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Justification for a taxonomic conservation update of the rodent genus *Tamiasciurus*: addressing marginalization and mis-prioritization of research efforts and conservation *laissez-faire* for a sustainability outlook

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Abstract

Taxonomy presents itself as the critical basis of any modern scientific decision-making approach in the living world, and therefore accurate classifications have to be sought. Due to ongoing species naming debates, here we would like to facilitate a discussion on the methods and validity used for taxonomic claims and their influence on conservation, ecology, and management for squirrels in the western world as a wider example. Following the established epigenetic approach, we examine the rodent genus *Tamiasciurus*. We include in our assessment all relevant species-interfering characteristics and present one new perspective, ecological niches. The ecological niche is essential for explaining the species' behavior patterns and their discrepancies among the congeners, adding insights into phylogenesis. We add the usage of mapping software such as geographic information systems (ArcGIS, Open QGIS) for this genus, as well as best-available open access data and the statistical aid from R. Misclassifications in the taxonomy are known to lead to conservation failures on a continental and societal scale, in part caused by a lack of knowledge by the public and the miscommunication between scientists and the public. As one possible solution, here we suggest a reclassification for Mearns's squirrel (*Tamiasciurus mearnsi*) and a description update for the entire *Tamiasciurus* genus to improve conservation success. Additional solutions are presented to simplify classification with reduced errors and confusion in the animal kingdom. A larger future effort of this style is sought to greatly decrease marginalization, to improve the current lack of research priority and "*laissez-faire*" attitudes on environmental issues for a better relationship between humans and the biotic world. In conclusion we present important topics and yet unaddressed problems, such as how the rodent's marginalization influences the pandemic disease transmission to humans (e.g. Covid-19, rabies, and bubonic plague), appropriately assigned budgets for their conservation, and the data transparency in a continuously accelerating climate-changing world.

Keywords: Squirrel, *Tamiasciurus*, taxonomy, conservation, marginalization

1. Introduction

A correct up-to-date taxonomy is essential for any science-based conservation effort (Focardi 2013; Von Staden et al. 2013 for South African flora; Tsang et al. 2016). However, after centuries of research, the biotic taxonomy is still heavily debated, unresolved, lacks data, is often even outdated and obsolete. It is usually understudied, not mutually accepted and poorly understood, that is especially true for small mammals (Bertolino et al. 2015; Tsang et al. 2016). Next to that, taxonomy persists still as a widely subjective

matter, hindering a collective delimitation and with this a combined conservation effort (Zachos 2016). For trustworthy and unambiguous decision-making in the public eye, modern taxonomy has to be strongly supported by all factors interfering with the examined species (Silva 1993). That is because mistakes and misclassifications can lead to conservation and management tragedies, lack of public trust, and policy dilemmas with substantial consequences including possible species extinction (Boltovskoy 1958; Dubois 2003; Zachos 2013). Taxonomy on a species or

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subspecies level, especially in small mammals, is still not stable and in continuous development due to new splitting/lumping of species, with possible negative impact on the taxa's conservation (Mori et al. 2019a, 2019b). Some globally relevant species which show taxonomic discrepancies, and which are important for conservation, are shown in Table I.

Ecological importance of conservation and speciation

In our assessment, we use squirrels as a model for improved taxonomic classification for conservation relevance. Squirrels are part of the mammalian order *Rodentia*, and they are widespread around the globe, with 286 extant species (as listed on <https://www.itis.gov/as> confirmed species. A clean and complete species list in a digital format can be obtained from MS on request). It is important to state here is that every online institutional source provides a different data set of squirrel species (GBIF accounts for 330 squirrel species as being valid entries, ITIS for 286 and Reference books such as "Squirrels of the world" reach 239 species (Thorington et al. 2012) without a good agreement overall.

Tracing the evolutionary history of squirrels, it is assumed that approximately 13 million years ago squirrels diverged from Eurasia via Beringia to the North American continent and evolved there into the genus *Tamiasciurus* (Mercer & Roth 2003). This genus contains the widespread American Red Squirrel (*Tamiasciurus hudsonicus*) and Douglas Squirrel (*Tamiasciurus douglasii*) located on the north-west of the North American continent. It also contains Mearns's Squirrel (*Tamiasciurus mearnsi*), which is Mexico's only endemic squirrel species with a restricted habitat on the peninsula of Baja California (Ramos-Lara 2012; Ramos-Lara et al. 2013). The life history of the examining genus is synthesized in Table II.

