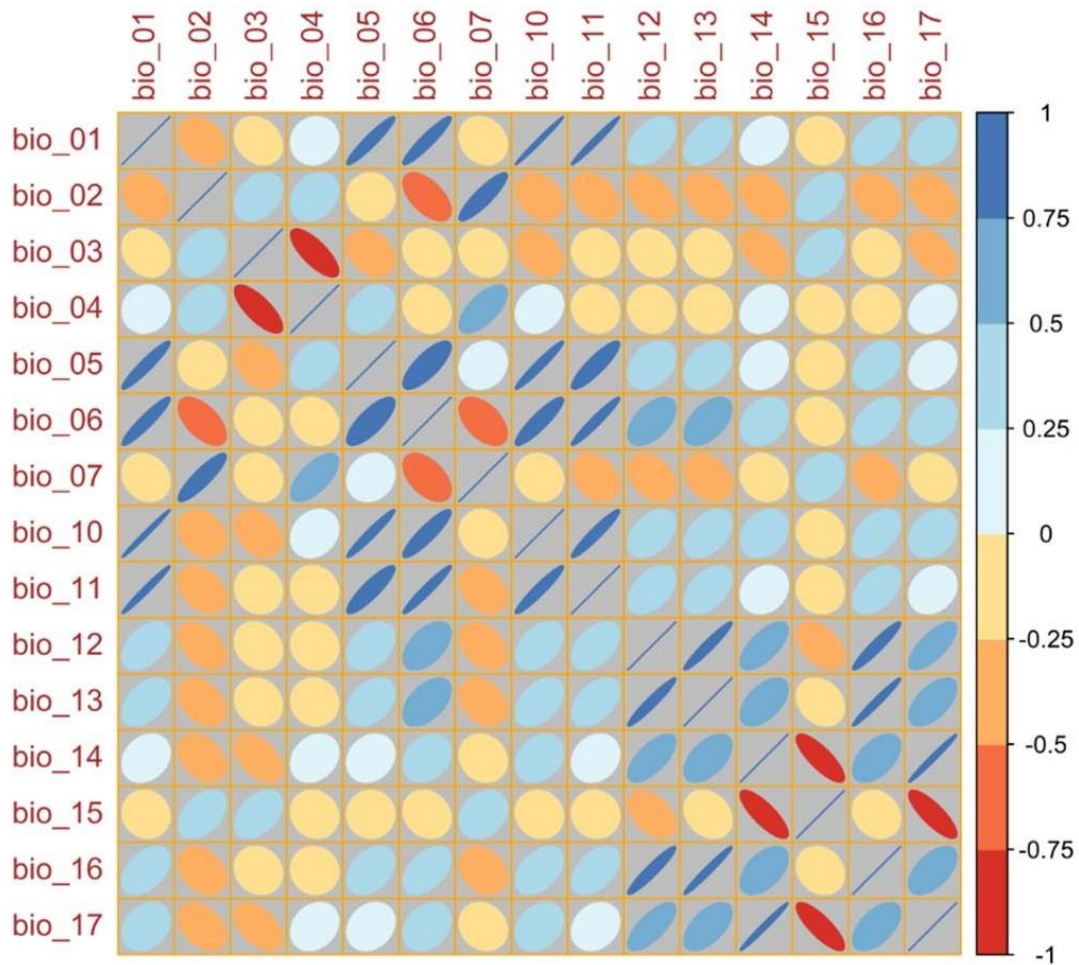
Supplementary Figure C. Background similarity tests based on PCA-env approach between

