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Revised checklist and conservation status of the mammals of Costa Rica

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Mammal diversity in Costa Rica is considerably high given the size of the country (51,100 km^2), and has increased in recent years. Taxonomic changes together with distribution extension records have contributed to such an increase. Here we present the revised and updated list of mammals confirmed for Costa Rica based on previous lists and recent additions obtained from literature, with notes on endemism and conservation status. This updated list was based on Rodríguez-Herrera *et al.* (2014a) list, compared and matched with the most updated taxonomic review. A total of 256 mammals are now confirmed for Costa Rica, with the order Chiroptera and Rodentia as the most representative. We report 30 endemics for Costa Rica, including those species whose distribution is limited to the country and one of its two neighboring countries, from which 21 are rodents. Compilation on conservation status information reveals 29.6 % of species within the list classified as threatened, either by Costa Rican or international environmental authorities. Increase in new studies on mammals all around the world is leading to the discovery of new species. While systematic and phylogenetic revisions is revealing new taxonomic relationships, and cryptic species. Mainly on highly diverse and taxonomically challenging groups, as bats, rodents, and shrews, as we evidence here. Several threatened and endemic species occur in Costa Rica, where the greatest endemism area is the high elevations, and most endemic species are mice. The creation and establishment of protected areas in a large part of the Costa Rican territory has favored the prevalence of a diverse mammalian assemblage.

La diversidad de mamíferos en Costa Rica es considerablemente alta a pesar del tamaño del país (51,100 km^2), y ha aumentado en los últimos años. Los cambios taxonómicos junto a registros de ampliaciones de distribución han contribuido a este aumento. Aquí presentamos la lista revisada y actualizada de mamíferos de Costa Rica, basada en listas anteriores y una revisión bibliográfica, con notas sobre el endemismo y el estado de conservación. Esta lista actualizada se basó en la lista de Rodíguez-Herrera *et al*. (2014a), comparada y cotejada con la revisión taxómica más actualizada. Confirmamos un total de 256 especies de mamíferos para Costa Rica, siendo los órdenes Chiroptera y Rodentia los más representativos. Reportamos 30 endémicas para Costa Rica, incluyendo aquellas especies cuya distribución se limita al país y alguno de sus dos países vecinos, de las cuales 21 son roedores. La compilación del estado de conservación revela que el 29.6 % de las especies en la lista están clasificadas bajo alguna categoría de amenaza, ya sea por las autoridades ambientales locales o internacionales. El aumento en nuevos estudios sobre mamíferos en todo el mundo está llevando al descubrimiento de nuevas especies. Mientras que las revisiones sistemáticas y filogenéticas están revelando nuevas relaciones taxonómicas y especies crípticas. Principalmente en grupos muy diversos y taxonómicamente desafiantes, como murciélagos, roedores y musarañas, como evidenciamos aquí. Varias especies con poblaciones amenazadas y endémicas ocurren en Costa Rica, donde la zona de mayor endemismo son las tierras altas, y la mayoría de las especies endémicas son ratones. La creación y el establecimiento de áreas protegidas en gran parte del territorio costarricense ha favorecido la prevalencia de un conjunto diverso de mamíferos.

Keywords: Central America; conservation status; Costa Rica endemic species; new records; taxonomic changes.

Introduction

Ecosystems around the world are losing biodiversity at an accelerated rate as a result of habitat loss, overexploitation, introduction of invasive species, and climate change (Naeem *et al.* 2012; Johnson *et al.* 2017; Ceballos *et al.* 2020). This loss of biodiversity has negative repercussions on ecological processes and the services they provide to human populations (Brodie *et al.* 2021). For example, the loss of primate species can have detrimental effects on seed dispersal and consequently on forest regeneration and tree community structure (Gardner *et al.* 2019). Knowing the diversity of mammal species in a given area can not only help to identify the impact of anthropogenic activities on it and its natural habitats (Rocha *et al.* 2014; González-Maya *et al.* 2016; Brodie *et al.* 2021), but also contributes to the creation of baseline studies on different biological

aspects (*e. g.*, biogeography, ecology), environmental education, disease prevention or control, and more. From this arises the importance and need to generate updated lists of mammal species at any geographical level, but especially in high diversity areas.

Costa Rica, located in Central America, is a small country with a land area of approximately 51,100 km^2, yet it is among the 20 most diverse countries in the world (Obando 2002; Kappelle 2016). Previous work has described a high richness and functional diversity of mammals (González-Maya *et al.* 2015; 2016) that results from its geographical location and geological history (Janzen 1991), and a complex biogeographic history as land bridge and barrier for different groups of mammals that originated in the north and south of the American continent, giving rise to a species composition with origins in both hemispheres (Carrillo *et al.* 2010; Rodríguez-Herrera *et al.* 2014a; Wilson *et al.* 2014; González-Maya *et al.* 2016).