The conservation status of *T. mearnsi* is classified by IUCN as "threatened", with a declining population trend (De Grammont & Cuarón 2018), thus, the conservation importance is significant for this species and the associated genus. Singular conservation management mistakes could lead to the extinction of the entire species, and should therefore be strongly avoided (Boltovskoy 1958; Dubois 2003; Zachos 2013).

Similar taxonomic cases of direct conservation concern in mammals

It is noteworthy that mammals, and specifically ones close to the rodent genus *Tamiasciurus*, but also many other species and genera, suffer under taxological

disagreements and misclassification. It affects their conservation effectiveness. Such cases are found worldwide and include prominent species like the Brown Bear (*Ursus arctos*), Red Wolf (*Canis rufus*), Gorilla (*Gorilla gorilla*), Indonesian monkeys (*Cercopithecinae sp.*), Langurs (*Semnopithecus sp.*), Bonobo (*Pan paniscus*), Red Panda (*Ailurus fulgens*), Boreal Woodland Caribou (*Rangifer tarandus caribou*), Serow (*Capricornis sp.*), Goral (*Naemorhedus sp.*), and Orca (*Orcinus orca*). For other species groups, misclassification is equally found in Snow Petrel (*Pagodroma nivea*), Birds of Paradise (*Paradisaeidae*), Canada Geese (Dusky Goose) (*Branta canadensis occidentalis*), Lizard (*Lacertilia sp.*), Arctic Cod (*Arctogadus glacialis*), Patagonian Toothfish (*Dissostichus eleginoides*), Zooplankton, cultivated plants, and Rhodophyta (*Gracilaria*) (More details shown in Table I). It is a pervasive problem found with many species of global conservation concern (Zachos et al. 2019).

Here we assess this problem and present a possible approach to resolve taxonomic issues using the sum of all the environmental, behavioral, and species-specific factors in the public arena. We guarantee a more modern and correct species classification and taxonomy by using publicly accessible – open-access - data. With this, we aim for the best-available conservation management options in the Anthropocene (as shown already for bats by Tsang et al. 2016).

As presented by Zachos (2013), not only the phylogenetic species concept has to be considered for guaranteeing a reliable and correct taxonomy, as it often dominates in a monopolized fashion. But instead, a combination of the phylogenetic and the biologic species concepts should be used for a wider agreement to have all facts in good agreement. Only the combination of these concepts identifies species in a defendable way.

2. A description of current discrepancies within the genus *Tamiasciurus* and their conservation

2.1 Current description of the genus (*Tamiasciurus*)

The genus *Tamiasciurus* underlies the tribe Sciurini and consists of three species, *T. hudsonicus*, *T. douglasii* and *T. mearnsi*. This rodent genus is primarily characterized by its hoarding behavior (= creating middens) for feeding, nesting, and hibernation purposes, giving the genus its name (*Tamiasciurus*, Greek for hoarder squirrel). Table III outlines the current taxonomic structure of the genus, based on the global taxonomic reference (Integrated Taxonomic Information System, www.itis.gov¹).

Table I. Cases of the living world where taxonomy and classification disputes exist and affect conservation efficiency.