evolutionary lineages within *Arremon brunneinucha* complex (left to right).
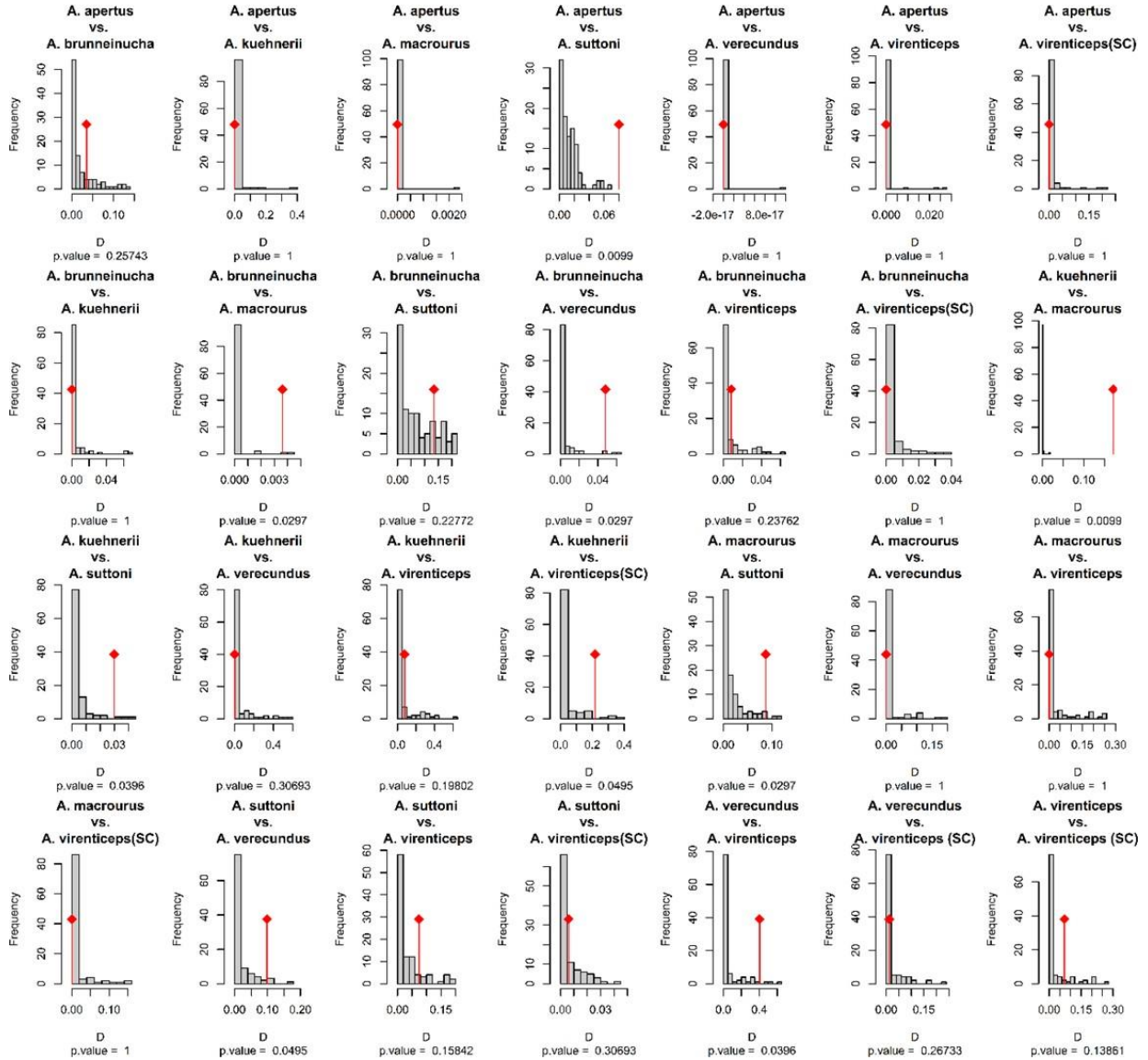
Supplementary Figure D. Background similarity tests based on PCA-env approach between

evolutionary lineages within *Arremon brunneinucha* complex (right to left).
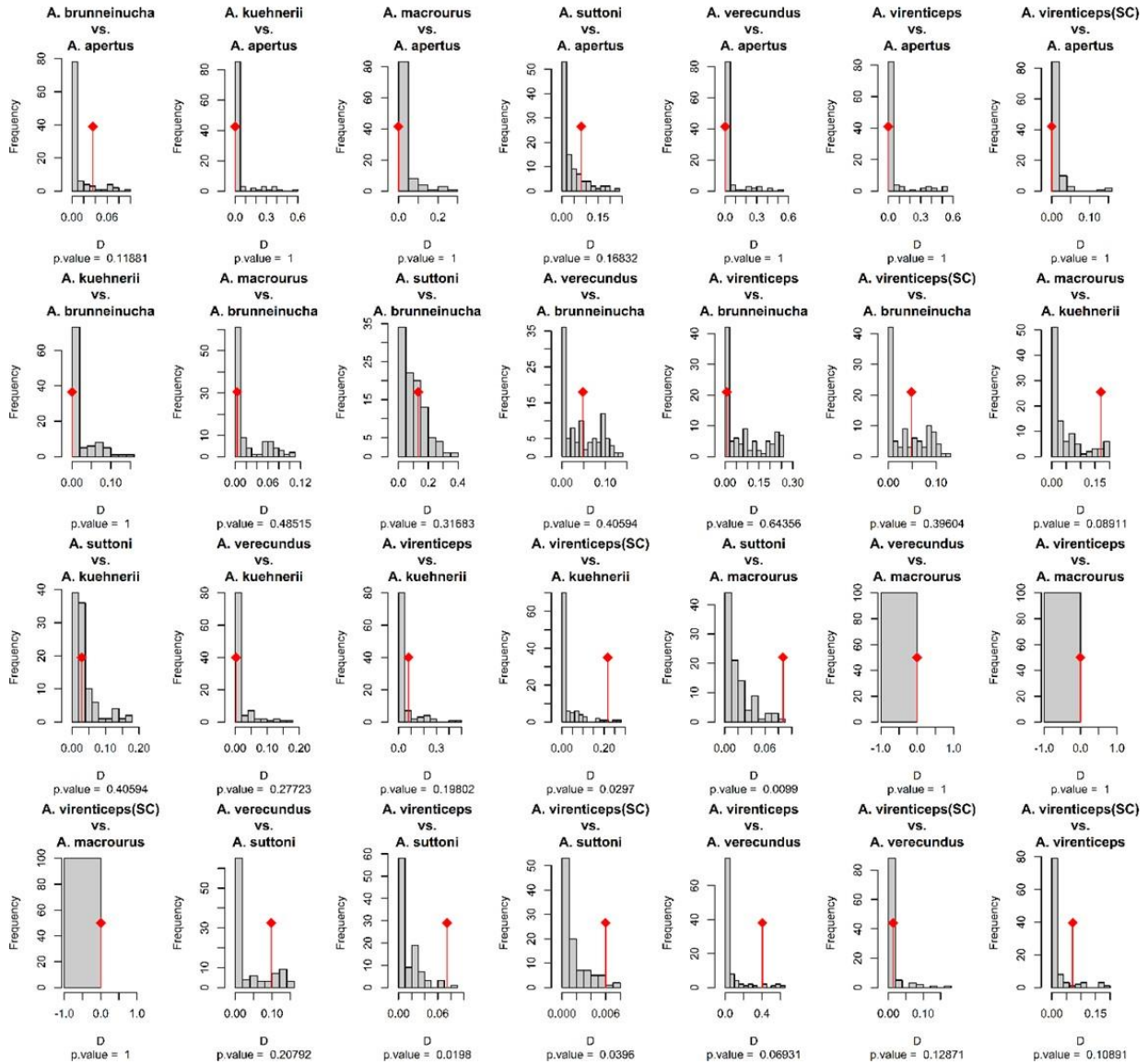
IV. DISCUSIÓN GENERAL Y CONCLUSIONES

