Knowledge shortfalls for titi monkeys: a poorly known clade of small-bodied South American primates

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Abstract

Titi monkeys (*Callicebus*, *Cheracebus*, and *Plecturocebus*) comprise the most species-rich group of primates in South America. Thirty-six currently recognized species composing this group inhabit a multitude of habitats across most of South America. While field-based and laboratory research has provided insights into the behavior, ecology, and physiology of some titis, multiple knowledge gaps regarding their biodiversity patterns persist. Here, we provide an overview of titi research and identify their biodiversity knowledge shortfalls. Using online databases, we collated the literature of all titi studies published up to December 31, 2021. We compiled 521 publications, with 48% representing *in situ* field studies of the monkeys. The majority of field-based publications focused on studies conducted in Brazil and Peru. We found that research efforts have increased in recent decades, as indicated by the increased number of publications on titis. However, given the large number of species and their wide distribution across South America, there is limited information about most of these species and their geographic ranges. By highlighting the focal points where conservation-related data are still required, our findings demonstrate the importance of expanding research efforts and investment on the full extent of titi species and their entire geographic regions; doing so will help fill the knowledge shortfalls rather than solely advancing the study of a restricted range of topics in one or two habitats or countries. These advances will contribute to fill knowledge gaps through the creation/expansion of data repositories, citizen science programs, and increased financial support to maintain long-term data collection.

Keywords: Atlantic Forest, Amazonia, behavioral ecology, diet, Platyrrhini, social behavior

1. Introduction

Awareness of the type and extent of biodiversity knowledge shortfalls (Hortal et al. 2015; Table I) is essential for determining the direction of future research on a particular taxon or region. Information that helps fill such gaps is even more important when these biodiversity shortfalls involve areas of knowledge needed for successful conservation and management (Mace 2004). Such knowledge shortfalls encompass a wide range of topics, including taxonomy, biogeography, ecological interactions, evolution, abiotic tolerances, populations, functional traits, and ecological functions (Table I; Hortal et al. 2015). Although they can appear intrinsic or exclusive, multiple shortfalls are often linked, so that information associated with (or missing from) one shortfall can assist in understanding another. For example, the Linnean shortfall, which is related to the description of new species (Brown and Lomolino 1998), could impact either the Wallacean shortfall, which defines what remains unknown of species' geographical distributions (Lomolino 2004), or the Prestonian shortfall, which is linked to deficit of knowledge or lack of data on abundance and population dynamics in space and time (Cardoso et al. 2011).

Most studies quantifying deficiencies in the current knowledge of species focus on a single shortfall (e.g., Lobo et al. 2007; Stropp et al. 2016; Troudet et al. 2017). This pragmatic approach, however, does not provide an overall picture of how scientific progress fills in knowledge gaps related to biodiversity and conservation. On the other hand, a set of shortfalls for a particular species or clade can lead to the compilation of a robust "state of the art" database (Freitas et al. 2020) that provides tools for future studies and conservation plans.

While there are serious concerns regarding global species loss from anthropogenic and climate changes, there remains an urgent need to quantify biodiversity at the regional level (Zhang 2011). Additionally, identifying new species increases knowledge of local and regional biodiversity filling this gap (Ferrier 2002). Moreover, establishing a high degree of certainty in taxonomic knowledge is likely to consolidate the known geographical range for a given species, thus assisting effective conservation assessment (Baranzelli et al. 2023). However, in some cases there is the risk that species may go extinct before they have been scientifically described; such scenarios are likely to be intensified due to a lack of investment in scientific research (Troudet et al. 2017; Thomson et al. 2018). Moreover, limits to our knowledge in multiple fields of study can complicate studies focused on feeding ecology, effects of the habitat and climate on reproductive behavior, and adaptability to current environmental conditions (Cardoso et al. 2011), as lack of associated knowledge means the full implication of the results in such fields may be neither appreciated nor applied. Consequently, identifying and quantifying current biodiversity knowledge shortfalls can help define priorities for future ecological and evolutionary research, as well as create effective conservation programs.

Overcoming knowledge shortfalls for a species increases the capacity to create and implement conservation actions more efficiently (Hortal et al. 2015). To accomplish such actions, it is necessary to understand the behavior, ecology, and biology of a species. It is also necessary to know the characteristics of its habitat (e.g., composition, structure, landscape) and the conservation threats (actual or potential) to aid the survival of that species. The creation of protected areas can function in the long term to conserve populations (Estrada et al. 2017). Moreover, ecological restoration programs based on the species' ecological needs can help increase habitat area (Rezende 2016; Chazdon et al. 2020). However, the conservation success of both protected areas and restoration programs depends on well-grounded ecological information concerning target or umbrella species. Lastly, the inclusion of local stakeholder communities in conservation actions is a well-established means to promote an appropriate understanding of the aims and intentions of conservation plans (Sterling et al. 2017). Furthermore, fostering local involvement, pride, and sense of ownership can promote collateral benefits (Mannigel 2008), including reductions in illegal pet trading, hunting, and inappropriate forest uses (Kleiman and Mallinson 1998). But, again, such actions only succeed when based on strong and well-researched ecological foundations and information (Estrada-Carmona et al. 2014).

In this context, understanding biodiversity and its intrinsic characteristics is a highly challenging task for highly understudied clades (Etard et al. 2020), Within the primates, titi monkeys (Pitheciidae: Callicebinae) form a salient example. Members of this group are the most species-rich clade of South American primates, with 36 currently recognized species, grouped into three genera (*Callicebus*, *Cheracebus* and *Plecturocebus*) based on variation in pelage, chromosomes, nuclear and mitochondrial loci, and habitat preference (Byrne et al. 2016). Collectively, titi monkeys occupy multiple biomes and ecosystems throughout South America, and are found in well conserved and protected landscapes as well as small, isolated, and highly disturbed forest fragments (Bicca-Marques and Heymann 2013). Additionally, there are regular descriptions of new species (Boubli et al. 2019; Gusmão et al. 2019) and populations (Rocha et al. 2019) of titi monkey, as well as documentation of new behaviors (Souza-Alves et al. 2021a; Martínez et al. 2022), and reports of new records for a species in a particular habitat or geographic location (Alonso et al. 2022; Costa-Araújo et al. 2022; Silva et al. 2022). While such discoveries provide further opportunities to increase our understanding of titi monkey biodiversity, pursuing these additional lines of scientific inquiry can be difficult, mainly because of the intense pressure humans can put on natural environments and the challenges of accessing remote environments for field studies (Pinto et al. 2013). Furthermore, titi monkeys can be quite cryptic and difficult to track in field studies. Therefore, many aspects of titi biology remain little studied.

Large and undisturbed forests provide suitable conditions (e.g., shelter, food) for the long-term maintenance and survival of primate populations which, among other things, aid in seed dispersal and pollination (Fleming and Kress 2013; Bufalo et al. 2016). However, habitat loss and fragmentation are primary threats to primate conservation in tropical forests (Estrada et al. 2017, 2018), and such loss and fragmentation has greatly impacted the geographic range of many titi monkey species (Boyle 2016). The variety of ecosystems occupied by titi monkeys has meant that there is significant variation in the extent and manner in which humans have transformed the habitat of an individual titi monkey species. A better understanding of the general behavior and ecology of this clade could help inform which conservation measures could be taken and how they might most effectively be implemented across multiple ecosystems and geographic localities.

This study provides an overview – what we know – of the progress made during the last 61 years (1960-2021) in our knowledge of titi monkey ecology, behavior, and genetics. Using the information obtained from our review of previous studies about titi monkeys, we identify which biodiversity knowledge shortfalls – what we do not know – exist for titi monkeys. This paper follows the taxonomic scheme proposed by Byrne et al. (2016), where titi monkeys were split into three genera: *Callicebus*, *Cheracebus,* and *Plecturocebus*. Consequently, earlier taxonomies deployed in the cited literature were updated to align with the most recent taxonomic scheme.

