Evolutionary Journal of the Linnean Society, 2024, 3, kzae032
https://doi.org/10.1093/evolinnean/kzae032
Advance access publication 6 November 2024
Perspective

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The ecomorphological radiation of phyllostomid bats

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ABSTRACT

Neotropical leaf-nosed bats (family Phyllostomidae) underwent an impressive adaptive radiation characterized primarily by the diversification of dietary strategies in tandem with functional morphological diversification of their craniodental and sensory systems. In this perspective, we integrate information from extensive research across multiple fields to outline the interplay between extrinsic and intrinsic drivers of the phyllostomid adaptive radiation and the resulting ecomorphological diversity of the clade. We begin by exploring the relationship between phyllostomids and their environments, focusing on the ecogeographical drivers of their radiation. Then, we detail current knowledge about the role of genes and development in enabling morphological diversification of the group. Finally, we describe the breathtaking ecomorphological diversification of phyllostomids, trying to unveil functional connections underlying their diverse dietary niches.

Keywords: adaptive radiation; Chiroptera; ecomorphology; evo-devo; diet; Phyllostomidae

INTRODUCTION

Adaptive radiations are exceptional instances of diversification in which a lineage rapidly speciates from a common ancestor in tandem with diversification of phenotypic traits that enhance performance within novel ecological niches (Schluter 2000, Gillespie *et al.* 2020). Mammals have diversified into thousands of species throughout their evolutionary history, but adaptive radiations—including their characteristic 'early burst' pattern (Simpson 1944)—seem to be rare or difficult to detect (Harmon *et al.* 2010). A suite of methodological issues may explain this difficulty, including the scarcity of ecomorphological studies that span whole mammal clades, the choice of nonfunctional phenotypic traits for phylogenetic comparative analyses, and the lack of well-resolved phylogenies with integration of fossil data (Slater *et al.* 2012, Mitchell 2015).

Nevertheless, some mammal lineages have emerged as models for investigating adaptive radiation. Bats (Chiroptera) are among these outstanding groups; they are the only mammals capable of powered flight and the second largest mammal order (>1400 extant species, Simmons and Cirranello 2024). Chiroptera probably radiated adaptively shortly after the evolution of powered flight (Teeling *et al.* 2005). However, rigorous tests of this hypothesis have not been possible due to a fossil record that is largely uninformative about the lineage's early diversification, and a poor understanding of how wing morphological traits relate to flight performance metrics and niche partitioning (e.g. Swartz *et al.* 2003, Hedenström and Christoffer Johansson 2015). Within bats, however, at least six instances of increased rates of species diversification have been detected (Dumont *et al.* 2011, Shi and Rabosky 2015, Almeida *et al.* 2021, Upham *et al.* 2023). Notably, three of these radiations occurred in tandem with diet shifts: (i) Pteropodidae (202 species), a Palaeotropical plantivorous clade; (ii) Phyllostomidae (227 spp.), a Neotropical clade spanning a wide dietary diversity; and (iii) Stenodermatinae (101 spp.), a clade of frugivorous phyllostomids (Fig. 1). Trophic transitions therefore seem to have played a salient role in chiropteran diversification.

We focus on the family Phyllostomidae (Fig. 1), which is the best known bat adaptive radiation due to extensive study of their systematics, development, natural history, ecology, and morphology (Fleming *et al.* 2020). Outcomes from this large body of work suggests that the phyllostomid radiation occurred relatively rapidly, over the course of ~30 Myr (with extant subfamilies represented in the fossil record and dietary diversification well underway in the Miocene, 13–11.5 Mya; Rojas *et al.* 2016, Simmons *et al.* 2020). During their radiation,

Received May 5 2024; revised October 30 2024; accepted for publication November 1 2024