Se han realizado diversos estudios de traslape de nichos ecológicos bajo diferentes condiciones (utilizando modelos de distribución de especies o datos ambientales sin procesar) y en varios taxa (Kozak y Wiens 2006; McCormack et al. 2010; Peterson 2011; Rödder y Engler 2011). Este enfoque es un tema de interés central en la biología, ya que permite una mejor comprensión de las relaciones entre la evolución y la ecología de las especies en paisajes cambiantes (Wiens 2004; Wiens y Graham 2005; Wiens 2008). Estudios pioneros en diferentes grupos taxonómicos han sugerido que el conservadurismo de nicho es uno de los principales impulsores de la especiación alopátrica y parapátrica (Peterson et al. 1999; Kozak y Wiens 2006; Hu et al. 2016). Por lo tanto, se ha vuelto cada vez más común combinar datos genéticos y morfológicos junto con modelos de nichos ecológicos para determinar la contribución relativa de los factores geográficos y ambientales en la divergencia de los linajes, que a su vez es importante para la delimitación de las especies (Wiens y Graham 2005; De Queiroz 2007).

Nuestros resultados utilizando el enfoque del PCA ambiental (PCA-env; Broennimann et al. 2012), sugieren que la mayoría de los linajes evolutivos alopátricos y parapátricos considerados en el complejo *A. brunneinucha* tienen un traslape de nichos climáticos de bajos a moderados. Este patrón es indicativo de que los nichos de estas unidades evolutivas se han adaptado a diferentes condiciones ambientales a lo largo de Mesoamérica. Es probable que tales diferencias reflejen la diversidad de los procesos evolutivos y ecológicos que han promovido la formación de nuevos linajes en cada caso. De hecho, el aislamiento genético entre estos linajes durante períodos significativos de tiempo (Peterson et al. 1992; Navarro-Sigüenza et al. 2008), la distinción filogenética (Cadena et al. 2007; Navarro-Sigüenza et al. 2013), y la incidencia de eventos históricos climáticos, como el establecimiento de condiciones cálidas y secas en los valles de las tierras bajas (Sánchez-González et al. 2008; Ornelas 2013), representan evidencias importantes sobre la separación de linajes hermanos montanos, así como sobre la promoción de la diferenciación de nichos antes o durante la fragmentación del hábitat a lo largo de las diferentes regiones de las cadenas montañosas mesoamericanas.

