Review

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Ecomorphology of familiy Plethodontidae (Amphibia: Caudata) in America: the state of art

Estado del arte de la ecomorfología de la familia Plethodontidae (Amphibia: Caudata) en América

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Abstract

Ecomorphological studies are essential to understanding how a species perform in an environment according to its morphology, allowing for further understanding of adaptation patterns and evolutionary diversification. Salamanders in the family Plethodontidae are widely distributed in the Americas, and their ecological specialization and philopatry make them highly vulnerable to environmental change. We compiled information on the ecomorphological aspects of the family to identify information patterns and gaps in data that could guide future research. We found that the United States is the country with the most significant number of studies (43), followed by Colombia (12) and Brazil (2). One of the most studied categories is life history and ecology, and the least studied are developmental biology, disturbance, and ecophysiology. *Bolitoglossa* was found to be 29% studied despite being one of the most diverse genera. Seventy-seven percent of the genera with altitudinal data prefer altitudinal ranges between 800-1200 m a. s. l., temperature between 15-20 °C and relative humidity above 80%. Finally, salamanders of lower weight (<1 g) and SVL (>60 mm) tend to use a higher perch height, probably related to a higher climbing ability or avoidance behavior. There is an opportunity for research on less studied genera, allowing future conservation decisions to be made.

Keywords: diet, distribution, ecology, habitat preference, morphology, salamanders

Resumen

Los estudios ecomorfológicos son importantes para comprender cómo una especie puede desempeñarse en un entorno de acuerdo con sus características morfológicas, permitiendo a futuro entender patrones de adaptación y diversificación evolutiva. Las salamandras en la familia Plethodontidae se encuentran ampliamente distribuidas en América y su especialización ecológica y filopatría las hace un grupo altamente vulnerable a cambios ambientales. En esta revisión, se buscó recopilar la información registrada sobre aspectos ecomorfológicos de la familia, para identificar patrones y vacíos de información que pueden encaminar futuras investigaciones. Por medio de una revisión sistemática de la literatura, se encontró que EEUU es el país que presenta mayor cantidad de estudios (43), seguido de Colombia (12) y Brasil (2). Una de las categorías más estudiadas es historia de vida y ecología y las menos estudiadas son biología del desarrollo,

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perturbación y ecofisiología. Se encontró que *Bolitoglossa* ha sido estudiada en un 29% a pesar de ser uno de los géneros más diversos. El 77% de los géneros con datos de altitud prefieren rangos altitudinales de los 800-1200 m s. n. m., temperatura entre los 15-20 °C y humedad relativa superior al 80%. Por último, salamandras de menor peso (<1 g) y SVL (>60 mm), tienden a usar una mayor altura de percha, probablemente relacionado a una mayor capacidad de escalada o un comportamiento de evasión. Se observa una oportunidad para investigar en géneros menos estudiados, puesto que esto permitirá tomar decisiones a futuro sobre su conservación.

Palabras clave: dieta, distribución, ecología, morfología, preferencia de hábitat, salamandras

INTRODUCTION

The interest in resolving scientific questions has led to the emergence of new fields of study in the last 65 years, such as understanding the adaptations of different living beings to their environment. The concepts ecology and morphology are naturally associated, since ecological factors play a key role in the variation in structural shapes and the performance of an individual in its environment. The field of study that analyzes both terms together is known as ecomorphology (Betz, 2006; Sherratt et al., 2018), which includes topics such as comparisons of adaptations between different organisms, modifications of morphological characteristics as a result of competition, and ecological community structure (Bock, 1994).

For example, the degradation of protected areas can limit the diversity of functional forms of anurans, given that there are phenotypes associated with specific microhabitats. Thus, it is important to plan conservation strategies that take into account these functional traits, as changes in ecological roles can have consequences on ecosystem function (Bolochio et al., 2020).

The evolution of morphological characteristics affects the performance of certain behaviors (swimming and jumping), and it has been found that anurans have different muscle mass in the limbs according to their aquatic or arboreal microhabitat. For example, arboreal frogs have less muscle mass for greater scalability, while frogs with aquatic microhabitat have a greater muscle mass in their limbs (Moen, 2019). For their part, tadpoles are an example of convergent evolution, body shape reflects niche use and locomotor strategies, and a relationship between tadpole morphological diversity and microhabitat use has been observed (Sherratt et al., 2018). Future ecomorphological studies will provide valuable information on adaptive processes and evolutionary diversification (Lopez, 2019).

The family Plethodontidae is the most diverse within the order Caudata, representing 66.1% of the global richness of salamanders (Parra-Olea et al., 2014), with approximately 520 species in 29 genera in the world (Frost, 2024) that are distributed mainly in North and South America (Solano-Zavaleta et al., 2009). Plethodontidae have important ecological functions including the flow of matter and energy in the food chain between terrestrial and aquatic environments, controlling invertebrate populations and facilitating soil dynamics (Davic & Welsh, 2004).

The Plethodontidae family has been used as a bioindicator given its endemism and low dispersal capacity, as they are highly sensitive to environmental changes such as floods, droughts and pollutants (Southerland et al., 2004). This is due to their morphological attributes, as amphibians are ectotherms dependent on the temperature of the environment and the characteristics of their highly permeable skin make them prone to water loss and pollutants (Flores et al., 2022). Additionally, the philopatry that amphibian populations have may be a reason for them to be threatened in the future (Flores et al., 2022; Galindo et al., 2018a).

Although studies have been conducted in Central and North America on the Plethodontidae salamander group, only 19% of in South American studies focused on ecomorphology and ecology in the last 50 years (Elmer et al., 2013). This is possibly related to the fragmented and isolated patchy distribution of species (Elmer et al., 2013). In addition, the richness of salamanders in the Neotropics is not sufficiently known due to their cryptic morphology. Therefore, an unexpectedly high diversity is present in the area with an increase of 22-350% over the known diversity, and in salamanders up to 400%, making the understanding of this group superficial (Jaramillo et al., 2020).