Since Rodríguez-Herrera *et al.* (2014a) mammal's list, where 249 species were reported for the country, there have been changes in the number of species and their taxonomy. This is remarkable, given that information about mammals in the country has been collected for more than 150 years (Rodríguez-Herrera *et al.* 2005, 2014b). The ongoing effort to document the mammalian community of Costa Rica has resulted in several updates to the list (*e. g.*, Wilson 1983; Rodríguez and Chinchilla 1996; Rodríguez-Herrera *et al.* 2002; Rodríguez-Herrera *et al.* 2014a), such that it reflects current taxonomic and systematic classifications (*e. g.*, Pérez Consuegra and Vázquez-Domínguez 2015; Lim *et al.* 2020), accounts for new records and species descriptions (*e. g.* Woodman and Timm 2017; Salas-Solano *et al.* 2020; Villalobos-Chaves *et al.* 2018), and changes in distribution range extensions (*e .g.*, González-Maya *et al.* 2017; Ramírez-Fernández *et al.* 2020). The continued addition of mammal species to the list over the years reflects increased efforts on biological research in the country. This study presents an updated list of the mammals of Costa Rica, including notes on their global and local conservation status.

Materials and methods

This updated list of the mammals of Costa Rica was based on the list of Rodríguez-Herrera *et al.* (2014a), compared and matched with the most updated taxonomic review made for the class Mammalia in the Mammal Diversity Database (MDD 2022), from where the original sources were obtained and consulted. Comments on species taxonomic changes and new additions to the list were provided according to a bibliographic review for the taxa differing between both lists. For changes in the total number of species and species by order, we reviewed previous species lists for the country (Frantzius 1869; Alfaro 1897; Harris 1943; Goodwin 1946; Wilson 1983; Rodríguez and Chinchilla 1996; Rodríguez-Herrera *et al.* 2002; Rodríguez-Herrera *et al.* 2014a). Information on the global conservation status of each species was compiled from the latest International Union for Conservation of Nature Red List assessment (IUCN 2022), and the national conservation status according to Costa Rican environmental authorities (SINAC 2017). Common names, and the phylogenetic order of the different orders, families, subfamilies and tribes follows the most recent publication of the Handbook of the Mammals of the World series (Mittermeier *et al.* 2013; Wilson *et al.* 2016, 2017; Wilson and Mittermeier 2009, 2011, 2014, 2015, 2018, 2019), with genera and species listed in alphabetical order.

Results

Species and family richness. In this study we report a total of 256 extant mammal species for Costa Rica, increasing the number of species by seven according to the last list published (Rodríguez-Herrera *et al.* 2014a; Figure 1). The order Chiroptera accounts for almost half (46 %) of the total number of species documented in Costa Rica with 118 species (9 families), followed by Rodentia (51 species, 8 families), Artiodactyla (31 species, 7 families) and Carnivora (25 species, 6 families; Figure 2). About 88 % of the species are primarily terrestrial environments and 12 % are fully adapted to an aquatic life. In terms of evolutionary distinctiveness (*i. e.*, a measurement of the uniqueness of a species evolutionary history), the updated list includes two artiodactyls *Physeter macrocephalus* and *Balaenoptera musculus*, the perissodactyl *Tapirus bairdii*, and the sirenian *Trichechus manatus* (May-Collado and Agnarsson 2011; Isaac *et al.* 2007).

Endemism. Within the list, we listed 30 mammal species that are endemics to some specific region within the geographic area ranging from southern Nicaragua to western Panama, as follows. A total of 20 species have a distribution that encompasses Costa Rica and Panama. These species include members of the orders Didelphimorphia (1 species), Lagomorpha (1), Rodentia (13), Primates (1), Eulipotyphla (2), and Chiroptera (2). The Nicaraguan woolly mouse opossum *Marmosa nicaraguae*, and two species of rodents *Reithrodontomys brevirostris* and *R. paradoxus* are distributed in northern Costa Rica and are shared only with Nicaragua. Seven species are exclusively found in Costa Rica, six rodents *Heterogeomys heterodus*, *Heteromys nubicolens*, *H. oresterus*, *Reithrodontomys cherrii*, *R. musseri*, *R. rodriguezi*, and one shrew *Cryptotis monteverdensis*. Among these species, the taxonomic group with the greatest endemism corresponds to the order Rodentia, with 21 species, followed by Eulipotyphla with three, and Chiroptera with two (Supplementary material).

Conservation status. According to the IUCN (IUCN 2022), eight species are reported as Endangered. These include the manatee *Trichechus manatus*, the tapir *Tapirus bairdii*, the primates *Aloautta palliata* and *Saimiri oerstedii*, the pinnipeds *Arctocephalus galapagoensis* and *Zalophus wollebaeki*, and the artiodactyls *Balaenoptera borealis*, and *B. musculus*. Six species are considered Vulnerable, including the giant anteater *Myrmecophaga tridactyla*, the primates *Ateles geoffroyi* and *Cebus imitator*, the oncilla *Leopardus tigrinus*, the white-lipped peccary *Tayassu pecari*, and the