2. Material and methods

We searched the titi monkey literature using PubMed-specific and EBSCOHost-specific filters "Callicebinae" following Cassidy et al. (2021). For the EBSCOHost search, we included 19 databases associated with EBSCOHost (e.g., Academic Search Premier, APA PsycInfo, OpenDissertations). We compiled peer-reviewed journal articles and book chapters, dissertations, and theses addressing any aspect of titi monkey biology (e.g., behavior, conservation, ecology, genetics, taxonomy), and sources that focused on the results of primate field surveys (Supplemental Material I). We then used Google Scholar (individual search terms: *Callicebus*, *Cheracebus*, *Plecturocebus*, titi monkey) and ResearchGate (individual search terms: *Callicebus*, *Cheracebus*, *Plecturocebus*, titi monkey) to supplement the list with additional material not located during the original searches. We used these databases to maximize the coverage of the published literature (Falagas et al. 2008). Our investigation included items published in English, Portuguese, and Spanish to avoid a sampling bias and best represent the published literature (Amano et al. 2021; Nuñez and Amano 2021). We included all literature published between January 1, 1960 and December 31, 2021.

We included field studies, laboratory studies, and literature reviews, but excluded conference abstracts, book reviews, and non-peer-reviewed material from our final list of titi monkey publications. We read each item to assure that it met our inclusion criteria. We then categorized each published article based on the type of study (field or laboratory or other - e.g., data from a genebank), geographic location and fieldwork duration, and the study topic (e.g., activity budget, anatomy/morphology, biomedical applications, conservation, diet, disease, genetics, physiology, social behavior, spatial use, surveys/distribution, taxonomy/phylogeny, vocalizations, and "other", which covered any topic that did not otherwise fit the existing topic list). Our literature search retrieved 538 published items. We discarded 17 (3.2%) because they did not meet our above-defined criteria, leaving a total of 521 publications for analysis.

We quantified the published studies by type, topic, and geographic region. We then used this information to identify the significant shortfalls (Table I) associated with titi monkey research, with the intention of identifying research foci for the effective conservation of these species. Review papers were tallied as one publication, using the main focal theme. Additionally, we mapped the spatial distribution of *in situ* field studies to identify areas within the geographic ranges (as defined by the IUCN Red List) of those titi monkeys that have been the subject of research versus geographic areas where titi monkeys have not been studied extensively. When a publication focused on findings from multiple sites (e.g., a survey of dozens of forest fragments in a region) or multiple species, we mapped it using the latitude and longitude for the most-centralized location surveyed. Using the findings from our literature review and the specific topics encountered by us during the research, we then identified the main conservation threats to titi monkeys and the conservation actions necessary to maintain their population viability.

3. Results

We found 521 published peer-reviewed journal articles (N=453; 86.9%), book chapters (N=27; 5.2%), and theses/dissertations (N=41; 7.9%) in our search of the literature on free-ranging and captive titi monkeys (Supplemental Material I). Although there are early accounts of titi monkey taxonomy and morphology (Johnston, 1919; Lönnberg, 1939; Thomas, 1903, 1927), the first published field studies of titi monkeys began in the 1960s. During the past six decades, the number of published studies has increased steadily from 1960 to 2019 (Fig. 1). In 2020 and

2021, the start of the seventh decade of publications on titi monkeys, we found an additional 49 publications (2020: 26; 2021: 23). Of the 521 publications we found and analyzed, 55.2% were published since January 2010.

Furthermore, the publications have become more collaborative over time. Prior to 1980, 54.1% of the titi monkey journal articles had a single author, 27% had two authors, and 18.9% had three or more authors. For journal articles published in 2000 or later, 73.1% had three or more authors, 18.9% had two authors, and only 8.0% had one author.

Based on a full review of the content of each published item, the most common topics across all published articles were: field surveys (26.4%), conservation (9.3%), anatomy/morphology (primarily captive, but also field studies; 8.9%), social behavior (11.1%; principally captivity-based [7.3%], but also field studies [3.8%]), diet (mostly field-based; 7.3%), and taxonomy/phylogeny (5.6%) (Fig. 2). Aside from site surveys, most of the "other" category consisted of studies focused on non-social behaviors (e.g., anecdotal reports of terrestrial behavior, predation avoidance, predation). Of the 521 total publications, 250 (48.3%) were field studies of titi monkey behavior, ecology, conservation, or presence/absence data in surveyed locations. Of these, the majority (52.9%) took place in Brazil. While most other South American countries were well represented (Fig. 3), we found only one publication on titi monkeys in Paraguay (Fig. 3), and it focused on *Trypanoxyruis* parasites in wild-caught titi monkey (Hugot et al. 1994). We found no published field studies of titi monkeys in Venezuela. Overall, studies of disease in free-ranging titi monkeys primarily focused on yellow fever (Sacchetto et al. 2020; Berthet et al. 2021; Fernandes et al. 2021) and parasites (Gómez-Puerta et al. 2009; Doležalová et al. 2015).

Of the 250 field-based publications, 154 (61.6%) addressed titi monkey behavior, ecology or genetics. Of these, most focused on titi monkeys in Brazil, followed by Peru (Fig. 3). Additionally, of these 154 publications, only seven addressed genetics in free-ranging individuals or groups.

The distribution of field studies across the geographic range of titi monkeys was also not uniform (Fig. 4). Overall, those publications addressing the behavior, ecology, and genetics of free-ranging titi monkeys were largely concentrated at a small number of field sites in Brazil (e.g., Estação Experimental Lemos Maia, Fazenda Trapsa, Mata do Junco Wildlife Refuge, Santuário do Caraça Private Nature Reserve, Parque Zoobotânico da Universidade Federal do Acre), Ecuador (Tiputini Biodiversity Station), and Peru (Estación Biológica Quebrada Blanco, Estación Biológica Cocha Cashu). Combined, these eight field sites represented 52.4% of the publications we gathered on the behavior, ecology, or genetics of free-ranging titi monkeys, suggesting that these topics remain unstudied over much of the geographic ranges of most species in the clade.

4. What do we know about titi monkeys?

4.1. Ecology

As a collective result of field studies across six decades, the overall ecology and behavior of titi monkeys as a clade is comparatively well-established. Titi monkeys use a range of habitat types, including rain forests, naturally open woodlands such as Chaco, highly disturbed habitats, edge forests, and secondary forests (Chagas and Ferrari 2010; Kulp and Heymann 2015). In these habitats, titi monkeys are predominantly frugivorous, with fruits comprising 36-86% of the diet (Bicca-Marques and Heymann 2013). Other food items, such as seeds, leaves, flowers, and insects have also been recorded (Norconk 2011). Seeds occur in titi monkey diets (Bicca-Marques and Heymann 2013), either during periods of low fleshy fruit availability (Caselli and Setz 2011; Acero-Murcia et al. 2018), or specifically during periods of bamboo masting year (dos Santos et al. 2012). The exploitation by titi monkeys of invertebrate prey (Souza-Alves et al. 2011a; Heymann and Nadjafzadeh 2013), and new leaves from lianas (Souza-Alves et al. 2011a; Nagy-Reis and Setz 2017) has been reported mainly during periods of low fruit availability. In contrast, small vertebrates have been documented as a food resource in titi monkeys only once (Vinhas and Souza-Alves 2014). Overall, dietary eclecticism is associated with the extensive variation between species and their geographic proximity: overall, the plant genera used as food resources is heavily associated with the geographic range of the titi monkey species (Boyle et al. 2016).

4.2.Behavior

Titi monkeys typically spend most of the time resting, followed by feeding/foraging, movement/travel, and social behavior, but such patterns vary between studies (DeLuycker 2021; Souza-Alves et al. 2021b). The distribution of food sources and their in-habitat availability is key to understanding the drivers of the behavioral and ecological adjustments made by South American primates (Hemingway & Bynum, 2005). This is also true for titi monkeys, where multiple studies have indicated that such adjustments are often highly correlated with the level of food resources available in a given habitat (Nagy-Reis and Setz 2017; Souza-Alves et al. 2021a).

Social behavior constitutes between 1% and 11% of titi monkey daily activity budgets (Bicca-Marques and Heymann 2013). This includes both allogrooming and affiliative behaviors such as tail twining (Kinzey and Becker 1983; Kinzey et al. 1977) and vocalizations (Adret et al. 2018). Bioacoustical studies of titi monkeys have shown that loud calls used by mated pairs are more strongly associated with the defense of food sources (e.g., fruits) than of a mate (Caselli et al. 2015). Additionally, alarm calls cause terrestrial predators (i.e., ocelot, *Leopardus pardalis*) to move away from the current location of a group; titi alarm calls have been shown to be predator-specific (Adams and Kitchen 2018; Cäsar et al. 2013). Calls may also be modified depending on the nature of the habitats (disturbed or not); *Plecturocebus modestus* living in continuous forests showed higher call rates than those in fragmented forests (Martínez and Wallace 2016). Titi monkeys also shorten their call duration to enhance the possibility of being heard and understood over anthropogenic noise (e.g., mining), which can obscure their territorial calls (Duarte et al. 2018 for *Callicebus nigrifrons*). *Plecturocebus donacophilus* reduced movement behavior when exposed to long periods of anthropogenic noise and decreased their alarm-calling behavior during periods of increased contact with humans (Hernani Lineros et al. 2020).