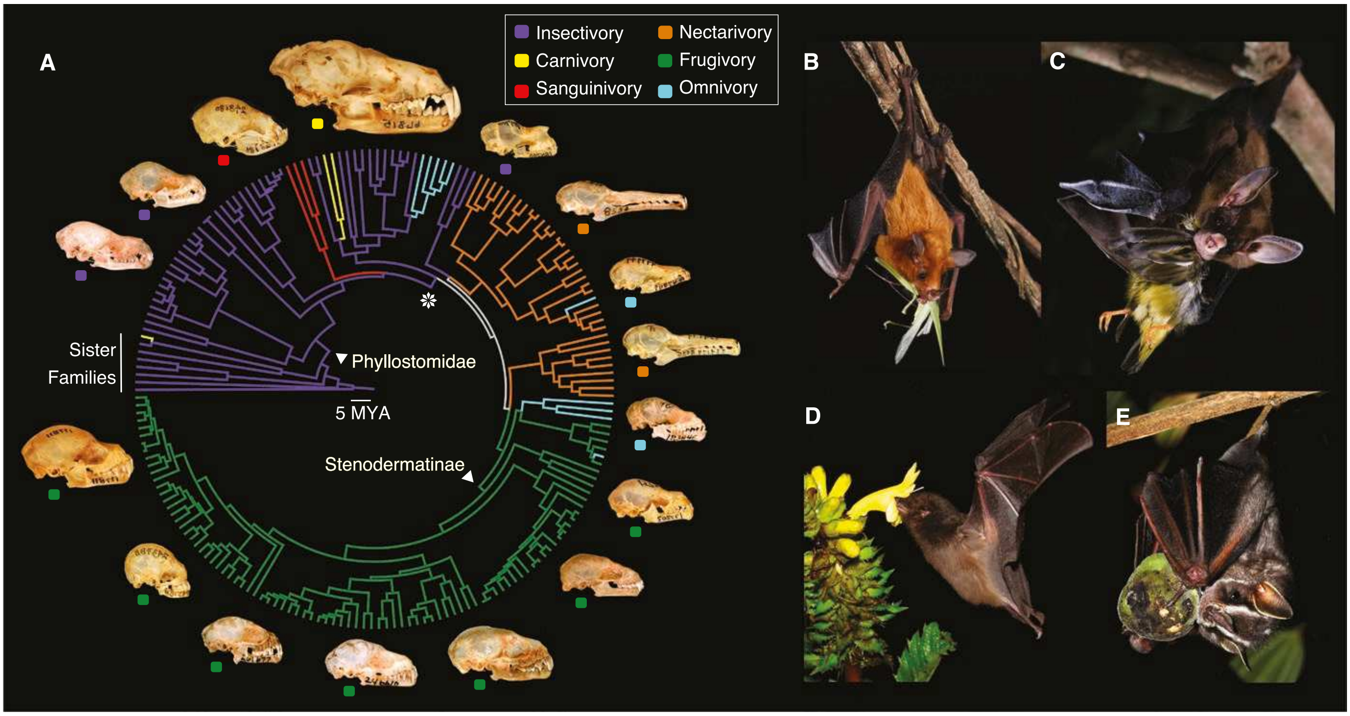


Figure 1. A, phylogeny of representative phyllostomid species and closely related families illustrating exceptional diversity in primary diet and skull morphology, particularly the degree of skull elongation; Δ: nodes with increased rates of species diversification, *: node with a diet-associated 'early burst' in molar shape evolution (see text for details). B–E, example phyllostomid species showcasing dietary diversity: *Trinycteris nicefori* (B, insectivore, credit: ©MerlinTuttle.org), *Vampyrum spectrum* (C, carnivore, credit: ©MerlinTuttle.org), *Anoura fistulata* (D, nectarivore, credit: Nathan Muchhala), and *Platyrrhinus lineatus* (E, frugivore, credit: Marco Mello).

phyllostomids evolved sensory specializations and extreme craniodental morphologies that allowed the exploitation of novel dietary niches (insectivory, frugivory, nectarivory, carnivory, sanguinivory, omnivory) across a multitude of ecosystems in the neotropics (Wetterer *et al.* 2000). In this perspective, we first detail the relationship between phyllostomids and their environments, identifying potential extrinsic drivers of their radiation. Then, we describe developmental and genetic factors underlying phyllostomids' diverse morphologies, to give a current outlook of the potential intrinsic drivers of the radiation. Finally, we describe how phenotypes are adapted to fulfil diverse ecological niches in this most striking—yet often overlooked—adaptive radiation of mammals.