The most recent ecomorphological studies (Ahumada-Carrillo et al. 2020; Brown, 2020; Capshaw et al. 2019; Drukker et al. 2018; Duarte-Marín et al. 2018; Galindo et al. 2018a; Gladstone et al. 2018; Hernandez, 2018; Hernández-Pacheco et al. 2019; Mendieta et al. 2019; Roach et al. 2020; Sasso et al. 2020), which account for their geographic ranges, behavior and taxonomic descriptions, allow for future comparative ecology studies (Hairston, 1949). However, further research on ecomorphological aspects is needed. For this reason, the objective of this study was to compile all the information recorded on the ecomorphological aspects of the family Plethodontidae. In this way, we sought to identify distribution patterns in terms of altitude, thermal and humidity preferences, the main diets for salamander species of the family Plethodontidae, their microhabitat preference, and the correlation between morphology (rostral-loach length (SVL) and mass) and microhabitat selection. Finally, information gaps were identified by taking into account publication trends at the university, country and journal levels, as well as more and less studied species that will allow us to direct future research.

MATERIALS AND METHODS

Search and collection of data

In 2020, a systematic review of the literature available in the virtual databases ScienceDirect, Scopus, Scielo, Elsevier, ResearchGate, JSTOR, BioOne, ProQuest, Wiley and university repositories was carried out to compile all existing information on the ecomorphology of salamanders belonging to the family Plethodontidae in the Americas.

The keywords Plethodontidae, ecomorphology, morphology and ecology in combination with the Boolean operators AND and OR were used to search in Spanish and English (Figure 1). Articles with ecological data on salamanders belonging to the family Plethodontidae, such as the type of microhabitat, temperature and humidity of the localities they inhabit, were included in this review. Morphological articles describing species were not considered for the review.

Additionally, with the data collected for each article (title, year, author affiliation, journal, country, distribution, ecological data and morphological data) a matrix was constructed in Excel, which can be consulted at supplementary material.

Categorization of thematic and microhabitat data

The main themes of the articles collected were analyzed in order to define the following categories: *life history and ecology*, which includes habitat, diet, climate-microclimate, reproduction and population estimators; *morphology*, which contains morphological data; *distribution*, which in this case refers to altitudinal data and the main ecosystems inhabited by these species; and *disturbance*, which deals with the influence of anthropogenic activities on the distribution of species of this family.

The *development* category was also considered, referring to how environmental conditions and microhabitat affect characters associated with life history (e.g., body size, *ethology* dealing with the behavior of salamanders in times of reproduction, foraging, behavioral adaptations and seasonal activity). Finally, *ecophysiology* deals with the influence of the environment on physiological responses in salamanders (e.g., temperature on locomotion).

The microhabitat used by salamanders in the family was grouped as follows: *aquatic*, which includes streams, wells, springs, marshes, seepage and stream banks; *soil*, which refers to leaf litter, rocks, logs and debris at ground level; *subterranean*, which are burrows (made by other species) used particularly by individuals living in seasonal locations; and salamanders found in vegetation greater than two meters (>2 m) were considered species with *arboreal* habits and in vegetation less than two meters (<2 m) were considered *shrubby.*

Statistical analysis

To evaluate whether the number of publications (output variable) is affected by the universities (input variable), the generalized linear model (GLM) was used, because the data do not follow a normal distribution. A Poisson distribution was used with this model, because the variable number of publications is discrete and corresponds to count data that are independent (Quinn & Keough, 2002). This analysis was performed using the R program (R Core Team, 2020).

To evaluate whether the number of species per genus (output variable) is being affected by altitude, temperature and humidity (input variables) independently, a Pearson chi-square test was used, since it does not require a normality assumption and the data are randomly sampled (Quinn & Keough, 2002). This analysis was performed using the JMP program® version 9.0.1 (2010).

RESULTS

Patterns by journal, university and country

A total of 189 publications were obtained, excluding duplicate articles, articles without full text access, and articles containing non-relevant subject matter. Therefore, 52% met the criteria established in the methodology (Figure 1, supplementary material). The journal with the highest number of articles related to Plethodontidae ecomorphology is the Journal of Herpetology with 13 publications, followed by Copeia with nine, and Ecology and Herpetologica with six each (supplementary material).

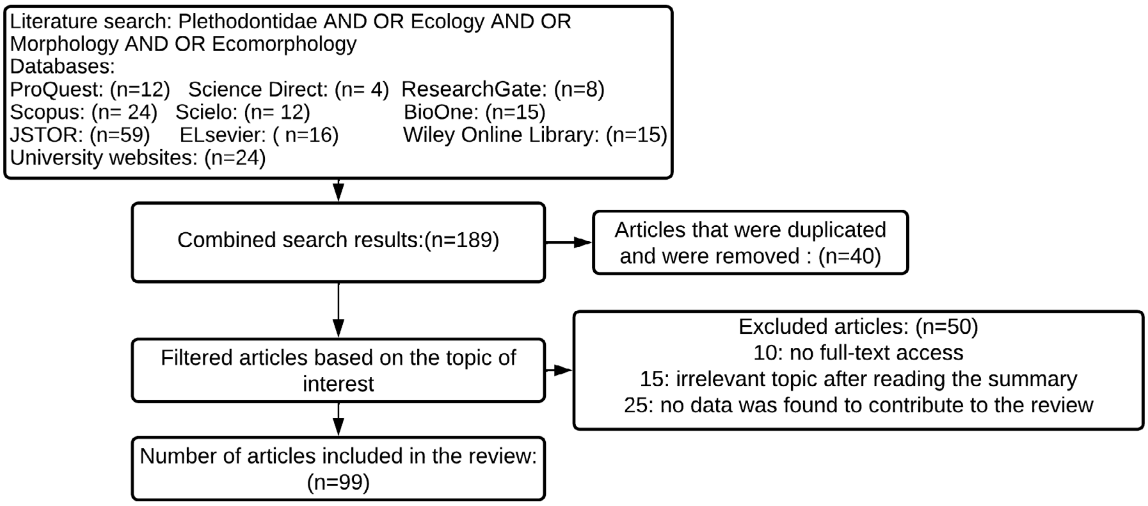

Figure 1. Methodology used to search for the articles included in this review.