Over the past ten years, the number of studies related to social behavior in titi monkeys has grown substantially. Here, we consider only investigations of such topics that were conducted in the wild, although there is extensive literature on captive titi monkeys, including the wide-ranging work conducted by Karen Bales' lab (some examples: Lau et al. 2020; Mercier et al. 2020; Rothwell et al. 2020; Savidge and Bales 2020). As a result of their monogamous social system and territoriality, titi monkey pair-mates often stay close to one other during daily activities (Kinzey and Wright 1982; Van Belle et al. 2021). In these events, the individuals demonstrate affiliation and social tolerance (Anzenberger 1988; Fernandez-Duque et al. 2013). In *Plecturocebus cupreus*, adult females appear primarily responsible for maintaining proximity and associated pair-bonding activities, and they contribute more often to grooming than do adult males (Dolotovskaya et al. 2020a). The arrival of infants results in substantial changes in group behavioral dynamics. Following a birth, adult females devote their time to nursing; thus they contribute to proximity and affiliation maintenance; contemporaneously, adult males carry infants and spend more time on territorial defense (Fernandez-Duque et al. 2013; DeLuycker 2014; Spence-Aizenberg et al. 2016; Dolotovskaya et al. 2020a). Additionally, adult females of *P. cupreus* eat more insects when lactating (Tirado Herrera and Heymann 2004); however, during the lactation period, females of *Plecturocebus discolor* did not increase the time devoted to feeding overall (Spence-Aizenberg et al, 2016; Fernandez-Duque et al. 2013).

Male-infant and mother-infant conflict and avoidance of infants by males were reported for *Plecturocebus oenanthe* in two small forest fragments (Hodges 2020). Such conflicts were also recorded during food-sharing events in *Callicebus coimbrai* (Correia et al. 2013; Souza-Alves et al. 2019a). Although the influence of habitat quality, seasonality, and home range size has been investigated, it remains unclear which factor(s) drive such behaviors. This is intriguing, especially since similar post-birth behavior has not been recorded for males of other titi monkey species (e.g. *P. discolor*: Fernandez-Duque et al. 2013; Spence-Aizenberg et al. 2016).

4.3. Genetics

The impacts of habitat loss and fragmentation on the genetic diversity in primates have not been extensively documented (Lino et al. 2019). Two studies have shown the effects of such events on titi monkeys within-population genetic diversity. In northern Bolivia, Pinto et al. (2019) found low levels of genetic variation in populations of *P. olallae* and *P. modestus* living in forest islands within natural savanna. In addition, *P. olallae* showed lower levels of consanguinity than *P. modestus*. Such findings appear to be linked to isolation, genetic drift, and selection as a by-product of habitat fragmentation. This appears to be more evident for *P. modestus* that inhabit forests on islands of higher grounds in a seasonally flooded grassland (Pinto et al. 2019). In addition, an unexpectedly low level of genetic diversity was found in *Plecturocebus moloch* living in patchy forest fragments in eastern Amazonian Brazil (Menescal et al. 2009); these were also likely a result of isolation. Both these studies highlight the risks of extinction in both naturally and anthropically isolated populations and the importance of implementing preventive measures to avoid such adverse effects (see Radespiel and Bruford 2014). Additionally, the single study to date to have used genetic analysis to document mate choice, relatedness, and potential inbreeding in titi monkeys found no evidence for mate choice, no between-sex differences in distances dispersed from the natal group, and no evidence of extra-pair paternity or evidence for relatedness- or heterozygosity-based mate choice (Dolotovskaya et al. 2020b). Thus, titi monkeys should be able to maintain populations in fragmented habitats, as long as the distances between suitable areas do not become so large that colonization rates drop below a critical threshold and inbreeding rates increase.

5. Current knowledge shortfalls for titi monkeys

An individual shortfall type does not occur in isolation, and only in combination can these shortfalls fully describe the various aspects of a given species. For example, the description of new species (Linnean shortfall), and the definition of their distributional range (Wallacean shortfall), both provide information on their behavioral and ecological patterns (Fig. 2 in Hortal et al. 2015). Given the extensive overall distributional range of titi monkeys as a group, it is unlikely that all shortfalls apply to all titi monkey species, as such knowledge is, to some extent, transferrable between species. Therefore, when using the data compiled from our literature search to assess the seven shortfalls identified by Hortal et al. (2015) for titi monkeys, we did not treat the shortfalls for each titi monkey species but took the overall clade as the unit of discussion.

5.1. Linnean shortfall

Knowledge of the total number of species within one group of animals or plants is essential for effective biological study. The lack of such information constitutes a Linnean shortfall (Lomolino 2004). However, abolishing this shortfall for a clade is challenging when it is composed of comparatively small-bodied animals with low abundance and restricted geographical ranges (Moura and Jetz 2021). Accordingly, additional titi monkey species likely remain to be discovered, further bolstering the status of the clade as the most species-rich of South American primates. Currently, there are more than 30 species distributed across seven countries (Bicca-Marques and Heymann 2013). However, the Linnean shortfall for titi monkeys is unlikely to be distributed uniformly. For example, the relative accessibility of the eastern portion in Brazil, the home of all members of the *Callicebus* (Byrne et al. 2016), could facilitate the encountering of any new species of this genus that remain undiscovered in the region. This is not the case, however, for the other two genera (*Cheracebus* and *Plecturocebus*); both restricted to Amazonia (Byrne et al. 2018) and adjacent areas (Boubli et al. 2019). As for many other taxa in the region (Brito 2010; Oliveira et al. 2016), the remoteness, distances, and difficulty of access are likely to be the main challenges faced to discovering new titi monkey species in this region. However, while historically, titi monkey taxonomy was beset with uncertainties (Byrne et al. 2020; Vendramel 2016), modern techniques such as mitochondrial DNA and genomic analysis have led to extensive clarifications and the establishment of a firm framework (Byrne et al. 2016) on which the description of new species (Boubli et al. 2019; Gusmão et al. 2019) can be based.

5.2. Wallacean shortfall

It is not only necessary to know the number of titi monkey species, but also to be sure of their geographical distributions. A complete knowledge of the distributional limits of each titi monkey is required so that studies can determine: 1) whether the habitat(s) in which a species occurs is undergoing (or has recently undergone) a high level of natural vegetation loss, 2) with which other primate species their geographical range overlaps, and 3) the nature of the boundaries that define range limits (biotic factors such as different types of vegetation, or abiotic ones such as rivers). Thus, a Wallacean shortfall involves uncertainties over where a species occurs and what limits its distribution (Lomolino 2004). Deficiencies in such data run the risk of introducing omission (reference sites left out – omitted – from the correct class in the classified map) and commission (revision of the classified sites but with an incorrect classification) errors in range maps and other forms of biodiversity-based cartography, thus complicating recommendations for reliable and effective management and conservation. Factors such as those cited above, combined with size, remoteness, and technically and logistically challenging nature of such areas, mean they are less sampled than those areas with easier access (Rodrigues et al. 2010). Reducing the extent of Wallacean shortfalls for titi monkeys is likely to require extensive investment in time and money. Thus, it will likely be most viable when conducted as part of a broader series of broad-based field visits that simultaneously aim to reduce Wallacean shortfalls for a wide variety of taxa.