Order/family/genus/species	Short family/genus/species description	Description of the misclassification/taxonomic chaos
Brown Bear (<i>Ursus arctos</i>)	The brown bear (<i>Ursus arctos</i>) is found across Eurasia and North America and is divided into five different clades, some of which coexist in different regions (McLellan et al. 2017; Servheen et al. 1999).	For several bear species, the same set of subspecies is listed and causes large confusion problems in its conservation effort (Wilson & Ruff 1999). In addition, a recent hybridization with polar bears creates management and legal problems in times of climate change.
Red Wolf (<i>Canis rufus</i>)	This species is native to the southeastern United States and its major characteristic is a reddish-tawny colored fur. This species is currently recognized as endangered and grants protected status (Hinton et al. 2013).	The species status here is unclear, scientists do not agree whether it is a wolf species itself, a subspecies or a hybrid between two subspecies (Phillips & Henry 1992).
Gorilla (<i>Gorilla gorilla</i>)	Inhabit the forest of central Sub-Saharan Africa, gorillas are ground-dwelling, predominantly herbivorous apes with a species division into eastern gorillas and western gorillas (both critically endangered).	Miscommunication between scientists can lead to taxonomic chaos and correspondingly to conservational interference (Cotterill et al. 2014), shown for this species and its conservation actions (see Groves 2002 for details).
Indonesian monkeys	Indonesia consists of over 17,500 islands (Indonesian Ministry of Trade), which are home to highly diverse ecosystems and habitat differentiations, causing enormous differentiations and adaptations in many living species, including primates (Gursky-Doyen & Supriatna 2010).	These differentiations and adaptations raise many taxonomic questions, including uncertainty how to solve findings in the field, whether subspecies should be proposed, if they should be raised to a new species level, how species should be grouped (genera) etc., this uncertainty can cause major conservational failures for 70% of the species threatened by extinction, and 84% of the 40 primates generally threatened (Gursky-Doyen & Supriatna, 2010).
Langurs (special focus on Black-crested Sumatran langur (<i>Presbytis melalophos</i>)	It is a primate species of the family <i>Cercopithecidae</i> , endemic to Sumatra in Indonesia. Its natural habitat is subtropical or tropical dry forests, which is shared with many congeners, however it is threatened by man-caused habitat loss (Traeholt & Setiawan 2020)	Taxonomy of this group in Sumatera has been based solely on the distinction in the pelage coloration and has been a subject of controversy (Aimi & Bakar 1992).
Bonobo (<i>Pan paniscus</i>)	This ape species shows extremely high genetic relationship with chimpanzees and humans. The taxonomy is in continuous evolution for this species and might change soon due to recent findings (Wildman et al. 2003).	This species shows accordingly to Wildman et al. (2003), 99.4% genetic overlap with humans and chimpanzees and proposals have been recently made to fuse these three species in one single genus (<i>Homo</i>).
Red Panda (<i>Ailurus fulgens</i>)	This mammal is native to the eastern Himalayas and southwestern China and is listed as endangered species on the IUCN Red List.	New research underlines taxonomic misalignments since the two subspecies should accordingly be divided into two species which further hinder successful conservation actions for this endangered species (Hu et al. 2020)
Boreal woodland caribou (<i>Rangifer tarandus caribou</i>)	This ungulate is a North American subspecies of the reindeer (or the caribou in North America). A distinctive characteristic of all caribou is large crescent-shaped hooves that change shape with the season and that are adapted to walking in snow-covered and soft ground such as swamps and peat lands.	It is in continuous discussion whether European Reindeer and North American Caribou are the same species. Additionally, it has been detected that some herds migrate, others not, which is probably an indicator of different subgroups of the species/subspecies and call for taxonomic clarification since it is otherwise impossible to handle it conservation-wise (Mallory & Hillis 1998).
Serow (<i>Capricornis</i> sp.) and Gorals	This medium-sized goat-antelope mammalian genera consist are endemic to Asia. The serow genus officially consist of 7 species and the goral genus of 6, out of these 13 species 8 are “Threatened” or “Near Threatened” (Mori et al., 2019b).	The taxonomy of these genera has been a debate for several decades already and it is still unagreed upon of how many species actually exist and whether some should be fused/reclassified (Mori et al., 2019b). Mori et al., (2019b) suggest a conservation supporting reclassification for these relatively rare and threatened genera.

(Continued)

Table I. (Continued).