The number of publications is not affected by the institutional affiliation of the authors (Central America z value = -0.802, Pr(>|z|) = 0.422; Europe z value = -0.471, Pr(>|z|) = 0.637; South America z value = 0.221, Pr(>|z|) = 0.825). However, the University of California had the largest number of papers in the family (eight publications) (Figure 2). It should be clarified that only the origin of the universities with more than two publications was taken into account. It was observed that universities in the United States (USA), Colombia and Brazil led the number of papers in the family with 43, 12 and two publications, respectively (Figure 2).

The countries with the highest proportion of studies compared to the number of species described in their territory are Peru, USA, Brazil and Colombia. The USA is the country with the highest number of described species of Plethodontidae, and at the same time the one with the highest number of studies on ecomorphology (table 1, supplementary material).

Trends in ecomorphological studies

Most ecomorphology papers are associated with life history and ecology (56%), followed by morphology (16%) and ethology (14%). The least studied categories were distribution (8%), developmental biology (2%), disturbance (2%), and ecophysiology (2%) (Figure 3, supplementary material). There was a general trend of increasing number of publications over the years, with 2016 and 2018 having the highest number of publications, followed by 2006 and 2019 (Figure 3, supplementary material).

Twenty-seven percent of the genera have addressed for their species 100% at the ecomorphological

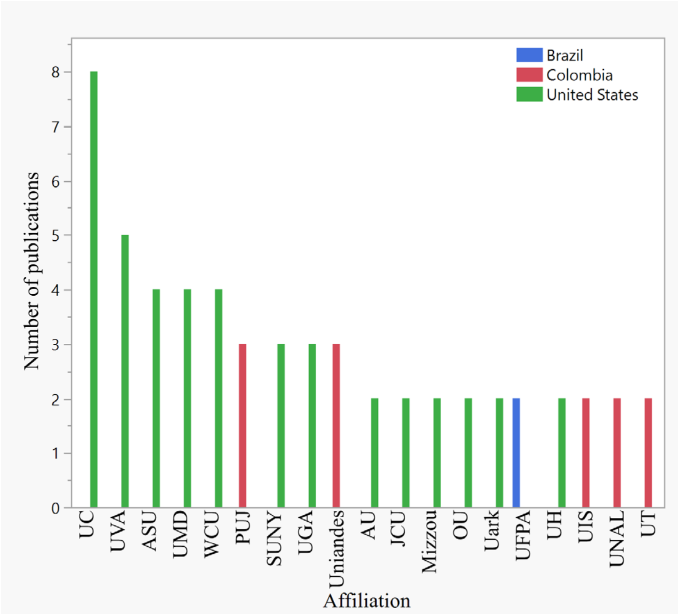

Figure 1. Number of publications by author affiliation addressing topics associated with Plethodontidae ecomorphology in the Americas. UC = University of California, UVA = University of Virginia, ASU = Arkansas State University, UMD = University of Maryland, WCU = Western Carolina University, PUJ = Pontificia Universidad Javeriana, SUNY = State University of New York, UGA = University of Georgia, Uniandes = Universidad de los Andes, AU = Auburn University, JCU = John Carroll University, Mizzou = University of Missouri, OU = Ohio University, UArk = University of Arkansas, UFPA = Universidade Federal do Pará, UH = University Heights, UIS = Universidad Industrial de Santander, UNAL = Universidad Nacional de Colombia, UT = Universidad del Tolima.

level within Plethodontidae (*Desmognathus*, *Gyrinophilus*, *Leurognathus*, *Parvimolge*, *Phaeognathus*, *Pseudotriton* and *Stereochilus*). The genera *Eurycea* and *Hydromantes* have been studied 79% and 67%, respectively, while the other 17 genera have approached 50% or less of their species: *Aneides* 50%, *Aquiloeurycea* 14%, *Batrachoseps* 10%, *Bolitoglossa* 29%, *Bradytriton* 33%, *Chiropterotriton* 22%, *Cryptotriton* 14%, *Dendrotriton* 13%, *Ensatina* 50%, *Hemidactylium*

Table 1. Percentage of species studied by country at the ecomorphological level.

Country	Number of species described (Frost, 2020)	Number of species studied	Species studied (%)
United States	165	103	62
Guatemala	63	15	24
Colombia	26	10	40
Panama	35	10	29
Mexico	137	10	7
Peru	4	3	75
Ecuador	12	3	25
Costa Rica	54	3	6
Brazil	5	2	40
Venezuela	7	2	29
Nicaragua	12	2	17
Honduras	44	2	5
Canada	10	1	10

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50%, *Isthmura* 43%, *Nototriton* 15%, *Oedipina* 5%, *Plethodon* 50%, *Pseudoeurycea* 17%, *Rhyacotriton* 50%, and *Thorius* 7% (Figure 4).

From the data recorded in the articles collected, information was found for 13 genera (Figure 4). The greatest number of species studied were located at altitudes between 800-1,600 meters above sea level (m a.s.l.) (Figure 5, supplementary material), and a decrease was observed when the

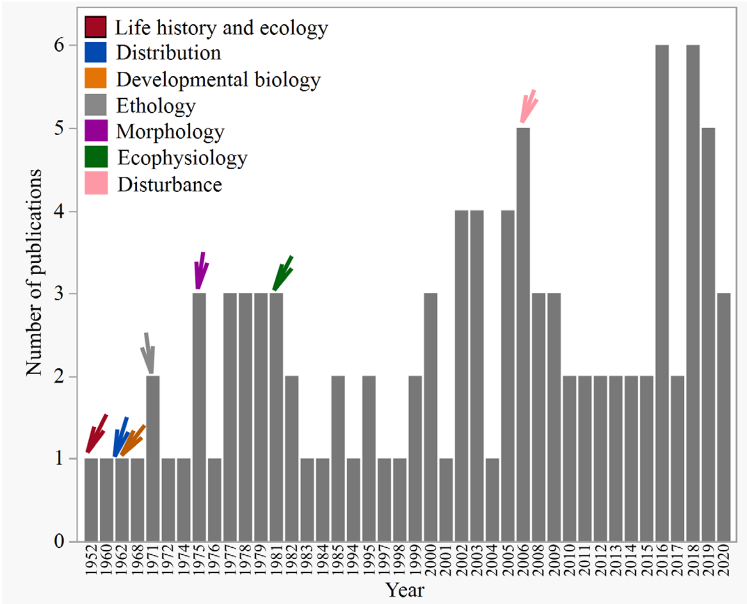

Figure 3. Number of publications per year on Plethodontidae ecomorphology in the Americas. The arrows indicate the occurrence of the different categories treated in articles on Plethodontidae in that year and the gray bars show the number of publications made on ecomorphology. The review was conducted up to December 2020.