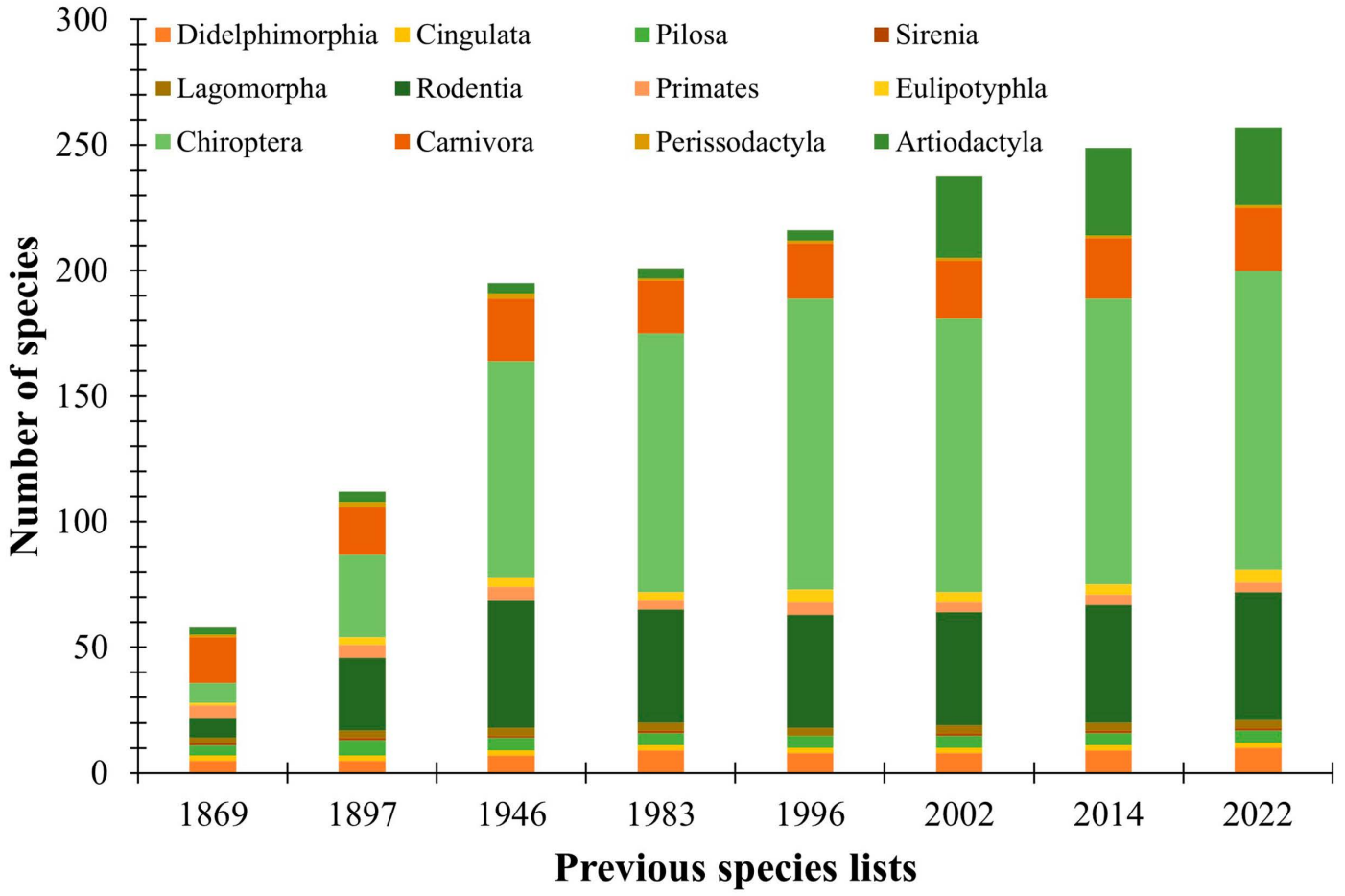

Figure 1. Changes in the number of mammal species from previous species lists for Costa Rica ranging from 1869 to date; orders taxonomic classification follows this work. References: Frantzius (1869), Alfaro (1897), Goodwin (1946), Wilson (1983), Rodríguez and Chinchilla (1996), Rodríguez-Herrera *et al.* (2002), Rodríguez-Herrera *et al.* (2014a).

endemic lagomorph species *Sylvilagus dicei*; nine species are listed as Near Threatened, and 11 as Data Deficient, with six endemics among them. Nationally, according to environmental authorities (SINAC 2017), 21 Costa Rican mammal species are endangered with extinction (Supplementary material). These include all six species of felids, three out of four monkey species, and the endemic rodents *Reithrodontomys musseri* and *Rheomys raptor*. In addition, a total of 42 species, including nine endemics, have seen their populations reduced or threatened (Supplementary material).

Changes in distribution. In terms of the distribution of localities of the recently recorded species *Cryptotis monteverdensis*, *Ichthyomys tweedii*, *Cynomops greenhalli*, *Diplomys labilis*, *Micronycteris tresamici*, *Molossus alvarezi*, *Mormoops megalophylla*, *Myotis armiensis*, *Nyctinomops laticaudatus*, and *Speothos venaticus* there is no clear pattern. Most of the new species are the result of taxonomic changes, although some indicate range expansion towards both borders of the country, with most of the new ones occurring in lowlands (Figure 3).

Taxonomic changes. Several taxonomic changes have occurred in the last decade at various taxonomic levels. These changes include:

Orders

Eulipotyphla. Based on phylogenetic analysis using molecular data (Douady *et al.* 2002), and following the classification proposed by Wilson and Mittermeier (2018), we acknowledge the inclusion of the former orders Soricomorpha (shrews) and Erinaceomorpha (hedgehogs) in the widely accepted order Eulipotyphla.

Artiodactyla. Following the International Code of Zoological Nomenclature (Asher and Helgen 2010), and according to the most recent morphological and molecular phylogenetic analyses (*e. g.*, Agnarsson and May-Collado 2008; Hassanin *et al.* 2012; Gatesy *et al.* 2013, 2017), we recognized Cetacea as an infraorder of the order Artiodactyla, along with their respective parvorders and families.