Order/family/genus/species	Short family/genus/species description	Description of the misclassification/taxonomic chaos
Orca (<i>Orcinus orca</i>)	This aquatic mammalian species has no defined conservation status according to the IUCN Red List (Reeves et al. 2017), as well as no defined habitat and population size. It is assumed that this species occurs in many parts of the world, however it is still assumed to be heavily threatened, especially in the Arctic (Reeves et al. 2017).	This immense uncertainty about this species raises questions whether all existing species or subgroups (pods) are even discovered yet, in the vast oceans, and how these animals interfere with their habitat (Hauser et al. 2007). Additional conservation efforts are promptly requested to guarantee a secure conservation status for this species in the future, starting with a strong and clear taxonomy.
Snow Petrel (<i>Pagodroma nivea</i>)	It is the only member of the genus <i>Pagodroma</i> and it is divided into two subspecies (<i>P. nivea nivea</i> and <i>P. nivea confusa</i>), where individuals primarily differ in their size (Henri & Schön 2017).	The taxonomic status of the Snow Petrel remains the subject of considerable controversy (Shirihai & Jarrett 2007; Del Hoyo & Collar 2014). Few “pure” populations of both “subspecies” are known whereas most colonies consist of hybrids which can make it highly difficult for conservation management, e.g. during climate change with Antarctica as one of the strongest affected areas in man-made climate change.
Birds of Paradise (<i>Paradisaeidae</i>)	The majority of species are found in Papua New Guinea, Indonesia and eastern Australia. The family has 42 species in 15 genera (Gill et al. 2020).	There is a long taxonomic debate for this species group for over 100 years. More taxonomic chaos has been created in the past years for this group by mixing instead of combining genetic taxonomic approach and the morphologic one. It resulted in classifications of several species and genera in different and multiple families (Irestedt et al. 2008). However, the conservation status for this group remains in peril.
Canada Geese (Dusky Goose) (<i>Branta canadensis occidentalis</i>)	Dusky Canada geese represent one of the smallest populations of Canada goose in North America (William L. Finley - U.S. Fish and Wildlife Service).	The dusky Canada goose is occasionally merged with the Vancouver Canada goose which causes misunderstandings with conservation management (Bromley 2003). It is of major legal concern for hunting.
Lizards (<i>Lacertilia</i> sp.)	Lizards are a widespread group of reptiles with over 6,000 species which are characterized by a small head and neck with a long body and tail.	The taxonomy has always been in debate for this group and is currently outdated for the entire suborder. The latest update dates back to 1988 (Gauthier et al. 1988).
Arctic Cod (<i>Arctogadus glacialis</i>)	Arctic Cod also called Polar Cod, is found circumpolar.	There are many genetic questions related to stocks and general biological characteristics, and thus resulting into fishing questions about quotas and their disputes in a changing Arctic (as summarized by Cohen et al. 1990).
Patagonian Toothfish (<i>Dissostichus eleginoides</i>)	The toothfish is found in many sub-Antarctic waters and replaces the shark species there.	This is a long-lived species, and its life history details are unknown, as needed for a valid fisheries management. Arguably, the Patagonian toothfish is a taxonomic group which is generally on the conservation decline and with Climate Change going on unabated (Huettmann 2012).
Charr (<i>Salvelinus</i>)	This genus contains primarily cold and fresh-water fish in the family Salmonidae, distributed circumpolar.	The diversity within this genus makes speciation difficult and confusing. The fish inhabit different habitats, where food availabilities differ as well as other circumstantial factors, leading to high polyphenism of several species and makes it difficult for diversification of species (Reist et al. 2013).
Zooplankton	This species group sits at the core of the global food chain, and is now even harvested in Antarctic waters, causing probable food shortages for the entire fauna of the Antarctic region (Trathan & Reid 2009).	Already the life history of this species group is complex, with many life stages to be identified. However, the species genetics remains to be resolved and with a matching morphological identification mutually accepted world-wide. Such an agreed classification, and subsequent conservation management does not exist, likely never will (Chiba et al. 2018).

(Continued)

Table I. (Continued).

Order/family/genus/species	Short family/genus/species description	Description of the misclassification/taxonomic chaos
Rhodophyta (<i>Gracilaria</i>)	Rhodophyta also called red algae, are one of the oldest eukaryotic algae (Lee 2008).	As seen in Junfu and Bangmei (1984), the taxonomy of some species remains unsolved till today because of their extreme polymorphism and the lack of authentic specimens for comparative studies.
<i>Lactobacillus acidophilus</i>	It is a species of gram-positive bacteria in the genus <i>Lactobacillus</i> and is a commercially significant bacterial probiotic.	<i>L. acidophilus</i> has struggled with misidentification and misrepresentation, caused by limitations of differentiating phenotypically similar species by morphological and biochemical means (Bull et al. 2013), with negative influences on the use in commercial field.
Purple sulfur bacteria (<i>Allochromatium</i> and <i>Thiocapsa</i>)	These two bacteria genera occur mostly in dark environments, far from what is often considered favorable living environment. Many members conduct anoxygenic photosynthesis.	At the species level a number of inconsistencies exist between the phenotypic and phylogenetic data, highlighting taxonomic problems within these genera (Herbert et al. 2005).