altitude was above 2,000 m a.s.l. Additionally, it was evidenced that *Bolitoglossa* is the only genus present in all altitudinal ranges while *Rhyacotriton* is only present at altitudes of 0-400 m a.s.l. and *Pseudotriton* at 1,200-1,600 m a.s.l. The number of species per genus was found to be affected by altitudinal range (Pearson chi-square = 145.949, p = 0.0088*). The number of items

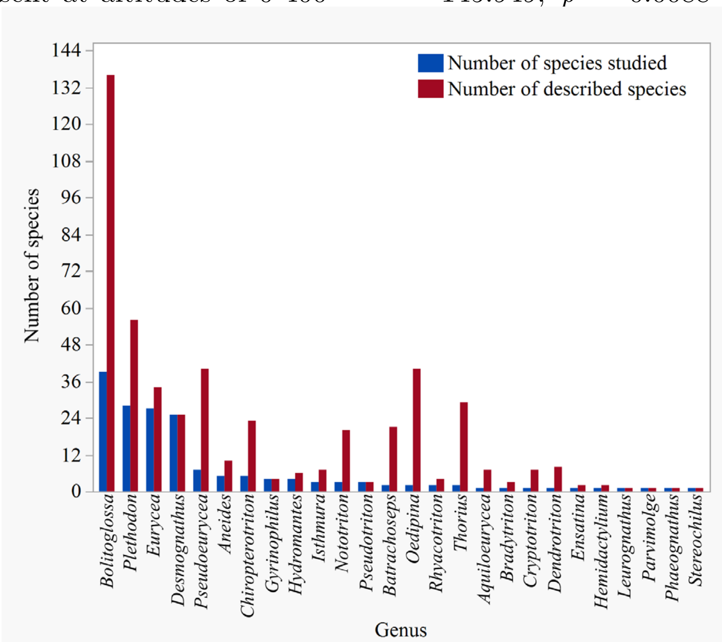

Figure 4. Number of described species taken from Frost (2020) and number of species studied by genus of the family Plethodontidae at the ecomorphological level in America. The graph is in descending order by number of species studied.

taken into account for each genus was *Bolitoglossa* (29), *Chiropterotriton* (1), *Dendrotriton* (1), *Desmognathus* (6), *Eurycea* (3), *Gyrinophilus* (3), *Leurognathus* (1), *Nototriton* (2), *Plethodon* (15), *Pseudoeurycea* (3), *Pseudotriton* (2), *Rhyacotriton* (1), and *Thorius* (1) (supplementary material).

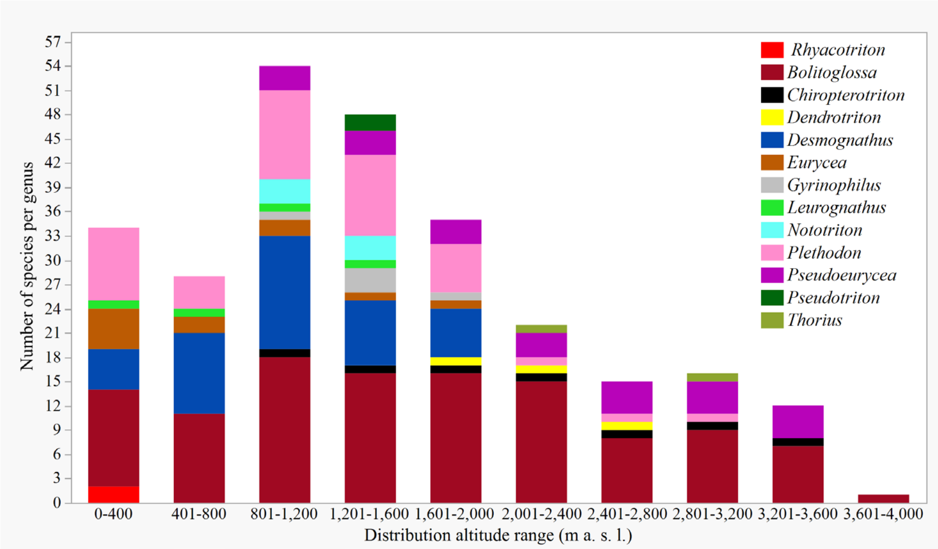

Figure 5. Altitudinal distribution of genera of the family Plethodontidae in the Americas.

The temperature where more Plethodontidae species were found according to the microhabitats usually used varied between 15-20 °C. Above 25 °C, a decrease of species was found (Figure 6, supplementary material). The variation in the number of Plethodontidae species is explained by the microhabitat temperature (Pearson chi-square = 99.6620, $p = 0.0002$). It should be clarified that not all genera of this family were included in the analysis, since not all have had ecomorphological studies with temperature data, for this case information is recorded for 12 genera. The number of articles considered for each genus was *Aneides* (1), *Batrachoseps* (1), *Bolitoglossa* (17), *Desmognathus* (9), *Eurycea* (8), *Gyrinophilus* (1), *Leurognathus* (1), *Nototriton* (2), *Phaeognathus* (2), *Plethodon* (14), *Pseudotriton* (1) and *Rhyacotriton* (3) (supplementary material).