EXTRINSIC DRIVERS

Habitat diversity is pivotal among the extrinsic drivers of the phyllostomid adaptive radiation. Phyllostomids thrive in a wide range of environments, from tropical rainforests to deserts and high-altitude regions, and in natural, rural, and urban environments (Stevens *et al.* 2020). Having evolved in the Neotropics, a region with high habitat heterogeneity, phyllostomids were presented with ample opportunity for diversification. Ultimately, their ability to exploit diverse habitats provided them with abundant ecological opportunities to excel in particular niches (Monteiro and Nogueira 2011), fostering speciation and resilience in the face of environmental fluctuations and habitat fragmentation (Festa *et al.* 2023). Presently, phyllostomids vary in their use of microhabitats within particular biomes or ecosystems; for instance, in sympatry, lineages such as the Phyllostominae are more frequently found in forests whereas Carolliinae are found in forest edges or open areas (Farneda *et al.* 2015). In complex habitat mosaics composed of forests, grasslands, plantations, and orchards, phyllostomid lineages differ in their habitat preferences according to their guilds, further leading to differences in microhabitat use between open and closed areas (Heer *et al.* 2015). Additionally, phyllostomid lineages differ in their vertical use of forests, as some species mainly occupy the canopy or the understorey, and others span multiple strata (Bernard 2001).

Phyllostomids are able to use a remarkable range of roost types within their habitats: from caves and tree hollows to foliage and human-made structures (Rodríguez-Durán 2020). This facilitates their expansion into new habitats and microhabitats, as well as access to distinct resources and protection against predators (Voss *et al* 2016, Rodríguez-Herrera *et al.* 2018). Further, over a dozen phyllostomid species have evolved the ability to modify leaves into tent roosts, a behaviour that opened another range of possible microhabitats within forests (Rodríguez-Herrera *et al.* 2018).

The astounding colonization of multiple habitats and microhabitats by phyllostomids is now better understood thanks to intensive phylogenetic scrutiny in recent decades. Molecular phylogenies have reshaped our understanding of phyllostomid evolution and biogeography (Teeling *et al.* 2005, Rojas *et al.* 2016), for example by highlighting the key role of continental-scale dispersal events and ecological determinants in genus-level cladogenesis (Dávalos *et al.* 2020). The Andes emerge as a significant factor in phyllostomid evolution, alongside lowland rainforests and large rivers, particularly for stenodermatine diversity (Villalobos and Arita 2010). In Central America, the Antilles represent a large-scale habitat mosaic that resulted in another hotspot of phyllostomid diversification (Dávalos 2007, Rojas *et al.* 2016). As family-wide analyses may oversimplify biogeographical patterns, there is a growing imperative to extend studies to genus or subfamily levels to validate emerging trends across the entire radiation and understand the interplay between geoclimatic factors and niche adaptations within the family.

Stemming from habitat diversity, dietary opportunity is key to understanding phyllostomid diversification; the evolution of frugivory and omnivory as primary diets is a remarkable feature that propelled this radiation (Rojas *et al.* 2011; Fig. 1). While many frugivorous species feed solely on fruits, omnivores supplement their diet with insects, nectar, pollen, or small vertebrates, and show a hierarchy among food types (Andrade *et al.* 2013). This dietary flexibility allows these species to exploit a wide range of resources, thereby reducing competition and niche overlap with coexisting species (Findley 1993, Kalko 1998, Giannini and Kalko 2004) and enabling adaptation to changing environmental conditions and resource availability (Lobova *et al.* 2009). More broadly, phyllostomids' dietary diversity has multiplied their interactions with other animals, plants, and microorganisms (Rossoni *et al.* 2017, Potter *et al.*; 2021, Caraballo 2022). These interactions between phyllostomids and other species range from mutualistic to antagonistic within local networks and have significantly influenced their adaptive radiation (Monteiro and Nogueira 2011, Mello and Muylaert 2020).