All the above-presented species and subspecies are accepted by ITIS as valid classifications. However, most of the classifications are outdated and reach back to the 1830s without recent adjustments. Additionally, some subspecies, and even the species name (*T. mearnsi*), are nomenclated inappropriately in a widely old-fashioned way and egocentrically discoverer-bound².

2.1.1 Short overview of the divergence history and development of the *Tamiasciurus* genus, and the influence of glaciation on their current distribution. According to Emry and Thorington (1982) and Mercer and Roth (2003), the first known ancestor of the *Tamiasciurus* genus is the *Douglassciurus jeffersoni*, which lived about 36 million years ago without any extant biologically similar individuals. Divergence of the *Tamiasciurus* happened around 13 million years ago from Eurasia via Beringia to the North American continent (Mercer & Roth 2003). *T. hudsonicus* remained in the cooler north, whereas *T. douglasii* moved toward the south (pacific northwest). From there, *T. mearnsi* evolved and diverged southwards (Baja California) around 2 million years ago. The species has been isolated there for more than 12,000 years without any opportunities to diverge back north due to climatic changes (concept details available from Stephen & Lindsay 1981). This isolation of the species has forced them to adapt to their unique climate. This adaptation is most likely explained by strong selection over generations for traits on morphology, behavior which are much more suited to the warmer climate (Via et al. 1995). All relevant evolutionary milestones for this genus are summarized in Table II.

The *Tamiasciurus* genus has since stayed stable: *T. hudsonicus* is now widespread over whole North

America, *T. douglasii* is common in British Columbia (Canada), Washington, Oregon, and California. Whereas *T. mearnsi* is locally restricted to its only known location in northern Baja California (Mexico) (see Figure 1 and Thorington et al. (2012) for details; Hope et al. 2016).

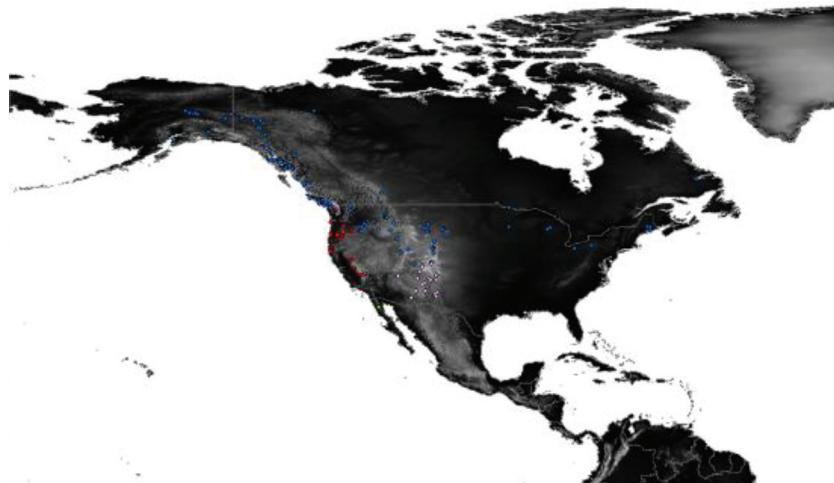
T. h. fremonti (pink), *T. douglasii* (red) and *T. mearnsi* (green) across the North American continent.)

2.1.2 Current Phylogeny of the genus *Tamiasciurus*. According to Pečnerová and Martinkova (2012), *T. hudsonicus* and *T. douglasii* are phylogenetically closely related. Additionally, it has been shown that *T. mearnsi* is a descendant of *T. douglasii*, phylogenetically as well as zoogeographically (Pečnerová & Martinkova 2012). This close relationship and the *T. mearnsi*'s recent (2 Mya) evolution from *T. douglasii* exhibit a high phylogenetic kinship between these two species (Mercer & Roth 2003; Pečnerová & Martinkova 2012).