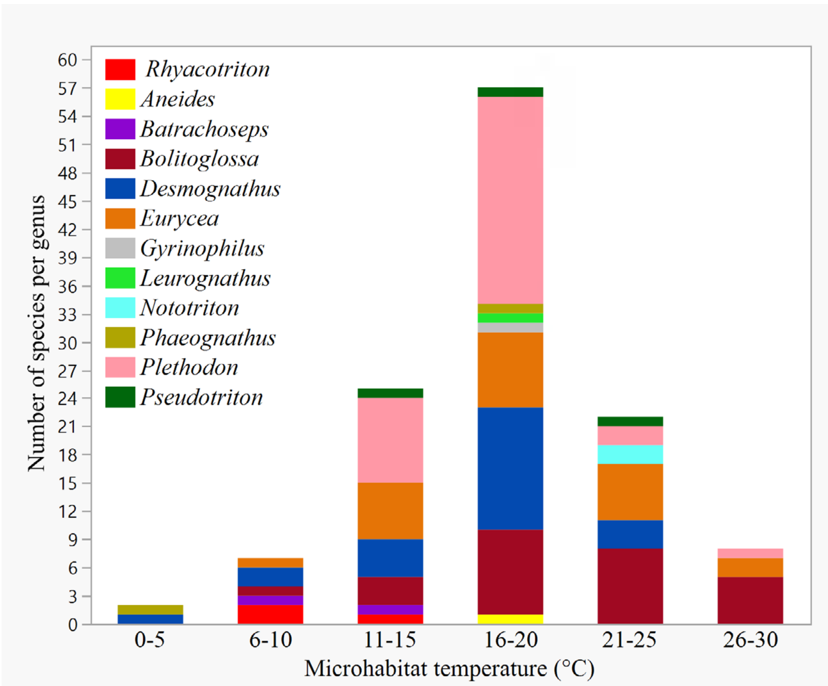

Figure 6. Microhabitat temperature of genera of the family Plethodontidae in the Americas.

The number of species in the nine genera evaluated is not affected by relative humidity (Pearson chi-square = 51.1030, p = 0.1122). However, it was observed that species prefer relative humidity above 80% (Figure 7, supplementary material). Decrease of species is observed when humidity is lower than 80%. The number of items considered for each genus were *Aneides* (1), *Batrachoseps* (1), *Bolitoglossa* (12), *Desmognathus* (3), *Eurycea* (4), *Gyrinophilus* (1), *Phaeognathus* (1), *Plethodon* (10) and *Pseudotriton* (1) (supplementary material).

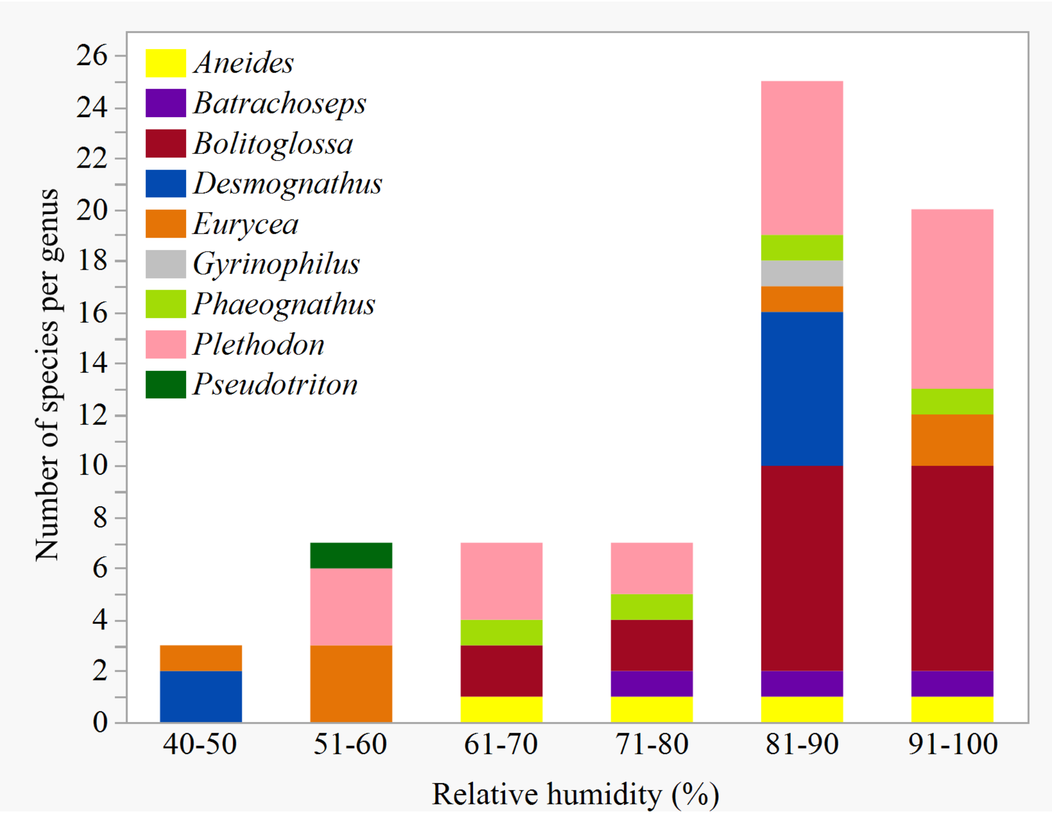

Figure 7. Relative humidity of localities inhabited by genera of the family Plethodontidae in the Americas.

A varied diet was evidenced for species of the family Plethodontidae, composed of 18 species distributed as follows: Hexapoda (11), Chelicerata (1), Crustacea (3), Myriapoda (1), Platyhelminthes (1), Annelida (1), and Caudata (1) (supplementary material). Hexapoda is the most representative group, with the following orders as the most abundant: Hymenoptera (16%), Coleoptera (15%), Collembola (13%), Diptera (13%), and Chelicerata represented by Araneae (12%) (supplementary material). The other food items are represented by less than 6%. *Eurycea*, *Desmognathus*, *Aneides*, *Leurognathus*, *Plethodon*, *Bolitoglossa*, *Gyrinophilus* and *Pseudoeurycea* are the only genera with associated diet studies.

Twenty-eight percent of the genera have aquatic habits while the remaining 72% have terrestrial habits, with soil being the most used microhabitat (Figure 8). It was observed that the genera *Desmognathus*, *Plethodon* and *Eurycea* can occupy a greater number of different microhabitats, four each, followed by *Bolitoglossa*, *Nototriton* and *Aneides* with three microhabitats, while *Chiropterotriton* and *Cryptotriton* are exclusively arboreal (Figure 8, supplementary material). Available microhabitat information is recorded for 18 genera. The number of items considered for each genus was *Bolitoglossa* (30), *Plethodon* (27), *Desmognathus* (24), *Eurycea* (12), *Nototriton* (3), *Aneides* (5), *Hydromantes* (2), *Gyrinophilus* (4), *Chiropterotriton* (2), *Batrachoseps* (2), *Pseudoeurycea* (5), *Rhyacotriton* (2), *Pseudotriton* (2), *Cryptotriton* (1) *Phaeognathus* (3), *Thorius* (1), *Dendrotriton* (2) and *Leurognathus* (1) (supplementary material).