On the mutualistic side of interaction networks, phyllostomids contribute to plant reproduction and community dynamics as pollinators and seed dispersers (Ramírez-Fráncel *et al.* 2022), which are critical roles for Neotropical forest conservation and restoration (Bianconi *et al.* 2007, Kelm *et al.* 2008, Reid *et al.* 2015). The intricate web of ecological interactions within which phyllostomids are embedded has probably facilitated their radiation by creating niche partitioning and coexistence opportunities (Saldaña-Vázquez 2014). Moving from mutualistic to antagonistic, interactions between phyllostomids and their competitors, predators, and parasites can impose selective pressures that influence species diversification and ultimately ecosystem functioning (Webber and Willis 2016, Tendu *et al.* 2022, Szentivanyi *et al.* 2023). Competitive antagonistic interactions among phyllostomid species have been hypothesized to contribute to their adaptive radiation, leading to character displacement and niche partitioning (e.g. Verde Arregoitia *et al.* 2018, Shi *et al.* 2018, López-Aguirre *et al.* 2023). This process is probably clade- and character-dependent; for example, while dental traits show signals of divergent, stabilizing, or nonselective evolution (López-Aguirre *et al.* 2023), size traits can converge among phyllostomid species in sympatry (Verde Arregoitia *et al.* 2018). Further in the realm of antagonisms, studies elucidating bat–ectoparasite interaction networks highlight the importance of relative abundance in determining species functional roles (Falcão *et al.* 2022) and the crucial role that phyllostomids play in mediating ecological interactions within their communities (Mello *et al.* 2021).

In this 'web of life' (*sensu* Humboldt), a combination of dietary specialization, relative abundance, and unique ecological interactions position phyllostomids as keystone species within many ecosystems (Muscarella and Fleming 2007, Kunz *et al.* 2011, Ramírez-Fráncel *et al.* 2022, Barbier *et al.* 2024). Dietary specialization and abundance greatly influence phyllostomid species' centrality in seed dispersal networks across the Neotropics (Mello *et al.* 2015, de Souza Laurindo *et al.* 2020). Notably, the centrality of specialized frugivores and nectarivores varies significantly within and among networks, underscoring the nuanced role that dietary preferences and abundance play in defining their importance within ecological networks (de Souza Laurindo *et al.* 2020, González-Gutiérrez *et al.* 2022). Moreover, multilayer network analyses involving frugivory and nectarivory interactions between phyllostomids and plants highlight phylogenetic constraints that segregate species into different layers (Mello *et al.* 2019). Within these networks, organismal traits related to fruit or nectar consumption dictate a species' module identity and centrality (Mello *et al.* 2019, Mello and Muylaert 2020). This underscores the intricate interplay between functional morphology, abundance, and complexity in shaping the roles of phyllostomid bats within their ecosystems.

INTRINSIC DRIVERS

Ecological adaptation is ultimately the result of selection on the raw materials provided by the intrinsic (genetic, constructional, developmental) qualities of organisms (Gilbert 2001). Therefore, adaptive radiations can stem from alterations in developmental programmes, including the timing of developmental events (heterochronies) and developmental genes, networks, or processes. Studies that consider these aspects in nonmodel organisms are exceptionally challenging and remain a frontier in bat research (Moczek *et al.* 2015, Sadier *et al.* 2020). However, evo-devo studies have already provided unprecedented insight into the origin and evolution of phyllostomid adaptations to their diverse foraging and roosting ecologies.