Families

Chlamyphoridae. Molecular phylogenetic analysis including fossils and extant species supports the division of the traditional family Dasypodidae into the families Chlamyphoridae and Dasypodidae (Delsuc *et al.* 2016; Gibb *et al.* 2016). Dasypodidae is currently restricted to the genus *Dasypus*, while all other modern armadillos, including *Cabassous*, and the extinct glyptodonts are grouped in Chlamyphoridae.

Choloepodidae. Two-toed sloths of the genus *Choloepus* are now placed in a new family, Choloepodidae, instead of the family Megalonychidae. This new placement is based on phylogenetic analysis of DNA data from fossils and extant species (Delsuc *et al.* 2019; Presslee *et al.* 2019).

Subfamilies

Former Phyllostominae. We follow the proposal of Baker *et al.* (2016), and Cirranelo *et al.* (2016), who recognized 11 subfamilies and 12 tribes within the family Phyllostomidae, adding the following subfamilies to the list: Glyphonycterinae, Lonchophyllinae, Lonchorhininae, and Micronycterinae.

Genera

Heterogeomys. Following the latest systematic revision of the genus *Orthogeomys* (Spradling *et al.* 2016), we recognize the genus *Heterogeomys* for the different species of the family Geomyidae occurring in Costa Rica. The genus *Orthogeomys* is restricted to the species *O. grandis*, distributed from México to Honduras.

Heteromys. Phylogenetic analysis based on molecular data of the family Heteromyidae shown that the genus *Liomys* is paraphyletic with respect to *Heteromys* (Hafner *et al.* 2007). Therefore, the formal taxonomy of the group suggests a synonymy between the two genera, and the name *Heteromys salvini* is accepted.

Coendou. According to the latest research in systematics and phylogeny of the family Erethizontidae (Voss 2011; Voss *et al.* 2013; Menezes *et al.* 2021), the correct and most commonly used genus is *Coendou* and not *Sphiggurus*, for *Coendou mexicanus*.

Gardnerycteris. According to phylogenetic analysis, the new genus *Gardnerycteris* is recognized for the former members of *Mimon* under the taxon "*Anthorhina*" (represented by *M. crenulatum* and *M. koepckeae*; Hurtado and Pacheco 2014). Thus, *Gardnerycteris crenulatum* is accepted as a valid species.

Artibeus. In accordance with the most recent morphological and molecular phylogenetic analysis (Baker *et al.* 2016; Cirranelo *et al.* 2016; Cirranelo and Simmons 2020), the genus *Artibeus* is used for the forms formerly assigned to the genus *Dermanura*.

Dasypterus. We follow the proposal of Baird *et al.* (2015, 2021) of three separate genera within the tribe Lasiurini: *Lasiurus* (red bats), *Dasypterus* (yellow bats), and *Aeorestes* (hoary bats). Thus, we recognize de genus *Dasypterus* for the yellow bats *L. ega* and *L. intermedius*.

Herpailurus. The species *Puma yagouaroundi* was reassigned to the genus *Herpailurus* according to morphometric analyses by Segura *et al.* (2013). Although some authors