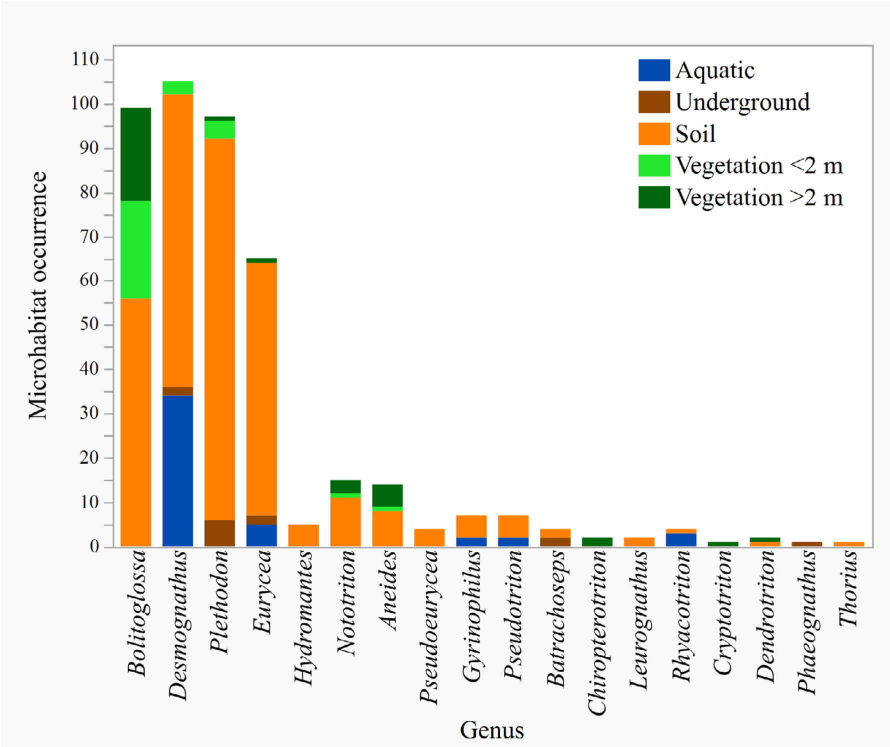

Figure 8. Microhabitats used by genera of the family Plethodontidae.

There was no clearly defined pattern of microhabitat choice associated with size in salamanders. However, it was observed that salamanders with a SVL less than 90 millimeters (mm) tended to select the ground more (Figure 9, supplementary material). In terms of body mass, in general terms, no differentiation was observed between microhabitats given by the weights of Plethodontidae species. However, species weighing between 0.1-0.5 grams (g) tended to have aquatic habits to a greater extent than salamanders with other masses (supplementary material).

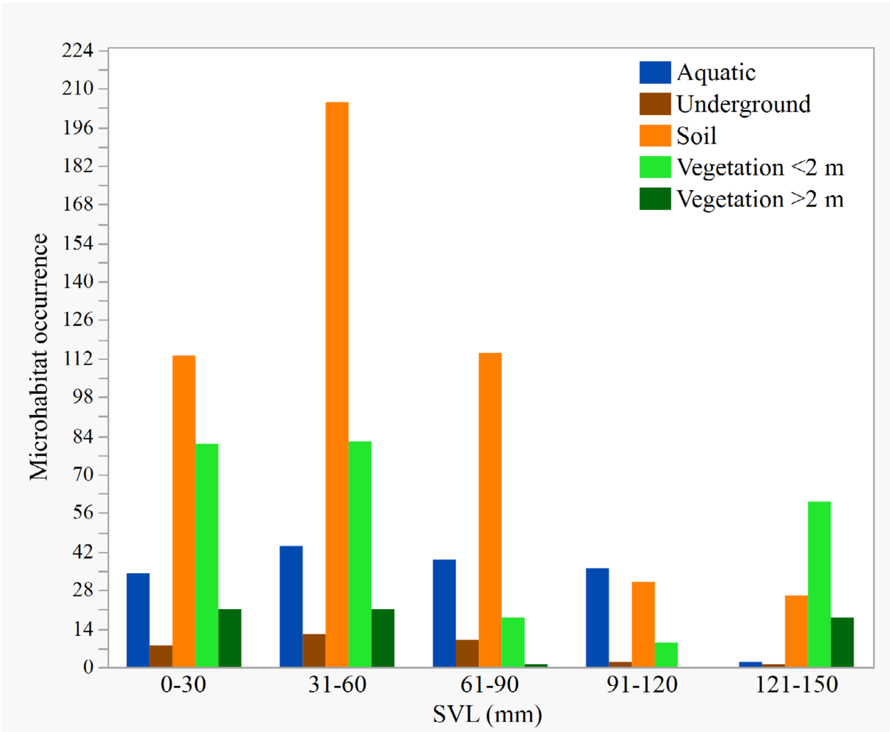

Figure 9. Microhabitats used according to the SVL of salamanders of the family Plethodontidae.

DISCUSSION

Patterns by journal, university and country

There was a trend of publications in North American journals (supplementary material) and this is supported by the fact that the leading universities in research on Plethodontidae ecomorphology are in the USA (supplementary material). One possible reason why research is focused on the USA is that there are many species described from this area of the continent (Table 1, supplementary material), particularly in the southern Appalachians where more than 50 species of salamanders are found (i.e., almost 10% of the global diversity), possibly due to the humid conditions and forest cover that the place offers and the good air quality (Martof, 1962). However, it is worth clarifying that there is another place where there may be a greater diversification of species and that is the Amazon, due to its geographical composition (longest mountain range and the second highest, and the largest rivers in the world); The lowlands of this area are still unexplored. Therefore, the diversity of salamanders is highly underestimated, and with studies more species may appear than expected (Jaramillo et al., 2020).