Heterochronies appear to be common at various organismal levels in phyllostomids. For example, earlier events in palate development are more conserved than later ones (Sears 2013), echoing variation in gestation length that results in species being born precocial or well-furred (Cretekos *et al.* 2005). Craniofacial development as a whole presents heterochronic shifts between species with different diets, with nectarivores and sanguinivores exhibiting peramorphosis, and frugivores exhibiting terminal acceleration to achieve their final forms (Camacho *et al.* 2019). This heterochronic variation seems to be explained by variation in growth rate during development through a differential cell division rate, which is also responsible for the difference in rostral length between nectarivores and frugivores (Camacho *et al.* 2020; Fig. 1). In turn, differential growth rate of the jaw influences the number and size of postcanine teeth, in some cases by breaking classical developmental constraints and allowing species to explore new morphologies that are unique in mammals (Sadier *et al.* 2023). Therefore, it appears that subtle variations in growth rate were sufficient to drive the morphological and functional diversification of phyllostomids (Sears 2013, Sorensen *et al.* 2014, Sadier *et al.* 2023), assuming that they evolved through a line of least resistance in rostral length (Hedrick *et al.* 2020; and see below). Specific developmental drivers have been proposed to regulate rostrum growth rate, in particular *RUNX2*, which has been shown to regulate face length in mammals (Pointer *et al.* 2012). The number of poly-glutamine, poly-alanine repetitions in this gene is linked to variation of palate width and length in phyllostomids, particularly in short-faced stenodermatines (Ferraz *et al.* 2018). Whether these mutations have a direct effect on morphology remains to be tested, but suggests one of many potential mechanisms driving the rapid variation in face length in phyllostomids (Sadier *et al.* 2023).

Over the past few years, differences in sensory organ development in phyllostomids have been linked to sensory specialization and tradeoffs among diverse dietary niches. For example, phyllostomid cochleas develop at their final size, constraining the development of other sensory organs by restraining the space available in the skull, particularly in nectarivores (Anthwal *et al.* 2023a). Some sensory-related genes such as *OPN1SW* or *TRPC2* are frequently lost in phyllostomids, suggesting these regions have the potential to drive diversification of colour vision and olfaction capabilities through rapid losses and potential regains (Gutierrez *et al.* 2018, Kries *et al.* 2018, Sadier *et al.* 2018, Yohe *et al.* 2018, 2021, Simões *et al.* 2019).

Finally, the development of the hallmark feature of bats, wing membranes, echoes the developmental patterns found in the phyllostomid cranium. For example, interspecific differences in wing membrane morphologies arise by processes that take place after the initial formation of the wing membrane (Anthwal *et al.* 2023b). Phyllostomids retain conserved mammalian mechanisms and candidate genes (e.g. *RIPK4*) for the emergence and diversification of membranes (Anthwal *et al.* 2023b), highlighting how selection has operated on ancestral developmental mechanisms to foster this mammalian adaptive radiation.