5.3. Prestonian shortfall

Population size is an essential predictor of the probability that a population will persist over time (Reed et al. 2003; Traill et al. 2007). As population density may vary considerably across the geographical distribution of a species (Brown et al. 1995; Pinto et al. 2009), identifying large areas of forest or extensive fragments with high population densities can be crucial for the effective conservation of a species. Databases for density or abundance exist for several titi monkey species (*C. personatus*: Price et al. 2002; *C. nigrifrons*: São Bernardo and Galetti 2004, and Trevelin et al. 2007; *C. coimbrai*: Chagas and Ferrari 2011; *C. barbarabrownae*: Freitas et al. 2011 and Corsini and Moura 2014). Preliminary data on abundance and density has been collected at several study sites, but the continuity of studies needed for effective population enumeration and monitoring of such demographic variables as sex ratio and age structure to model titi monkey population dynamics is infrequent. As noted by Hortal et al. (2015), three primary factors cause such limitations: 1) the absence of accurate data between years, 2) the cost of maintaining long-term projects, and 3) the requirement for frequent resampling to capture any rapid fluctuations in population size. Although new techniques are being deployed to estimate the abundance and density of primates (*Prolemur simus*: Olson et al. 2012; *Pan troglodytes verus*: Cappelle et al. 2019; *Macaca fuscata*: Enari et al. 2019), the long-established method of the line transect (Peres 1999; Marshall et al. 2008; Buckland et al. 2010) is still a standard and often employed. This has led to variations in data collected due to inter-observer interpretation in capacity and experience (Plumtre et al. 2013). Therefore, a large part of the Amazon is gaining data on abundance and density for remote areas where access is difficult.

5.4. Darwinian shortfall

According to Diniz-Filho et al. (2013), there are three components to Darwinian shortfalls: 1) absence of fully resolved phylogenies, 2) poor knowledge of edge lengths and difficulties with absolute time calibrations, and 3) unknown nature of the evolutionary processes linking ecological traits and life-history changes within these phylogenies. In addition, as pointed out by Assis (2018), there may be problems related to the current form of the reconstructed phylogeny, which could influence this shortfall. The first studies aimed at constructing a phylogeny for titi monkeys was by Hershkovitz (1988, 1990), using morphological characteristics and a metachromic analysis of evolutionary significance of color pattern to reorganize the sole genus recognized at that time (*Callicebus*) into 13 species and 17 subspecies grouped in four distinct species-groups (*donacophilus, modestus, moloch*, and *torquatus*). Five years later, Kobayashi (1995) used similar parameters and identified an additional titi monkey lineage (*personatus*). This was the only titi lineage present in the Atlantic Forest, Caatinga, and Cerrado biomes of Brazil (Bicca-Marques and Heymann 2013), and Carneiro et al. (2018) subsequently confirmed the validity of the *personatus* lineage. Changes have also occurred in what is accepted as a species; this began with van Roosmalen et al. (2002), whose review of titi monkey taxonomy elevated all sub-species to species level, resulting in 28 species at that time.

Even though such studies have had a strong influence on subsequent phylogenetic analysis in titi monkeys, the variables used (e.g., morphology, specimen locations) are no longer considered the most reliable sources for inferences. However, refined and robust new procedures, such as molecular analysis, have allowed various aspects of titi monkey phylogeny and phylogeography to be investigated, along with previously totally understudied factors such as the evolutionary history of the clade. Of the recent studies that have filled this shortfall, arguably the most complete was performed by Byrne (2017), who used a large multi-locus molecular dataset and showed the existence of four distinct titi monkey clades. Two major divergence events were identified in the Miocene, with the division of sister species estimated to have occurred c. 2-1 Mya in the Pleistocene. As a result, Byrne et al. (2016) proposed splitting *Callicebus* into three genera: *Callicebus*, *Cheracebus,* and *Plecturocebus*. Subsequent work resolved species-level relationships (Byrne et al. 2018, 2020), with support derived from additional studies (Carneiro et al. 2016, 2020; Hoyos et al. 2016).

However, a shortfall still exists for the third component identified by Diniz-Filho et al. (2013): absence of phylogenies linking life-history and ecological traits. It should be pointed out that further studies could usefully deploy existing databases to analyze associations between titi monkey ecology and life-history traits and phylogenies. This approach may become particularly pertinent because such studies may permit predictions of likely responses by individual titi monkey species to climate change, so indicating potential extinction resilience or vulnerability, as shown with other primate species (Sales et al. 2020; Stewart et al. 2020; Pinto et al. 2023). This is extremely pertinent as the deleterious effects of climatic change can reduce and homogeneity the suitable areas for primates, leading to decreases in both populations and species richness, increases in competition with phylogenetically-related species, and modifications to life-history traits (Lima et al. 2019; Silva et al. 2022; Pinto et al. 2023).

5.5. Raunkiæran shortfall

The Raunkiæran shortfall is defined as the absence of knowledge on the species' traits and their ecological functions within and between populations (Roy and Foote 1997; Kingsolver et al. 2001). Such functions can be determined by response to pressures (response traits) and their effects on processes and ecosystems services (effect traits) (de Bello et al. 2010). These traits can be combined with life history, behavior, and feeding habits (de Bello et al. 2010). The behavior and feeding ecology of titi monkeys are well-documented. Nevertheless, there is an essential Raunkiæran shortfall in titi monkey studies: seed dispersal and its role in habitat restoration (ecosystem process). The strong patterns of frugivory shown by titi monkeys make it very likely that these primates contribute to ecological restoration via seed dispersal. Although primates are often essential participants in this process (Chapman et al. 2020), including such erstwhile pithecine seed predators as *Cacajao* and *Chiropotes* (Barnett et al. 2012), this research theme has been almost entirely absent from titi monkey studies except for a few investigations (Correia 2014; Baião et al. 2015; Gestich et al. 2019b). During a six-month study in Atlantic Forest fragments, Baião et al. (2015) recorded *C. coimbrai* groups collectively defecating seeds of 22 plant species, although germination was not recorded. Meanwhile, Gestich et al. (2019b) found 49 species of seeds in the feces of *C. nigrifrons* in the Brazilian Atlantic Forest, the majority of which germinated; however, passage through the gut reduced germination success in three of the five seed species evaluated. Given their established capacities as seed dispersers (Baião et al. 2015; Gestich et al. 2019b), calls have been made for the enhanced deployment of primates as seed dispersers in habitat restoration projects (Chapman et al. 2020).

A second type of Raunkiæran shortfall concerns the importance of sleeping trees on the predation avoidance and foraging strategy in titi monkeys; this has been the subject of just two dedicated studies (Souza-Alves et al. 2011b; Caselli et al. 2017). Other studies have mentioned various aspects of this behavior (Kinzey et al. 1977; Kinzey 1978; Kinzey and Becker 1983; Heiduck 2002), but it was not the focus of the study. Field studies that document the use of sleeping trees and sites are extremely important for understanding species' behavior in avoiding predation, facilitating foraging, reducing diseases, and increasing sociability between individuals of a group (Anderson 1998). Titi monkeys may exhibit a preference for only one tree species (Souza-Alves et al. 2011b), use tallest branches covered in epiphytes and vines on trees, probably to avoid predation mainly by scansorial carnivores (Caselli et al. 2017), but may also choose the sleeping trees located close to important feeding sites (Caselli et al. 2017). We suggest investigating whether associations are linked to predator avoidance or to enhance the effectiveness of food source location after a night of non-feeding. We could expect that sleeping trees would be close to food sources to reduce the distance to access the food after waking up. Moreover, we also could expect large and tall sleeping trees with closed canopy (i.e., presence of lianas and dense foliage) would contribute to the avoidance of potential predators (e.g., preference for such trees has been reported by Barnett et al. 2012 for golden-backed uacaris, *Cacajao melanocephalus ouakary*). An additional aspect could include tests of whether day-resting and night-sleeping sites differ, depending on the most likely predator type, as reported by Jucá et al. (2020) for howler monkeys (*Alouatta nigerrima* and *A. discolor*).

5.6. Hutchinsonian shortfall

Given the extent to which titi monkeys use a variety of habitats across a large geographic area of South America, but with more than half of published field studies representing eight field sites, there is not full documentation of the extent to which titi monkeys, as a clade, tolerate and respond to various abiotic conditions. As a whole, there has been little to no study of titi monkeys throughout much of their geographic ranges, which makes it difficult to describe tolerance to abiotic factors. The Hutchinsonian shortfall addresses these abiotic tolerances (Hortal et al. 2015), but this shortfall can also include knowledge gaps of life-history traits and the functional role of the species in various habitat types and degrees to which habitats have been modified (Cardoso et al. 2011). In this context, studies of Hutchinsonian shortfall can help define a species' lack of tolerance or response to particular abiotic conditions or to changes to such conditions (Soberón 2007), whether these conditions are indicative of a particular habitat or ecosystem, or these conditions represent relatively recent changes due to human activities.