It has been found that the extension, population and gross domestic product of each country influence the number of researchers, again highlighting the USA as the leader (Ibañez, 2017). On the other hand, according to the United Nations Educational, Scientific and Cultural Organization (UNESCO), the USA is one of the largest investors in science, taking into account that it has more funds with respect to other Latin American countries, allowing to encourage research and that each university can have a group of researchers in each area (Lemarchand, 2018).

On the other hand, one of the limitations of science in Latin America is the perception that authors have regarding the quality of regional journals and the language in which they are published. Since 81% of the scientific production is published in English, journals in this language have a wider target audience, causing institutions to promote the dissemination of research in North American and European journals to generate a greater impact (Ronda-Pupo, 2021).

As for the countries that have studied less than 40% of their species, these are mostly Latin American, to begin with, very little funding has been allocated there and growth in terms of innovation and science has occurred in recent years with respect to other countries in the world; it is estimated that Latin American researchers represent 3.9% of the world total, so there is less research in this part of the continent given that there are not enough resources (Paz-Enrique et al., 2022).

Trends in ecomorphological studies

It was observed that in the years when publications began (1952-1972) most categories were covered, with life history and ecology (57%) being the most addressed (Figure 3, supplementary material). Further, it was evident that topics such as disturbance (2%) and ecophysiology (2%), which are the least addressed, appeared in relatively recent years with respect to the others. This is probably due to the fact that in the 1980s and early 1990s the scientific community began to gather information about amphibian population declines, finding alarming figures where entire populations had disappeared, and since then efforts to monitor threatened species have doubled (Tejedo, 2003).

There is particular interest in the study of the genus *Desmognathus* as all of its species (25) have studies associated with their ecomorphology (Figure 4). This is because the genus is distributed in the USA and southern Canada (Vitt & Caldwell, 2014) and as mentioned above, this area has a greater potential for publication given that there is greater investment, the journals have a wider target audience and a larger extension, population and gross domestic product, making it possible to cover more species of this North American genus (Ibañez, 2017; Lemarchand, 2018; Ronda-Pupo, 2021). A probable reason why some genera have 100% of their species with some ecomorphological study is that they possess few if compared to those genera that possess more than 100 species (Figure 4).

On the other hand, the genus *Bolitoglossa* with 136 species, is one of the most diverse genera of the family. However, only a small percentage has been studied at the ecomorphological level, because they are fractal in nature. That is, they are distributed in patches in little explored areas of the Amazon; their small size and the absence of distribution data makes their search and study complex and in addition to this, few are interested in them (Elmer et al., 2013). The greatest number of *Bolitoglossa* species are distributed in Central America (Frost, 2024) and in view of the fact that fewer studies are conducted in these countries due to factors such as lack of resources and funding, there is greater uncertainty with these species (Lemarchand, 2018).

Although latitude data were not taken into account for this review, it is worth mentioning that this variable influences the distribution and richness of species and may be affecting climatic variables. For example, in temperate regions there is extreme temperature variation, causing extinction rates to be higher than in tropical zones where there are more stable climatic conditions (Wiens, 2007). Particularly, individuals experience lower temperatures at higher latitudes, restricting their activity and in turn affecting their breeding seasons (fewer clutches or young in season) making them more vulnerable to extinction processes (Morrison & Hero, 2003). However, species in tropical areas are less able to undergo thermal acclimatization as they experience less thermal variability in their environments (Feder & Lynch, 1982).

Species from higher latitudes undergo shorter periods of growth and development, and therefore take longer to reach the minimum size required for sexual maturity than tropical species. Therefore, individuals from temperate zones, growing more slowly, tend to be larger when they reach reproductive age (Morrison & Hero, 2003).

The inclusion of the latitude variable does not contradict the patterns presented and could give it more support. For example, the genus *Phaeognathus*, which is endemic to the USA, has species with a temperature range of 0-5 °C. According to the data collected for this review (supplementary material); *Phaeognathus* has one of the largest body sizes (268 mm), second only to the genus *Isthmura* (327 mm) endemic to Mexico, which coincides with the large body sizes reported for high latitude species by Morrison and Hero (2003). Species from tropical areas, for example, *Bolitoglossa* presents sizes that do not exceed 60 mm with the exception of *Bolitoglossa dofleini* which has been reported to have sizes up to 203 mm, however, this size is still smaller than the North American salamanders mentioned above.

In terms of ecology, Plethodontidae species probably have a preference for low and medium altitudes (Figure 5, supplementary material). This altitude coincides with the location of some habitats frequented by salamanders of the family Plethodontidae, among which we find in tropical areas the premontane rainforest (1,000-2,000 m a.s.l.) and tropical rainforest (0-1,000 m a.s.l.) (Gutiérrez, 2002). In temperate zones, the habitats frequented are deciduous forest (152 m a.s.l.) (Quinn & Graves, 1999; Rissler et al., 2000) and temperate forest (45 m a.s.l.) (Hernández-Pacheco et al., 2019).

Additionally, it has been found that species of the genera *Nototriton*, *Bolitoglossa*, *Chiropterotriton* and *Pseudoeurycea*, have preferences for medium altitudes (1,000-2,000 m a.s.l.), because areas with this altitude in North America were colonized earlier (historically) with respect to high or low altitudes. Therefore, there has been greater accumulation of species and greater diversity (Wiens et al., 2007). On the other hand, species from South America have a preference for lowlands, explained by the geographical conditions offered by the Amazon, which is a place with great diversification of amphibians (Jaramillo et al., 2020).

It was evidenced that the *Bolitoglossa* genus is found in almost all altitudinal ranges recorded so far and this is because it has many species distributed widely. Therefore, its altitudinal distribution ranges between 0-2,054 m a.s.l., being able to inhabit deforested forests, coffee plantations, premontane forest and tropical forests (Frost, 2024), this may be possible as long as high relative humidity can be found at these altitudes. In general, in the articles consulted salamanders were always found near humid microhabitats, since for them hydro-regulation is more important than thermoregulation (Galindo, et al., 2018b).

However, within the family Plethodontidae the genus *Rhyacotriton* and *Pseudotriton*, are the only genera that are restricted to an altitudinal range, explicitly distributed from 0-400 m a.s.l. and 1201-1600 m a.s.l., respectively, in the USA, the above because the species present low dispersal, reporting that adults can register movements of 2.2 meters per year (Evelyn & Sweet, 2018).