ECOMORPHOLOGICAL DIVERSIFICATION

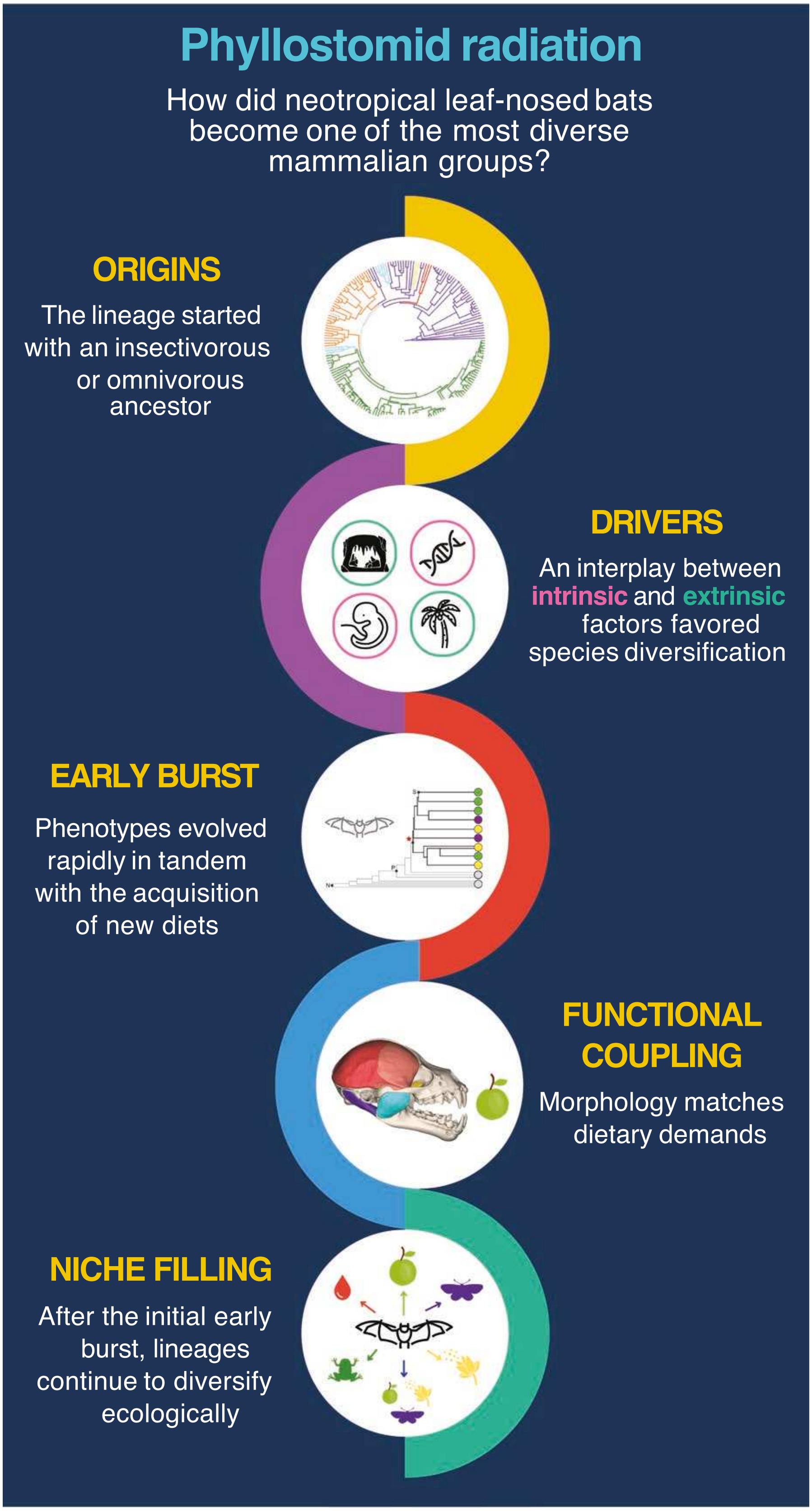
Resulting from the extrinsic and intrinsic drivers outlined above, phyllostomids evolved specialized phenotypes during their adaptive radiation. Many of these morphological and behavioural traits have direct functional significance by enhancing performance of the sensory and feeding systems towards specific dietary niches.

Given their diverse habitats and diets, phyllostomids are adapted to process information from various sensory channels. They typically forage in dense habitats or glean prey from surfaces using frequency-modulated multiharmonic echolocation calls for navigation and prey detection (Yoh *et al.* 2020, but see Gessinger *et al.* 2019). In addition to echolocation, carnivorous species eavesdrop on sounds produced by their prey (e.g. frog-eating bats; Page *et al.* 2012), frugivorous and nectarivorous species sniff out scent cues produced by fruits or flowers (Thies *et al.* 1998, Gonzalez-Terrazas *et al.* 2016, Leiser-Miller *et al.* 2020), and vampire bats use thermosensation to locate their vertebrate prey (Gracheva *et al.* 2011).