Encontramos que los linajes parapátricos (*A. kuehnerii* y *A. b. suttoni*) muestran evidencia de que sus nichos ecológicos fueron generados o han sido mantenidos por gradientes climáticos agudos. Para este caso, observamos que *A. kuehnerii* mantuvo un nicho similar cuando sus datos de ocurrencias se asignaron al azar en el contexto ambiental de *A. b. suttoni*, pero no al contrario. Una posible interpretación para este patrón es que los límites de la distribución para ambos linajes puedan

deberse a interacciones ecológicas con linajes hermanos en lugar de tolerancias climáticas (Remsen & Graves 1995), así como por barreras físicas, como los principales ríos de tierras bajas que limitan la distribución de ambos linajes a lo largo de la Sierra Madre del Sur central, lo que posiblemente impide el flujo genético (Kozak y Wiens 2006). Es posible que especies hermanas parapátricas se hayan originado en la alopatría y luego hayan tenido un contacto secundario a lo largo de un fuerte gradiente ambiental (Hua y Wiens 2013) en la región más oriental de la Sierra Madre del Sur, como en *A. b. suttoni*. Ambos linajes de la Sierra Madre del Sur no solo comparten nichos grinnellianos algo similares, sino también patrones de plumajes parecidos. Desde esta perspectiva, asumimos que la plasticidad de las características del plumaje entre los linajes del complejo *A. brunneinucha* es sobresaliente (Parkes 1954; Parkes 1957), debido a las adaptaciones para forrajeo y eficiencia de vuelo, camuflaje y termorregulación (Zink y Remsen 1986).

Por otro lado, observamos que los linajes de rayas verdes no ocurren en ambientes más húmedos que los linajes de color castaño. Teniendo en cuenta que los límites de la distribución parapátrica están generalmente asociados con gradientes ambientales (Kozak et al. 2008), es importante tener en cuenta que, en el caso de especies estrechamente relacionadas en regiones montañosas, el norte de Mesoamérica (desde el sur de México hasta el norte de Nicaragua) se caracteriza por una mayor estacionalidad tanto en temperatura como en precipitación en comparación con la región sur (Ortiz-Rodriguez et al. 2018); por lo tanto, la diferenciación de estas poblaciones puede atribuirse a la presencia de importantes barreras topográficas y ecológicas para la dispersión (por ejemplo, el Istmo de Tehuantepec y la Depresión del Balsas) (Sánchez-González et al. 2008; Ornelas et al. 2013). De hecho, un estudio reciente que evalúa el traslape ambiental dentro del clado *Desmopsis-Stenanona* (Annonaceae), apoya la idea de que el conservadurismo de nicho en las tolerancias climáticas ha sido uno de los principales impulsores de diversidad en las selvas tropicales de Mesoamérica (Ortiz-Rodriguez et al. 2018).

Encontramos que tanto los linajes de rascadores cejas verdes (grupo *A. virenticeps*) como los rascadores de gorra castaña (*A. kuehnerii*) tienen nichos ecológicos más restringidos, lo que es probable que refleje los requisitos climáticos específicos que pueden limitar sus respectivas áreas de distribución geográficos. Muchos géneros y familias de vertebrados están restringidos geográficamente y, por lo tanto, experimentan un rango limitado de variación ambiental, lo que dificulta la detección del conservadurismo climático de nichos (Wiens & Graham 2005). Una caracterización más refinada de los nichos ecológicos de los linajes que hemos examinado requeriría estudios de campo detallados y espacialmente extensos y sin duda incluir variables más allá de las

variables climáticas y de vegetación (Peterson & Holt 2003; McCormack et al. 2010). Teniendo en cuenta la longitud de las ramas en la filogenia, en aquellos linajes evolutivos con nichos más restringidos (es decir, *A. kuehnerii* y *A. virenticeps*), los procesos de divergencia son todavía muy recientes y, por lo tanto, la predicción se mantiene al menos en una dirección dentro de la prueba de similitud. Se observa esta propensión a conservar los componentes principales de su nicho ancestral, porque la mayoría de ellos comparten parcialmente el espacio ambiental del primer linaje divergente (*A. b. suttoni*) en la filogenia (Fig. II y Fig. III) (Navarro-Sigüenza et al. 2008, 2013).

Finalmente, a pesar de estudios previos que muestran patrones de plumaje mixtos en poblaciones de aves (Núñez-Zapata et al. 2018), los análisis geográficos y ecológicos trazan una historia evolutiva para el complejo *Arremon brunneinucha* conformado por el aislamiento de poblaciones a través de barreras topográficas ecológicas que pueden favorecer la divergencia genética entre linajes. Sin embargo, el grado en que dicha divergencia se combina con cambios en la variación ecológica entre linajes no es similar entre las poblaciones alopátricas y parapátricas estrechamente relacionadas. Por lo tanto, sería interesante evaluar si las poblaciones aisladas pueden responder a diferentes presiones selectivas que promueven o restringen la evolución. Este estudio también puede ser útil para orientar investigación con respecto a la diversificación de linajes y la evolución de nichos en ecosistemas amenazados globalmente bajo una planeación sistemática de la conservación (Peterson et al. 2011; Ornelas et al. 2013).

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