In terms of temperature, there is a preference for ranges of 10-25 °C (Figure 6, supplementary material). This is because salamanders are less active in extreme temperatures. Species distributed in seasonally distributed countries seek refugia and come back out when conditions are slightly more favorable with temperatures around 19 °C (Anthony et al., 2008; Bakkegard, 2002; Davis, 2002; Herbeck & Semlitsch, 2000). When temperatures are below 10 °C, individuals show reactions such as loss of locomotion (Feder & Pough, 1975), while others lose their tails in response to stress (Maiorana, 1977).

The species distributed in the tropics, try to be in protected places to avoid dry conditions, since they have a preference for temperatures between 10 and 16 °C, the instability of environmental conditions can become critical for salamanders at the ecological level (Vial, 1967).

The relative humidity of the environment in which salamanders live should be above 80% (Figure 7, supplementary material), as salamanders are highly dependent on humidity. Salamanders seek refugia to slow water loss as much as possible, as 8-12% water loss will lose their ability to forage and locomote, and water depletion of 18-26% can be lethal (Marcum & Sievert, 2001). Any movement away from their moist refuge means loss of water in one form or another (Marcum & Sievert, 2001). Therefore, there may be a risk of desiccation in any microhabitat whose relative humidity is less than 80-100% (Camp et al., 2013). However, in some studies salamanders have been reported in environments with relative humidity of 40-50%, but these in most cases were found under cover objects or in subterranean habitats.

In tropical zones, salamanders have a preference for high relative humidity, since when this is below 95%, their activity decreases, as there is a lower locomotor performance, and therefore they prefer to protect themselves from moisture loss (Galindo, et al., 2023). It has been found that the body temperatures of tropical salamanders are similar to those of the environment, while the body temperature of salamanders from temperate zones tends to be higher due to their adaptations, so this factor is related to latitude (Feder & Lynch, 1982).

For neotropical species, in this case *Bolitoglossa*, the temperature varies according to the thermal floor and that is why it can be found in wide ranges of humidity and temperature, which makes it an interesting group to study at the level of physiological and morphological changes associated with these environmental variables.

The diet does not have a marked pattern since it is considered varied, given that it is being evaluated at the family level. In addition, it should be taken into account that the richness and abundance of prey varies with the time of year and their availability in the different microhabitats used by salamanders, as in the case of *Aneides flavipunctatus* (Lynch, 1985).

Finally, regarding the choice of microhabitat, taking into account morphological characteristics, it is observed that smaller salamanders tend to be arboreal with respect to those with a larger size (SVL) (Figure 9). This is possibly because a smaller size there increases the probability of climbing (Correa & Chagas, 2017; Mezebish et al., 2018). In addition, it can be seen that cover objects such as rocks, logs and debris (Figure 8, supplementary material) are the main microhabitat for many species, as these refuges allow them to avoid desiccation and predation (Marcum & Sievert, 2001; Pierce et al., 2010).

Future prospects

Based on the results obtained in the review, there is a need to strengthen research in Central and South America (Ibañez, 2017; Jaramillo et al., 2020; Lemarchand, 2018; Ronda-Pupo, 2021). First, because it is there where large groups of salamanders are found, as is the example of the genus *Bolitoglossa* widely distributed in Central America. On the other hand, the diversity of species in the Amazon is highly underestimated because there are many unexplored areas, so it is worthwhile to encourage research in this area of the continent and for this it is necessary to manage resources for research and publication in regional journals. There is a lack of research on many species of salamanders in the Americas; 85% of the countries have investigated less than 50% of the total species described, generating information gaps in a topic as relevant as ecomorphology.

Researching the described species of each country will allow us to know their distribution ranges and ecological data, so that we can prioritize inhabited areas according to their specific ecomorphs and avoid population decline. Species in temperate zones that are more vulnerable to extinction processes should be extensively studied in order to make decisions on their conservation and microhabitats with high humidity levels should be protected since it was found that salamanders have preferences for humidity > 80%. Tropical species such as those found in the Amazon that have not yet been described, should be a focus of study not only nationally but worldwide.

It is recommended that the *Oedipina*, *Thorius* and *Batrachoseps* genera be covered more, since they have less than 10% of their species studied and their lack of knowledge may hinder their conservation in the future; knowing their biodiversity and distribution will allow the creation of management and conservation plans and the evaluation of threat categories. On the other hand, it is important to cover more of the *Bolitoglossa* genus since it is one of the most diverse, having only 29% of its species studied, and its lack of knowledge could lead to the fragmentation of key habitats for them.

It is considered necessary to give more visibility to this little known group (salamanders) not only in the scientific community, since anurans are usually the most popular group, and it is worthwhile to start disseminating more information on salamanders in the media and schools; also join efforts between universities (i.e., create a network of authors to keep existing information updated and that research on the same species are not repeated and go covering studies for new species).

It is suggested that research be directed to topics such as distribution, developmental biology, disturbance and ecophysiology, which were the least studied categories because they are relatively recent and are considered to be of utmost importance. For future studies, it is important to take into account the species description articles, since they contain threat data that contribute to conservation strategies. On the other hand, it is relevant to include latitudinal data since latitude strongly influences environmental variables such as temperature and humidity.

There are very few articles that focus only on diet, since this is only mentioned in broad strokes in articles on ecology, so it would be worthwhile to investigate this aspect. It should be clarified that there are very few studies that relate morphology and microhabitat choice, which is considered relevant to investigate so that in the future these microhabitats can be protected to a greater extent.

Finally, it should be noted that the results of temperature and humidity trends show how essential optimal conditions are for this family of salamanders to survive in the future, so paying special attention to the habitats on which these species depend can ensure their long-term conservation, also take into account the microhabitats used by salamanders to avoid future fragmentation and decrease over time populations.

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AUTHOR CONTRIBUTION

PAMM data collection, tabulation, charting and paper writing, NAB advice for tabulation, charting and paper writing, and NRPS research planning and paper writing.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

SUPPLEMENTARY MATERIAL

Available at: Supplementary Material

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