The geographic range of titi monkeys has been impacted by human activities (Ferrari et al. 2013b; Porter et al. 2013), specifically forest loss (Boyle 2016). Therefore, an understanding of abiotic tolerance and response to abiotic conditions is needed for understanding how quickly changing habitats impact titi monkey species. Compared to other primate species in the Americas (Boyle and Smith 2010; Chaves et al. 2011a,b), there has not been as great a focus on the effects of habitat loss and fragmentation to changes in titi ecology and behavior (Boyle 2016). Identifying and comparing the behavioral and ecological flexibility of titi monkeys in the context of the adverse effects of such disturbances is essential for the effective development of appropriate conservation strategies. For example, Souza-Alves et al. (2021a) recorded different behavioral and ecological strategies of the *C. coimbrai* groups living in one large (522 ha) and one small (14 ha) Atlantic Forest fragment. Variations in feeding and habitat use in primates are generally related to body mass and metabolic rate. However, abiotic and habitat variables must be considered so that, when making such comparisons (i.e., between species), similar-sized forest fragments in the same landscape are used (Estrada et al. 2012; Benchimol and Peres 2014). Primates are known for their sensitivity to ecological changes (Cowlishaw and Dunbar 2000), and such an accumulation of additional data should allow more accurate inference of the adverse effects that have been encountered in the past and what may occur in the future (Cardoso et al. 2010; Triantis et al. 2010).

Additionally, studies of habitat loss and fragmentation should investigate the influence of variables such as habitat and the surrounding matrix on individual and group dispersal and new group formation. Although dispersal events have been recorded for titi monkeys (see Bicca-Marques and Heymann 2013), the role of habitat loss and fragmentation on dispersal events and the formation of new titi monkey groups remain poorly understood. Disturbance and fragmentation affect the forest cover of titi populations across the great majority of their distributional range (Boyle 2016). The outcomes of the fragmentation process in its extreme form - small and isolated areas – have a strong influence on the frequency, distance, and success of individual dispersal events in titi monkeys (Ferrari et al. 2013a). In titi monkeys, upon reaching sexual maturity (*ca*. 40 months), individuals tend to disperse from the natal group and attempt to form or (perhaps) join a new group (Wright 1985). In fragmented landscapes, the availability of suitable habitat may influence social organization; in a highly fragmented landscape in the coastal Atlantic Forest in Sergipe, Brazil, Souza-Alves and Ferrari (2012) found that a young adult *C. coimbrai* male, apparently unable to find suitable habitat elsewhere, returned to the natal group one year after initial emigration. This study group inhabited a small and isolated fragment, and, as a result, the group had more than one adult male. Titi monkeys live in breeding pairs and the presence of other sexual competitors can result in non-affiliative behaviors (i.e., fighting) that may potentially disrupt the group's social dynamics, reduce time spent on foraging, and vigilance behavior (Souza-Alves & Ferrari 2012).

There is a strong need for additional field studies of genetic variability in titi monkeys. While previous studies have considered the detrimental effects of fragmented landscapes on titi monkey genetics hypothetically (Menescal et al. 2009; Pinto et al. 2019), few have done so *via* actual field studies. A thorough study of genetic variation and population structure is essential for a better understanding of how species evolve, adapt, and co-exist and for the formulation of effective and practical conservation and management strategies (Eguiarte 1990). Many titi monkey populations exist in highly fragmented landscapes that include a non-forested matrix. This scenario of a fragmented landscape, for example, might result in the reduction of the movement of titi monkeys between areas, as well as overabundance in small and isolated fragments. It is likely that both scenarios could cause negative genetic effects on titi monkey populations.

Although titi monkeys can travel on the ground (Souza-Alves et al. 2019b), movement between forest fragments has been documented only for *P. olallae* (Martínez and Wallace 2011). The difficulties and risks for individuals when moving between forest fragments can be correlated with the matrix type surrounding the forest fragments and linked to increased exposure to parasites and increased predation risk (Barnett et al. 2005; Nunn and Altizer 2006). Moreover, living in small and isolated areas can considerably increase the density of individuals, causing a crowding effect (reviewed by Fahrig et al. 2019). Therefore, while habitat loss is the main threat to primate populations (Galán-Acedo et al. 2019), habitat fragmentation can also contribute *via* reduced genetic variability, increasing consanguinity, and possibly extinction (Gravitol et al. 2001; Pinto et al. 2019; Solórzano-Garcia et al. 2021), as well as increasing competition, thereby leading to physiological stress and increased spread of disease (Arroyo-Rodríguez & Dias 2010; Marsh et al. 2013; Gabriel et al. 2018). The potential absence of functional structure (e.g., ecological corridors) and long distances can contribute negatively to the movement of the titi monkeys between forest fragments, thus likely limiting dispersal (Costa-Araújo et al. 2021). The negative effects of such limitations on genetic variability in titi monkeys remains poorly understood and deserves attention in future studies of highly fragmented landscapes. Recently, in a study developed with 14 groups of *P. cupreus*, Dolotovskaya et al. (2020b) evaluated genetically the link between mating system, mate choice, and dispersal. Although the study was preliminary, the authors indicated that adult individuals of both sexes were able to disperse in varied and similar distances across a variety of habitat types, thus avoiding inbreeding.

5.7. Eltonian shortfall

Our understanding of titi monkey behavior, ecology, evolution, and conservation would be enhanced by studies of the association – positive or negative – of titi monkeys with other primates and with other animals in general, e.g., predators, non-primate competitors. Therefore, addressing an Eltonian shortfall should also be considered a necessary aim when planning future titi monkey studies.

Interspecific associations with other primate species (also known as mixed-species groups) can be a central part of the ecology of a species; while these associations may sometimes have no discernible benefits to the primate involved (Barnett and Shaw 2014), it is common for them to contribute positively to either improve the acquisition of the food resources or increasing capacity against potential predators (Goodale et al. 2017). Furthermore, ecological network analysis is often used to understand social relationships within a primate group (see Brent et al. 2011). However, this analysis is poorly applied in studies related directly to the role of primates within the ecological food web (Dáttilo et al. 2014; Bufalo et al. 2016; Benitez-Malvido et al. 2016). As a result, this knowledge gap can be filled by studies of how intragroup differences (sex and age) may act on ecological processes such as seed dispersal, and these studies can then identify the main drivers of an ecological network in diverse groups of titi monkeys using such considerations of fragment size, isolation, habitat quality, and landscape matrix.

An additional case of an Eltonian shortfall involves the study of titi monkey vocalizations. Social communication has been investigated, both in captivity (Hoffman et al. 1995; Lau et al. 2020) and in the field (Adret et al. 2018). However, while many within-group calls are structurally designed to carry only short distances, long calls have a territorial function and can be detected at a distance (Caselli et al. 2014). Long calls appear to be species-distinct, allowing them to be used in survey work (Aldrich et al. 2008), thus aiding in the diminution of Wallacean shortfall. Such studies would be helpful because titi monkeys are known to respond to call playbacks (Dacier et al. 2011; Caselli et al. 2015). These studies could also be supplemented by remote sound monitoring (e.g., Bastos et al. 2019), permitting an analysis of densities and assisting in knowledge related to Prestonian shortfall. However, this will only be possible with the full complement of vocal repertoires from all titi monkey species.

6. Discussion

The identification of knowledge shortfalls is essential for planning future research on titi monkeys across the geographic range of the clade. To develop such studies, it is clearly essential to secure adequate financial and logistic support and people (future researchers: graduate and undergraduate students) who have the required capacity, desire, and dedication. Based on our findings, it is evident that across the distributional range of titi monkeys, only a few species have been well investigated but, even then, mostly at a handful of study sites primarily in Brazil and Peru. Therefore, there exist important knowledge shortfalls.