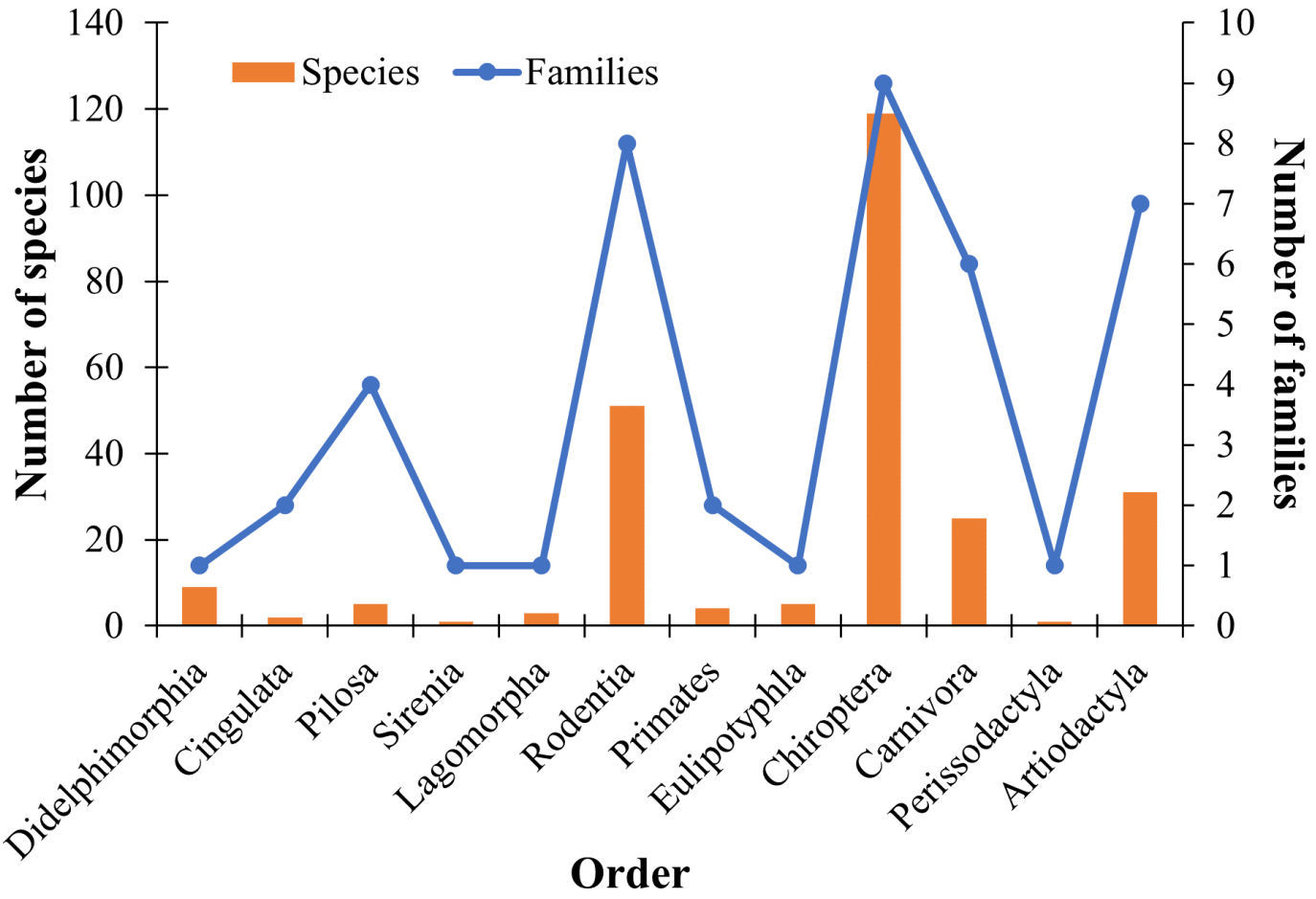

Figure 2. Distribution of the number of mammal species and families according to orders in Costa Rica.

still use the genus *Puma* for the species (*e. g.*, Li *et al.* 2016; Tamazian *et al.* 2021), we follow the designation from the Cat Classification Task Force of the IUCN Cat Specialist Group (Kitchener *et al.* 2017).

Neogale. According to the latest review of the phylogeny and nomenclature of the genus *Mustela*, *M. frenata* should now be recognized in the genus *Neogale* (Patterson *et al.* 2021).

Dicotyles. In accordance with the International Code of Zoological Nomenclature the genus *Dicotyles* is accepted as valid, and the former genus *Pecari* becomes a junior synonym of it (Acosta *et al.* 2020).

Species

Marmosa nicaraguae. According to the latest phylogenetic revision using molecular data of the didelphid marsupial genus *Marmosa*, *M. nicaraguae* was separated and recognized as a valid species from *M. alstoni* (Voss *et al.* 2021). Therefore, both species deserve an endemic status, *M. nicaraguae* with a distribution limited to Nicaragua and Costa Rica, and *M. alstoni* distributed in Costa Rica and Panama (Voss *et al.* 2021; Carter 2022).

Philander melanurus. This species was splitted from the *Philander opossum* species complex and validated as a species after phylogenetic and morphological analysis (Voss et al. 2018).

Cyclopes dorsalis. Based on phylogenetic analyses using molecular data, coalescent analyses of species delimitation, cranial diagnostic characters, and patterns of coloration and fur structure, we accept the proposal of Miranda *et al.* (2018) to separate the species *Cyclopes didactylus* into seven equally valid species. Therefore, the species recognized for Costa Rica, with a Mesoamerican distribution, corresponds to *C. dorsalis*, while *C. didactylus* is restricted to the northeastern region of South America.

Cryptotis orophilus. Following the International Commission on Zoological Nomenclature (2006) the specific epithet changes from *orophila* to *orophilus* because *Cryptotis* gender is masculine.

Peromyscus nicaraguae. This species was separated from the *P. mexicanus* species complex and revalidated as a species by Pérez Consuegra and Vázquez-Domínguez (2015). The distribution reported by the authors includes only Honduras and Nicaragua, however two subspecies of *P. nudipes*, *hesperus* and *orientalis*, are included as synonyms of *P. nicaraguae* (Bradley *et al.* 2016), which have been reported in the past for the northern and central mountain