Phyllostomids are one of several chiropteran lineages that evolved nasophonation—a mode of echolocation that relies on laryngeally produced, ultrasonic calls that are transmitted through the nasal cavity and emitted via the nostrils (Jones 2005). Characteristic of phyllostomids is their noseleaf, a fleshy and often spear-shaped structure putatively implicated in sound modification, and after which they get their common name: the neotropical leaf-nosed bats. Across species, the three-dimensional shape of the noseleaf is correlated with echolocation call maximum frequency and bandwidth, and has evolved in a modular fashion to produce morphological differences among species that fall into broad dietary categories (mobile prey vs. immobile food items; Leiser-Miller and Santana 2020). Similarly, external ear shape and the morphology of the malleus and incus vary among species that specialize on different diets (Leiser-Miller and Santana 2020, Dickinson *et al.* 2023), probably related to differences in hearing sensitivity found at even finer levels of niche differentiation (Geipel *et al.* 2021). Further, phyllostomids exhibit thinner laryngeal cartilages and greater laryngeal diversity, probably due to reliance on senses other than echolocation for foraging (Brualla *et al.* 2024) and supporting the notion of tradeoffs between senses (Thiagavel *et al.* 2018). Phyllostomid echolocation morphologies therefore appear to be fine-tuned to the different demands imposed by the detection of specific food items in their respective habitats.

Phyllostomid skulls provide a wealth of information about how they adaptively radiated to occupy diverse dietary niches. Cranial anatomical modules related to sensory systems evolved at faster rates prior to accelerated changes in mechanical (feeding-related) modules (Mutumi *et al.* 2023). This emphasizes the possibility that sensory evolution was the first step to facilitating the phyllostomid radiation (Hall *et al.* 2021, Mutumi *et al.* 2023). Subsequently, cranial evolution underwent shifts to adaptive zones that largely match dietary transitions (Arbour *et al.* 2019). This process is characterized by exceptionally fast rates of rostral length evolution and high selective pressures leading to extremes in cranial elongation—from long-faced nectarivores to short-faced frugivores (Rossoni *et al.* 2017, Arbour *et al.* 2021; Fig. 1). The evolution of the mandible shows an even tighter association with diet; adaptive shifts in mandible shape—predominantly length—match transitions in diet (Monteiro and Nogueira 2011, Arbour *et al.* 2019), with resulting differences in mechanical advantage, peak bite force and its position along the tooth row, and tooth number also corresponding to dietary groupings (Nogueira *et al.* 2009, Santana *et al.* 2022, Sadier *et al.* 2023). Therefore, skull elongation appears to have facilitated the rapid dietary evolution of phyllostomids by acting as a line of least resistance for ecomorphological changes (Dumont *et al.* 2011, Ferraz *et al.* 2018, Hedrick and Dumont 2018, Arbour *et al.* 2019, Camacho *et al.* 2019, Hedrick *et al.* 2020). This idea is further supported by recent studies correlating rapid evolution in jaw length and tooth gains/losses and proportions in phyllostomids and close relatives (Sadier *et al.* 2023). While some integration patterns that possibly affected the evolution of phyllostomid skull elongation have been identified (see previous section), the underlying mechanisms have just started to be investigated.

The jaw muscles that connect the cranium and mandible to enable biting and mastication also show differences in physiological cross-sections and internal architecture among phyllostomid diet groups (Santana *et al.* 2010, Santana 2018). These range from reduced cross-sections in nectarivores (which



Phyllostomid radiation

How did neotropical leaf-nosed bats become one of the most diverse mammalian groups?