Expanding the understanding of interspecific and populational-level differences in varied traits is necessary. Nevertheless, the absence of data from multiple populations makes it unfeasible to fill gaps for Darwinian, Raunkiæran, Hutchinsonian, and Eltonian shortfalls for titi monkey species. Additionally, many forested areas with titi monkeys have few or no studies. Paraguay and Venezuela each have only one titi monkey species, *Plecturocebus pallascens* and *Cheracebus lugens*, respectively. In Paraguay, titi monkeys occur in various environments such as Dry Chaco, Pantanal, and Cerrado (Smith et al. 2021), and in Venezuela, they occupy forested areas (Lehman et al. 2013). Furthermore, a large portion of Brazilian Amazonia lacks research titi monkeys. We recommend that future studies focus overall on the clade, but also on individual species, and interactions between populations and species. Such knowledge would reduce the homogenization of the data for the clade.

Although the titi monkey clade is the most species-rich clade of South American primates, there is potentially a knowledge gap in species richness (Linnean shortfall). This gap appears to occur in inhospitable and hard-access sites inserted in the Amazon (see Freitas et al. 2020 for fishes and Carvalho et al. 2023 for multiple taxa). These poorly known regions are of paramount importance for registering new species (Hortal et al. 2015; Mora et al. 2008; Wheeler, 2004). The inability to access these sites and the lack of investment in this type of research in most countries jeopardize the reduction of the shortfall. To expand our knowledge of potential titi monkey species, government agencies, non-government organizations, universities, and research centers should invest in inventory surveys at regional and local scales. Eighteen years ago in Brazil, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) promoted the development of taxonomy-related projects (PROTAX:Programa de Capacitação em Taxonomia); additional financial assistance came from other state foundations. Like Brazil, other South American countries could also stimulate the development and financial support of projects linked to expanding knowledge of regional and local biodiversity.

Diminishing the Linnean shortfall would also help reduce the Wallacean shortfall. Together, addressing the Linnean and Wallacean shortfalls would increase the ability to design robust and effective conservation strategies (Jones et al. 2009). For Hortal et al. (2015), both shortfalls demonstrate a wider influence on conservation issues; such data are essential to identify broad-scale patterns in biodiversity and the process that lead to extinction. For example, surveys for *C. coimbrai* in Atlantic Forest fragments in northeastern Brazil demonstrated a local extinction (Hilário et al. 2017). Reduction of the Wallacean shortfall can have a huge impact on the evaluation of the IUCN Red List as estimates of conservation threat status. Evenly distributed data tend to increase the accuracy of species distribution models, thereby allowing for the formation of robust and strong hypotheses. Also, range areas are frequently used for conservation planning, where species with small ranges often present a higher priority on a global scale (IUCN 2001). Thus, reducing this gap could highlight certain taxa or regions as priorities for conservation. First, one could compile data in public, online repositories (e.g., Culot et al. 2019) to facilitate the sharing of information on localities; such data are important in conservation planning (Margules & Pressey, 2000). Second, citizen science programs with local communities can facilitate the sharing of species distribution data (Braschler, 2009; Cohn, 2008). Although research scientists are involved in the field research, data analysis, and writing the final report, most of the direct conservation actions are applied by local communities.

To discover and describe all titi monkey species (Linnean shortfall), define their geographical distributions (Wallacean shortfall), and understand population dynamics (Prestonian shortfall), habitat conservation is critical. South American primates and their habitats have suffered extensively from anthropogenic actions (Estrada et al. 2017). Extensive habitat loss, which can reduce geographical ranges and result in population decreases, may negatively affect the likelihood of discovering new species. Creating a network of protected areas is extremely important for the conservation of currently isolated populations of titi monkeys, given that protected areas can be the most effective short-term means of conserving biodiversity (Magioli et al. 2021). This is important for the long-term conservation of the titi monkey clade because the existing protected area network does not form a functional network; there is an urgent need for the creation of further protected areas (Michalski and Peres 2005; Boyle 2008; Ometto et al. 2011; Costa-Araújo et al. 2022). Under current and future scenarios for land cover, landscape features such as total forest remnant cover, patch size, and functional connectivity would negatively impact the occurrence of all *Callicebus* spp. (Gouveia et al. 2016). Similarly, Alvarez (2019) used both optimistic and pessimistic future climate change scenarios to examine habitat loss and distribution of *P. oenanthe* in Peru. Landscape characteristics could also affect titi monkey density (Gestich et al. 2019a; Hilário et al. 2022), occurrence (da Silva et al. 2015; Costa-Araújo et al. 2021), and abundance (Carretero-Pinzón et al. 2017).

Prestonian shortfall occur when we do not have adequate information on species abundance and population dynamics, specifically in time and space (Hortal et al. 2015). For titi monkeys, obtaining abundance data on a spatial scale is relatively practical. Nevertheless, a standardized protocol needs to be applied. There have been two common approaches: line transect (São Bernardo & Galetti, 2004; Chagas & Ferrari, 2011; Freitas et al. 2011) and playback (Dacier et al. 2011; Gestich et al. 2019a; Hilário et al. 2022). Although both present powerful outcomes, comparisons between them are still not fully feasible. On the other hand, the lack of investments in long-term projects and the workforce (e.g., graduate and undergraduate students) make it difficult to obtain data on a long temporal scale. The absence of these data under local and regional scales hinders the establishment of conservation measures that address the maintenance or reestablishment of titi monkey populations; for example, currently there are not reliable estimates of the amount of forested area necessary to support a minimum viable population. Such measures can vary from creating protected areas to maintain the populations, to programs of habitat restoration to increase the population size. However, a primary concern for effective conservation measures is the lack of data from a temporal perspective, which would help promote actions to mitigate the deleterious effects of habitat loss and degradation.

According to Hortal et al. (2015) Raunkiæran, Hutchinsonian, and Eltonian shortfalls are intrinsically related. The data necessary to fill these gaps are also critical in understanding the extent to which human pressures negatively impact habitats and species. the negative effects of massive human pressures on habitats and species. For primates like titi monkeys, systematic monitoring in fragmented and continuous habitats will be crucial for obtaining good indicators linked to ecological, behavioral, genetic, and reproductive parameters, both within species and between species. For example, life history traits such as interbirth intervals, number of offspring, lactation time, and gestation length allow us a more comprehensible and suitable populational viability analysis for the species. Moreover, further understanding titi monkey diets can help define the role of titi monkeys in the process of natural restoration of forests.

A robust and effective ecological restoration program should be pursued in specific target regions. Restored habitats would increase the ability for individuals to move between forest fragments to either encounter a potential new mate and form a new group or integrate into an established group. Such actions would help maintain the genetic diversity of a local population, reducing consanguinity rates (Dolotovskaya et al. 2020b). Additionally, habitat size could be increased; well-managed restoration programs have mitigated the deleterious effects of habitat loss and fragmentation on other primates (Chapman et al. 2018; Chazdon et al. 2020). It is possible to design effective restoration programs using a robust and reliable database either of plant species known as foodstuffs of the primates of concern or via floristic composition of habitats (Rezende 2016). Enhanced knowledge of ecological networks, feeding habits, and seed dispersal by titi monkeys of various plant species (Eltonian shortfall) would improve the conservation success of these plant species in these restoration programs. For example, a restoration project initiated between 1994 and 1996 regenerated a forest fragment (23.5 ha) from an area of pasture and croplands in Peru; *P. oenanthe* was initially absent from the fragment, but, in 2010, a group of *P. oenanthe* was recorded there and, some years later, a total of 27 individuals were recorded with the density estimated at 35 groups/km^2 and 124 individuals/km^2 (Allgas et al. 2017). Such results demonstrate the importance of ecological restoration projects for increasing the long-term viability of titi species and illustrate the capacity of titi monkeys to use ground-based access to colonize isolated forest areas (Souza-Alves et al. 2019b). Furthermore, long-term studies that document the effects of habitat loss and fragmentation on titi monkeys (Hutchinsonian and Raunkiæran shortfalls) would enable us to understand how some populations are surviving in these heavily impacted areas. Collection of such data, including life-history traits, requires a massive effort; information is available for only a handful of titi monkey species (Valeggia et al. 1999; Van Belle et al. 2016; Souza-Alves et al. 2019c; Acero-Murcia et al. 2021), illustrating a component of the Darwinian shortfall.