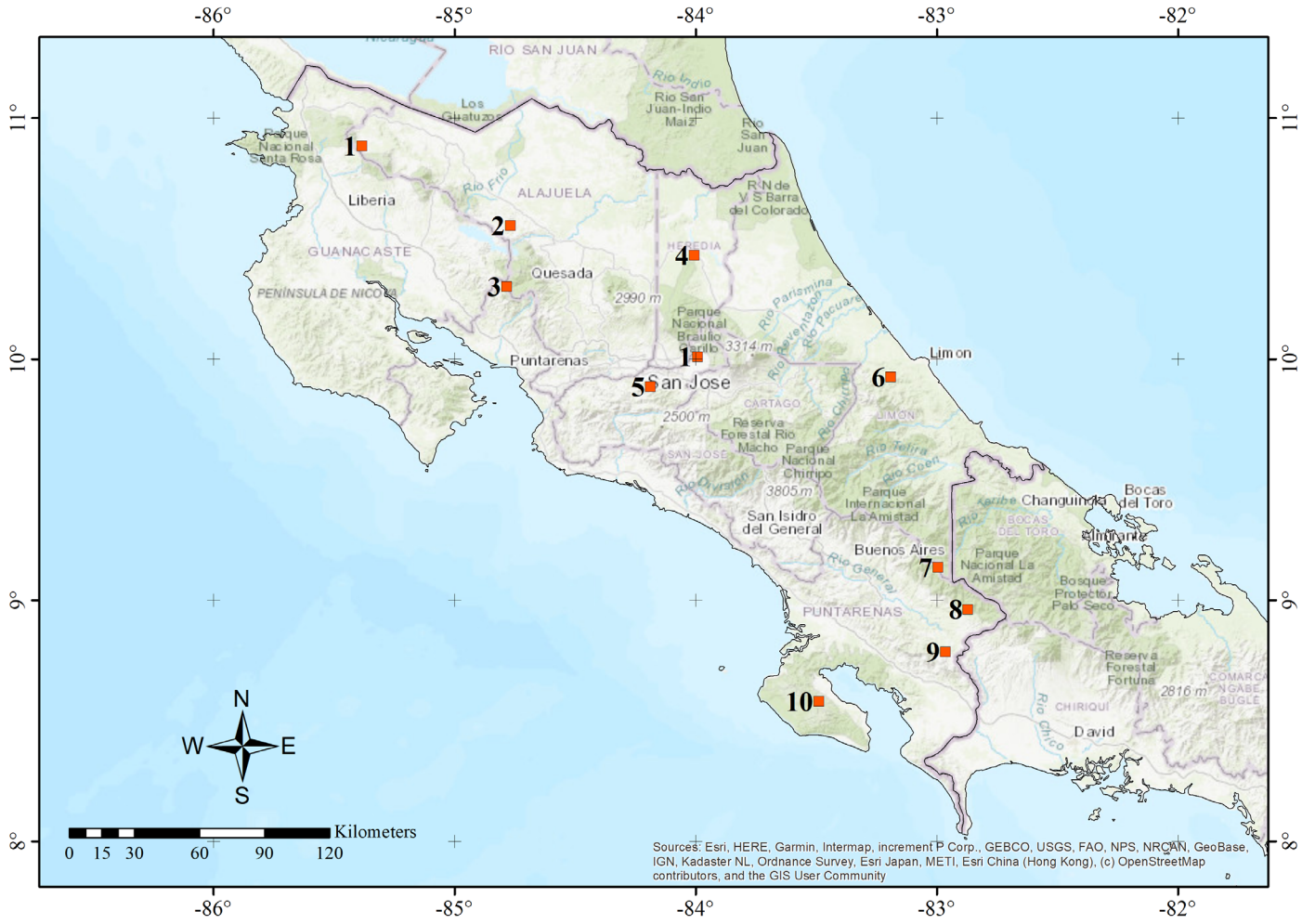

Figure 3. Map showing localities of recorded new mammal species for Costa Rica since Rodríguez-Herrera *et al.* (2014) list: 1, *Micronycteris tresamici*; 2, *Mormoops megalophylla*; 3, *Cryptotis monteverdensis*; 4, *Molossus alvarezi*; 5, *Nyctinomops laticaudatus*; 6, *Cynomops greenhalli*; 7, *Myotis armiensis*; 8, *Speothos venaticus*; 9, *Ichthyomys tweedii*; 10, *Diplomys labilis*.

ranges of Costa Rica respectively, confirming its presence in the country.

Peromyscus nudipes. Mitochondrial cytochrome-*b* gene data revealed that the *Peromyscus mexicanus* species complex has a polyphyletic origin (Pérez Consuegra and Vázquez-Domínguez 2015). Therefore, it was decided to elevate *P. nudipes* to specific level, due to its monophyletic origin (Bradley *et al.* 2016). This species has a restricted distribution to the highlands of the Talamanca Mountain Range in Costa Rica and Panama.

Reithrodontomys cherrii. According to molecular (Arellano *et al.* 2005), and morphological data (Gardner and Carleton 2009), *R. cherrii* was separated from *R. mexicanus* and is recognized as a valid species. Recently, this condition was also reinforced with ecological data (Martínez-Borrego *et al.* 2022). *R. cherri* is an endemic species and its distribution is restricted to the highlands of central Costa Rica.

Reithrodontomys garichensis. This species was recognized as such and separated from the *R. mexicanus* species complex based on morphological data (Gardner and Carleton 2009). *R. garichensis* is distributed in the Talamanca Mountain Range in Costa Rica and Panama.

Melanomys chrysomelas. Using mitochondrial DNA nucleotide sequences of the cytochrome-*b* gene, phylogenetic relationships were inferred in *Melanomys caliginosus* (Hanson and Bradley 2008). This study included samples from populations in Nicaragua, Costa Rica, Panama, Venezuela and Ecuador, resulting in the elevation of these four groups to a specific level. Thus, the accepted species for Costa Rica is *M. chrysomelas*, and is distributed in Honduras, Nicaragua and Costa Rica (Hanson and Bradley 2008; Wilson *et al.* 2017).

Oligoryzomys costaricensis. This species was separated from the *Oligoryzomys fulvescens* species complex according to Bayesian analyses of the mitochondrial cytochrome-*b* gene (Hanson *et al.* 2011). According to this study the form of this species complex accepted for Nicaragua, Costa Rica and Panama is *O. costaricensis*.

Gardnerycteris keenani. Based on genetic analyses and morphological comparisons, it was proposed to elevate the subspecies *Gardnerycteris crenulatum keenani* to specific level (Hurtado and D'Elía 2018).

Diaemus youngii. The correct original spelling of the species epithet is *youngii* and not *youngi* (Kwon and Gardner 2008).

Lophostoma silvicola. The specific epithet changes from *silvicolum* to *silvicola* because it is an invariable noun (MDD 2022).