ORIGINS

The lineage started with an insectivorous or omnivorous ancestor

DRIVERS

An interplay between intrinsic and extrinsic factors favored species diversification

EARLY BURST

Phenotypes evolved rapidly in tandem with the acquisition of new diets

FUNCTIONAL COUPLING

Morphology matches dietary demands

NICHE FILLING

After the initial early burst, lineages continue to diversify ecologically

Figure 2. Summary of the main drivers and processes underlying the adaptive radiation of phyllostomid bats.

in turn have elongated and specialized tongues; Freeman 1995, Winter and Helversen 2003, Quinche *et al.* 2023, Muchhala *et al.* 2024), to robust temporalis muscles in species that feed on tough food items (e.g. vertebrates, hard fruit; Santana *et al.* 2010). Together, these features function to produce bite forces that match dietary mechanical demands, from weak bites in species that feed on liquids and soft foods, to forceful bites in species that feed on vertebrates or tough fruits (Aguirre *et al.* 2002, Dumont *et al.* 2009, Santana *et al.* 2010).

Teeth tell the most compelling story about the phyllostomid adaptive radiation's tempo and modes of evolution. Phyllostomid molars are specialized for efficient processing of different foods: insectivorous and omnivorous species have dilambdodont molars with shearing crests that cut through insect exoskeleton, frugivores have flattened molars that help mash up fruit pulp, whereas nectarivorous and sanguinivorous species have reduced molar morphologies (Freeman 1988, Santana *et al.* 2011, López-Aguirre *et al.* 2022). Diet-associated components of 3D molar shape exhibit an 'early burst' pattern in molar shape diversification within the phyllostomid subclade that underwent rapid dietary evolution (Grossnickle *et al.* 2024; Fig. 1). This early burst in morphological diversification was then followed by less dramatic morphological changes within the dietary adaptive zones, probably reflecting finer-scale niche partitioning (Grossnickle *et al.* 2024; Fig. 2). Initial shifts to derived diets probably posed strong selective pressures on molar development mechanisms, which freed molars from functional constraints associated with the ancestral molar morphotype and molar proportions found in most mammals (Kavanagh *et al.* 2007, Polly 2007, Sadier *et al.* 2023). Altogether, the evolution of phyllostomid craniodental morphologies fits traditional models of adaptive radiation (Simpson 1944, Schluter 2000), which are characterized by an initial explosive phase of ecomorphological diversification, followed by slower evolution in the resulting adaptive zones.

CONCLUDING REMARKS

A complex interplay of extrinsic (habitat, roosts, diet, and interactions) and intrinsic (integration, heterochrony, cell division rates, and modification of developmental programmes) factors appear to have driven the phyllostomid adaptive radiation. By colonizing and then thriving in diverse niches, phyllostomids diversified into a remarkable array of species, many with morphologies finely tuned to specific ecologies. Understanding the multifaceted drivers of the phyllostomid adaptive radiation has only been possible due to intensive research by hundreds of scientists who have helped establish phyllostomids as a model of mammalian adaptive radiation. Future research that directly and quantitatively integrates evidence across fields and organismal scales in this system has exciting potential to continue furthering our understanding of the mechanisms that generate and maintain biodiversity.

ACKNOWLEDGEMENTS

We thank all scientists who have been studying phyllostomid bats in the field, labs, museums, zoos, and computers in the past decades. The integration of natural history, classical and novel methods, and theoretical synthesis has helped considerably to advance our knowledge of this outstanding lineage, an endeavour that needs to be further promoted in the future. We thank Dr María del Rosario Castañeda and the rest of the editorial team of the *Evolutionary Journal of the Linnean Society* for the invitation to make this contribution, and members of the Santana Lab and two anonymous reviewers who provided comments that helped improve the manuscript.

FUNDING

S.E.S. is funded by the National Science Foundation (awards 2017738 and 2202271). A.S. is funded by the European Union (ERC-CoG-2023, NOVELTEETH, 01125917). The views and opinions expressed are, however, those of the author(s) only and do not necessarily reflect those of the European Union or the European Research Council Executive Agency. Neither the European Union nor the granting authority can be held responsible for them. M.A.R.M. was supported by grants and fellowships given to him and his team by the Alexander von Humboldt Foundation (AvH, 1134644), São Paulo Research Foundation (FAPESP, 2023/03083-6, 2023/02881-6, and 2023/17728-9), and Consulate General of France in São Paulo.

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