In general, titi monkey species have been the focus of a number of conservation efforts, and have included the creation of specific protected areas in Brazil, Peru, and Bolivia to help maintain titi monkey populations (Gaultier et al. 2015; Sergipe 2007; Shanee 2016; Wallace et al. 2013). Government actions, including action plans, have also provided valuable tools with which to establish conservation agendas for titi monkeys; Brazil has implemented an action plan to conserve *C. coimbrai*, *Callicebus barbarabrownae*, *Callicebus melanochir*, and *Callicebus personatus* populations (Brasil 2011; Brasil 2018; Brasil 2019; Escarlate-Tavares et al. 2016), Ecuador has created action plans for *Cheracebus lucifer* and *P. discolor* populations (Cervera et al. 2017), while Peru has provided these for *P. oenanthe* and *C. lucifer* (Serfor 2020). Moreover, government agencies and conservation NGOs have actively engaged with local communities, ranchers, and schoolchildren to provide opportunities for participants to learn more about titi monkeys (e.g., *P. oenanthe* in Peru: Shanee 2016; Shanee et al. 2018; *P. modestus* and *P. olallae* in Bolivia: Siles et al. 2019; Wallace et al. 2013). We believe it is very important that such action plans are maintained, supported, and further developed by researchers, governments, and local communities in the countries where titi monkeys live. To date, such public policy has gained strength and has led to the creation of financial and logistical resources for titi monkey conservation.

Another priority is to standardize the quantification of habitat structure and quality; such variables impact the ecology, behavior, demography, and effective conservation of primates (Xiang et al. 2007; Boubli et al. 2011; Akers et al. 2013; Rafidimanana et al. 2017; Paim et al. 2018; Oliveira et al. 2019; Cardenas et al. 2021; Souza-Alves et al. 2021b; Souza-Alves et al. 2022; Guedes et al. 2023). For titi monkeys, few studies have reported the habitat structure and quality, especially in fragmented habitats (see Santana et al. 2021; Souza-Alves et al. 2021b). Understanding how forest fragments are structured can provide a sense of their current conservation status, as well as aid in the design of the site- recovery and maintenance strategies, that are appropriate to both the site and needs of the focal primate species (Oliveira and Amaral 2004; Giehl and Budke 2011; Paim et al. 2018).

7. Concluding Remarks

Although it is rarely mentioned in the academic literature, a distinct priority for future studies of titi monkeys is securing financial support. However, obtaining this support can be an obstacle for many countries, like Brazil, with almost 90% of the titi monkey species diversity divided among four biomes: Atlantic Forest, Cerrado, Caatinga, and Amazonia (Printes et al. 2013). Conserving and maintaining these titi monkey populations should primarily focus on research efforts. Between 2018 and 2021, Brazilian science has experienced significant reductions in financial support (Hallal 2021) through the actions of the past president of Brazil. Furthermore, Brazil's environmental policy adopted by the Ministry of Environmental from 2019 to 2022 sought to minimize the extent of naturally forested areas, thereby promoting accelerated deforestation. Without adequate funding for the future, it will be practically impossible to fully address the shortfalls identified in this study. In this sense, we hope that the information presented here can provide a baseline for ideas to address the knowledge shortfalls and contribute to the conservation of titi monkeys in South America.

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Figure Legends

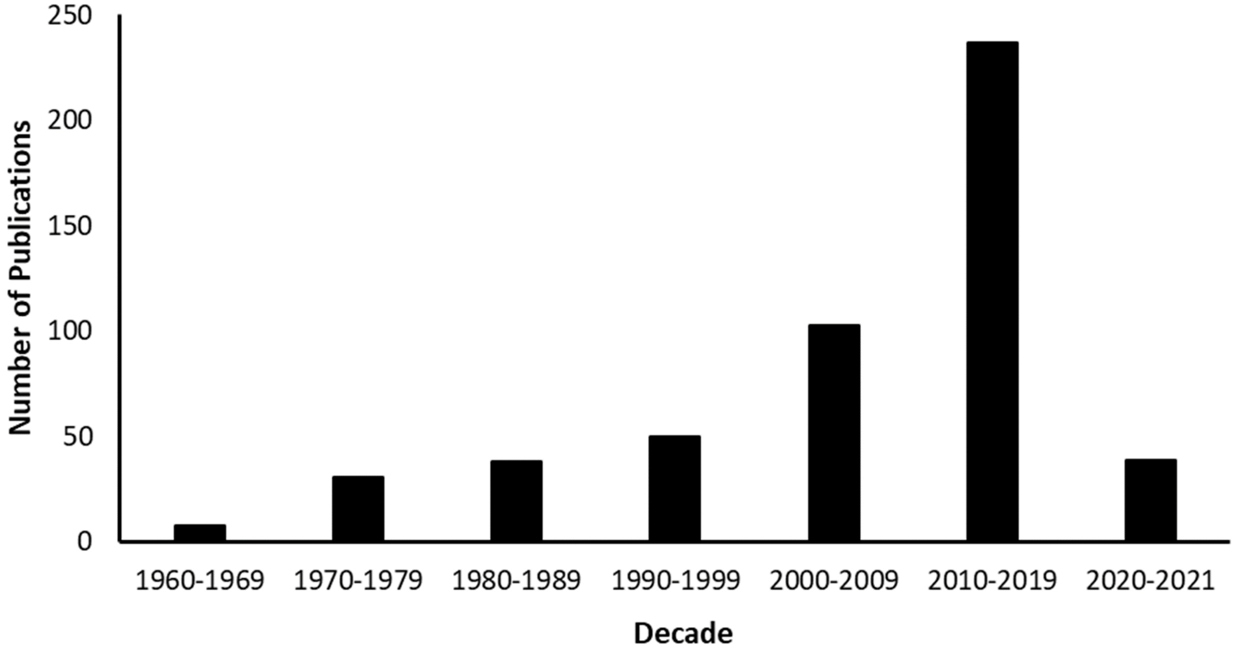

Fig. 1. The number of publications on titi monkeys has increased during the past six decades, especially from 2010-2021. The publications quantified in this analysis represent peer-reviewed journal articles, book chapters, and dissertations focused on free-ranging and captive titi monkeys.

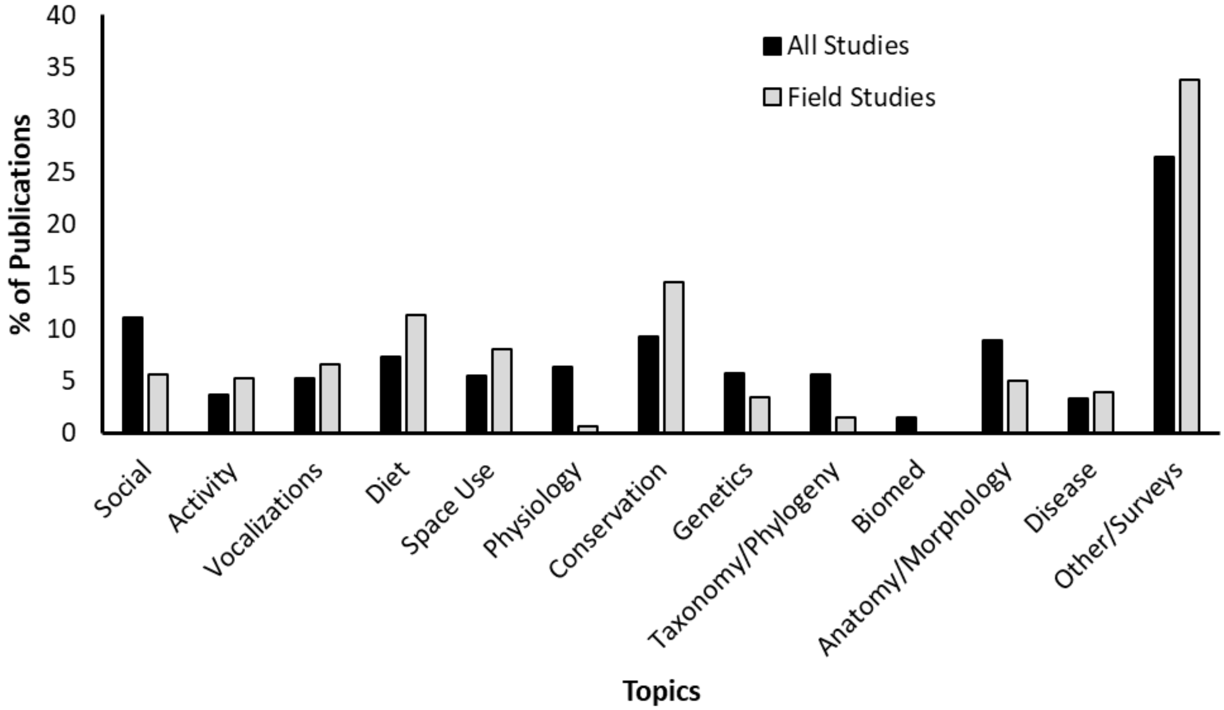

Fig. 2. The range of topics covered in the 521 publications on titi monkeys reviewed in this study.