Tonatia bakeri. Based on descriptions and morphometric analyses, and a phylogenetic reconstruction, the three recognized subspecies of *T. saurophila* were recognized and elevated to species level (Basantes *et al.* 2020). *Tonatia bakeri* is distributed from southeastern México to northern South America (Wilson and Mittermeier 2019).

Glossophaga mutica. Based on morphometric analyses with cranial characteristics and their relationship with environmental variables, the four subspecies of *Glossophaga soricina* were elevated to specific level (Calahorra-Oliart *et al.* 2021). The distribution of *G. mutica* includes Central America.

Artibeus aztecus and *A. toltecus*. It is appropriate to use the specific epithets *aztecus* and *toltecus* instead of *azteca* and *tolteca* because *Artibeus* gender is masculine.

Chiroderma gorgasi. According to the latest phylogenetic revision of the genus *Chiroderma* (Lim *et al.* 2020), based on morphological and molecular analyses, the trans-Andean populations of *C. trinitatum* should be elevated to specific level, adopting the name *C. gorgasi*.

Uroderma convexum. The trans-Andean subspecies of *U. bilobatum* was elevated to specific level according to a review of the genus *Uroderma*, through analyses of morphological, karyotypic, and molecular variation, and taxonomic affinities between geographic variants (Mantilla-Meluk 2014).

Eumops ferox. Based on morphological and genetic analyses, the *Eumops glaucinus* species complex was separated into four entities (McDonough *et al.* 2008). The species *E. ferox* was defined for the Caribbean region, México and Central America, while *E. glaucinus* has a South American distribution.

Molossus nigricans. Based on the most recent phylogenetic analysis of the genus *Molossus* (Loureiro *et al.* 2020), *M. nigricans* is revalidated and recognized as a distinct species from *M. rufus*. The former has a Mesoamerican distribution, and the latter is restricted to South America.

Lasiurus frantzii. According to a molecular systematic review of the tribe Lasiurini, *L. frantzii* was recognized as a distinct species from *L. blossevillii*, leaving the former with a Mesoamerican distribution (Baird *et al.* 2015), including Costa Rica.

Myotis pilosatibialis. The subspecies *Myotis keasy pilosatibialis* was elevated to specific level and separated from *M. keaysi* according to morphological and phylogenetic studies (Mantilla-Meluk and Muñoz-Garay 2014; Carrion-Bonilla and Cook 2020); this being the species present in Costa Rica.

Kogia sima. The specific epithet changes from *simus* to *sima* (McGowen *et al.* 2020).

Recent records since Rodríguez-Herrera et al. (2014) list

Cryptotis monteverdensis. We add a new species of shrew, belonging to the *Cryptotis thomasi* group, described for the Monteverde Cloud Forest Biological Reserve, Puntarenas Province (Woodman and Timm 2017).

Ichthyomys tweedii. This species was recorded for southern Costa Rica, at the Las Cruces Biological Station (Ramírez-Fernández *et al.* 2020). This record represents the northern distribution limit for the genus *Ichthyomys*.

Diplomys labilis. Reported for the Osa Peninsula, Puntarenas Province, in the south of the country (Ramírez-Fernández *et al.* 2015).

Mormoops megalophylla. Captured at the Venado Caves, Alajuela Province (Vicente and Ledezma comm. pers.; see York *et al.* 2019).

Micronycteris tresamici. A new species described based on morphometric analysis, and cariological and morphological comparisons (Siles and Baker 2020). Confirmed for Alajuela and Guanacaste provinces in Costa Rica, and Honduras.

Molossus alvarezi. Described by González-Ruiz *et al.* (2011), apparently this species used to be misidentified as *Molossus sinaloae*, from which it differs in size, fur coloration, and other morphological characteristics. *M. sinaloae* distribution is restricted to México, therefore we replaced it with the new species *M. alvarezi*.

Cynomops greenhalli. Reported for Veragua Rainforest, Liverpool, Limón Province, and confirmed in scientific collections by Salas-Solano *et al.* (2020). This represents a distribution range extension into the Caribbean for the species in Central America.

Nyctinomops laticaudatus. Reported for Santa Ana, San José Province (Villalobos-Chaves *et al.* 2018).

Myotis armiensis. This species was described by Carrion-Bonilla and Cook (2020). Its distribution includes the premontane and montane forests of Chiriquí (Panama), Valle del Silencio (Costa Rica), and the Cordillera Oriental (Ecuador).

Speothos venaticus. Reported for Zona Protectora Las Tablas, Talamanca Mountain Range (González-Maya *et al.* 2017).

Discussion

Increasing interest in studying mammals, not only abroad, but also locally in Costa Rica (Rodríguez-Herrera *et al.* 2005, 2014b) is leading to the discovery of new species. Ongoing systematic and phylogenetic revisions using a combination of fossils, morphology, and molecular data is revealing cryptic species, and more powerful hypotheses about the evolutionary relationships of mammals at various taxonomic levels. This is particularly evident in the orders Chiroptera, Rodentia and Eulipotyphla which are not only small-sized mammals from very diverse groups, but also more taxonomically challenging (*e. g.*, cryptic species, species complexes) than other orders of mammals. This is reflected in the new additions to the list, where six bat species, two rodent species, and one shrew are among the ten recent records. Of these, four correspond to new species descriptions to science: the bats *M. tresamici*, *M. alvarezi*, and *M. armiensis*; and the shrew *C. monteverdensis*. The latter stands out for being an endemic species for Costa Rica, known only for the Monteverde region, Puntarenas Province (Woodman and Timm 2017).

Another species that stands out among the new records, belonging to the well-studied group of the carnivores, is the bush dog *Speothos venaticus*. This poorly known species, reported to be rare throughout its distribution, was recorded in camera traps for southern Costa Rica (González-Maya *et al.* 2017). According to the authors, the low frequency of records of this species in the study area is consistent with and reinforces the idea of its cryptic habits and natural rarity. This also highlights the great importance and scope of modern technologies for field work, such as camera traps, and long-term research, in developing complete mammal inventories, making it possible to record species that would otherwise go unnoticed.

Regarding aquatic species, as expected the cetaceans are the most diverse group of marine mammals within the Costa Rican Exclusive Economic Zone with 27 species. However, it is important to highlight that this is likely an underestimation. While monitoring efforts in terrestrial habitats continue to grow in Costa Rica, the aquatic environments remain largely unexplored. Deep diving and offshore species are likely missed in opportunistic boat surveys. To this day, no dedicated effort to evaluate the species richness and abundance of cetaceans in Costa Rican waters have taken place. Most survey efforts are near the coast, and temporally and spatially limited (May-Collado *et al.* 2018).

Regarding the last list of mammals published for the country (Rodríguez-Herrera *et al.* 2014a), two bat species, *Sturnira hondurensis* and *M. sinaloae*, and four cetaceans, *Kogia breviceps*, *Mesoplodon europaeus*, *M. ginkgodens* and *Stenella clymene*, were removed from our list. The bats were previously included, most likely given they are cryptic species with respect to *S. burtonlimi* and *M. alvarezi*, respectively, and having little knowledge about their taxonomy, their correct identification has been mistaken since the first records. In the case of cetaceans, these were included in the list based on distribution maps from various sources, that generalize their presence throughout the Pacific or Indian Ocean (*e. g.*, MacLeod *et al.* 2006; Jefferson and Braulik 2018; Kiszka and Braulik 2020). However, these species have not yet been documented in the field or in strandings in Costa Rican territory.

The main areas of mammal endemism in Costa Rica correspond to the high parts of the different mountain ranges, with 21 of the 30 endemic species restricted to these regions, mainly in the mountainous extension of the Talamanca Mountain Range in Costa Rica and Panama. This mountain range presents the highest elevations in the country, reaching a maximum of 3820 masl (Kappelle and Horn 2005), is considered one of the five great forests of Mesoamerica, and is home to the largest forest extension in the country, with more than 400,000 ha of protected areas. These high elevation regions are considered endemism hotspots because of its historical biogeographical formation that has served as a refugee for some species, due to the isolation of relatively small areas with specific climate ranges enhancing speciation rates (Obando 2002; Savage 2002; Kluge and Kessler 2006). It is important to highlight rodents among the endemic species in the country, which comprises 70 % of the total, being at the same time one of the least known groups and with most uncertain conservation status.

Among the Mesoamerican countries, Costa Rica has historically stood out as a leader in conservation. Costa Rica has 166 protected areas that cover approximately 25 % of the national territory (Alvarado *et al.* 2012; González-Maya *et al.* 2015). These protected areas include 50 % of the coastline and 20 of them are exclusive marine protected areas (Alvarado *et al.* 2012). In addition, the land administration has favored the prevalence of wildlife populations in much of the country, including species categorized as threatened and with a special conservation status, both nationally and globally (SINAC 2017; IUCN 2022). In groups such as primates and felids, all species are under some category of threat, and the same happens with the tapir *T. bairdii*, the largest land mammal in the region. In the case of the giant anteater, listed by both SINAC (2017) and IUCN (2022), this has been considered as extirpated from Costa Rica by some authors (Ruiz León 2019).

For other members of the Costa Rican mammal assemblage, long-term monitoring efforts are urgently needed to help identify the impact of direct and indirect anthropogenic activities on their populations. In particular for endemic species, most of which are not included under any threat category despite poor knowledge on its biology and its reduced global distribution range, so its conservation status should be carefully reviewed. Management of protected areas in Costa Rica over time has provided space for the mammal diversity recorded in this study; however, it is necessary to invest in conservation efforts, especially on species that receive less attention, to guarantee their survival and presence in Costa Rican territory in the future.

Although some researchers consider Costa Rican mammalian diversity well known, still new species are continuously being described and some are even periodically reported for the first time for the country. This is reinforced not only by cientific research, but it encompasses constant informal field work, observation and documentation of wildlife by local naturalists; furthermore, growing citizen science and participatory research initiatives (*e. g.*, camera-trapping monitoring, bird counts) are now surveying many areas across the country and will provide new information about multiples groups in the coming years (Gómez Hoyos *et al.* 2021). Moreover, contributions on systematics have proved their need and value as taxonomic boundaries between species from complex groups, as bats and rodents, are being clarified adding more changes to the list.

Although multiple threats still exert pressure over many mammal populations in the country (González-Maya *et al.* 2015, 2016), Costa Rica stood globaly as a leader in conservation, and the country's economy benefits largely from ecotourism (Echeverri *et al.* 2022). This is reflected in the recent creation of new protected areas (Presidencia de la República de Costa Rica 2022), where more than 15,000,000 hectares were added. So we expect that the country will continue towards a conservation-minded path for the future, maintaining committed efforts for safeguarding its biodiversity for the long term, although still many challenges remain to be covered by local government and policies.

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Supplementary material

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