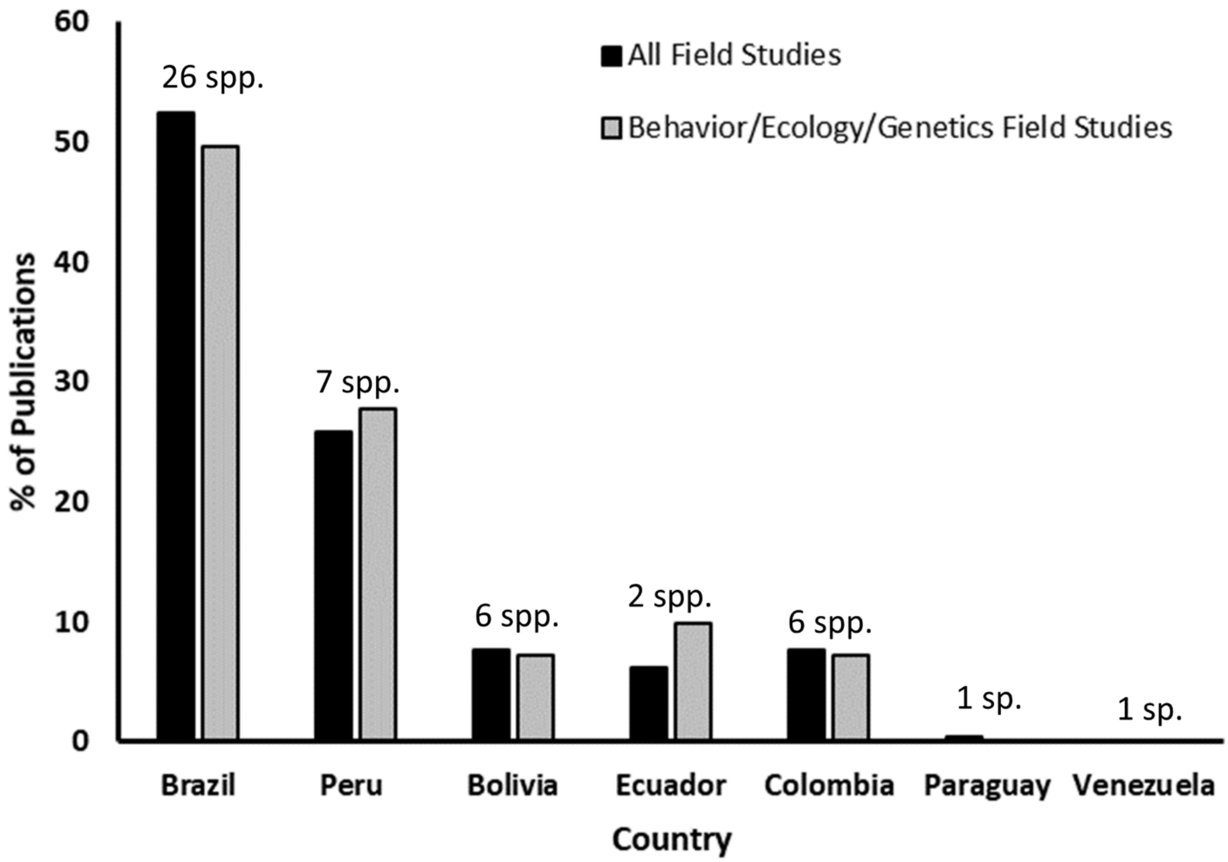

Fig. 3. Distribution of publications from field studies on titi monkeys by habitat countries. Percentages add up to more than 100 because five publications addressed field studies in more than one country. None of the publications focused on field studies of titi monkeys in Venezuela.

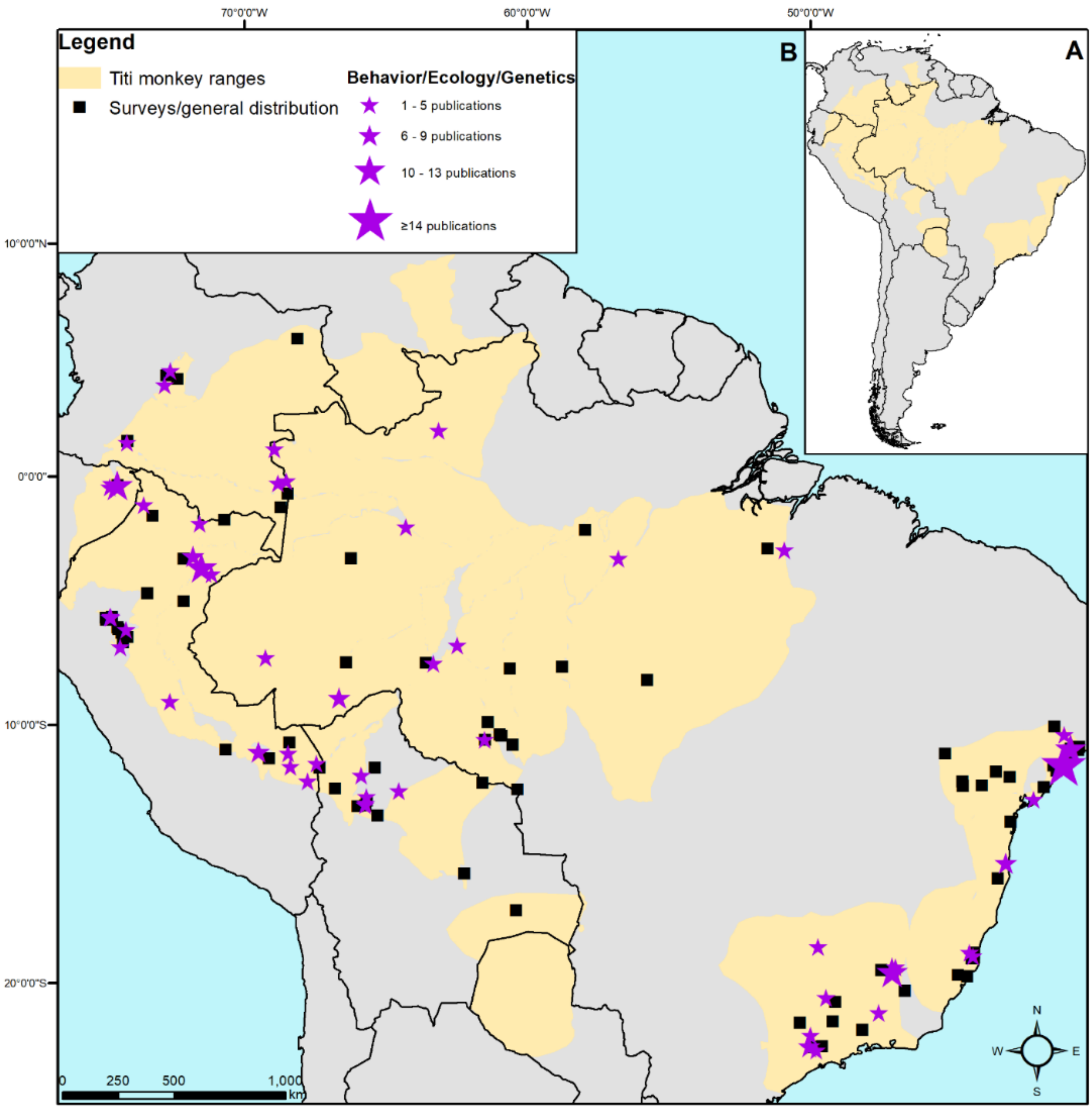

Fig. 4. Titi monkeys range across much of South America (A), but the titi monkey field studies we located in the literature search were not evenly distributed across the geographic ranges of titi monkey species (B). We did not include locations were field specimens were collected but there was no study of the animals' free-ranging behavior or ecology; hence, there are no behavioral or

ecological field studies representing Paraguay. The data source for geographic range: IUCN Red List.