2.1.3 Epigenetic perspective. The overall goal of this study is to review and investigate current taxonomy, and subsequently propose a method showing how the current taxonomic misalignment can be resolved. Therefore, here we consider all of the relevant species-interfering parameters and combine them to identify the best available taxonomy and subsequent conservation measures. The approach presented here is a template which conservationists can sustainably build on. When considering all the relevant species-specific parameters, some may contradict or overlap with others. Such a case can be seen with the phylogeny and its comparison with all the other parameters used in this study. The phylogeny indicates a close relationship among the examined species, however, the objective here is to assess the differences between

Table II. Evolutionary history of the species from the genus *Tamiasciurus*.

Important events	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Common ancestor	All the species share the same common ancestor, namely the <i>Douglassciurus jeffersoni</i> , lived approximately 36 Mya (Mercer & Roth 2003).		
Divergence from Eurasia to North America	Approximately 13 Mya the common ancestor of the genus <i>Tamiasciurus</i> diverged from Eurasia, via Beringia to the North American continent (Mercer & Roth 2003).		
Divergence across the North American continent	<i>T. hudsonicus</i> remained in the north and mid of the North American continent (Figure 1).	<i>T. douglasii</i> evolved towards the south-west, with the location focused on the pacific northwest (Figure 1).	<i>T. mearnsi</i> evolved from <i>T. douglasii</i> and diverged finally from the pacific southwest towards the south (Table I). This divergence happened presumably around 2 million years ago, from where the species has been isolated for more than 12.000 years without any opportunities to migrate/diverge back north due to climatic changes (Lindsay 1981).
Species current territory	The species is vastly distributed across most of the northern and middle part of the North American continent (Hope et al. 2016).	This species has found their optimal habitat between British Columbia (Canada), Washington, Oregon, and California (Hope et al. 2016).	The species has its natural habitat restricted to the northern Baja California (Mexico) (Ramos-Lara 2012). It is important to underline the small size of this species' habitat, which is estimated to be only 266 miles ² (689 km ²) (De Grammont & Cuarón 2018).

Figure 1. Mapped distribution of *T. hudsonicus* (blue) (with subspecies *T. h. fremonti* (pink)), *T. douglasii* (red) and *T. mearnsi* (green) across the North American continent.

T. hudsonicus, *T. douglasii* and *T. mearnsi*. Consequently, an epigenetic approach will be followed. This is done not to ignore the close genetic relationship, a parameter not fully supporting our proposal. Instead, we present the information more holistically to reach a wider consensus among known facts. Epigenetics (see Dupont et al. 2009 for definitions) underlines the approach to modern taxonomy from all the species-interfering factors, including genetics (however,

without direct alterations of the genetic information – but instead with a bigger influence of the environment and evolution), and supports our assessment by showing the importance of all species characteristics such as behavior and morphological differences. Here, we focus on the identification of the species' unique climate niche, in addition to the mentioned metrics, with the primary goal of eventually guaranteeing a higher conservation success (Ramos-Lara et al. 2013).

2.1.4 Morphological comparison within the genus *Tamiasciurus*. Evolution and environmental adaptations lead to morphological differences in isolated species (shown by Ruff 1994), such as the case with *T. mearnsi* and its congeners. Morphological adaptations, similarly to behavioral adaptations, are presumably caused by changes in the circumstantial habitat (e.g. glaciations, cold/hot climate periods, unique climate niche etc.). *T. mearnsi* shows not only behavioral adaptations but also morphological differences compared to its congeners (presented in Table IV).

2.1.5 Behavioral description for the genus *Tamiasciurus*. *Tamiasciurus* originates from the Greek “Ταμίας” “Σκιουρος” for “hoarder squirrel”, which describes the species characteristic behavior of hoarding conifer cones, small branch ends and even entire small spruce (*Picea sp.*) and pine (*Pinus sp.*) cones. These hoardings are stored in middens (“caches”), serving to store the squirrels’ nutrition over winter. Otherwise, these resources would be unavailable for the squirrel, buried under seasonal snow or ice and eventually decaying.

Table III. Taxonomic overview of the genus *Tamiasciurus*.

Species	Subspecies	Taxonomic serial number	Accepted names by itis.gov
American red squirrel (<i>Tamiasciurus hudsonicus</i>) reference: Thorington & Hoffmann 2005)	<i>T. h. hudsonicus</i>	202352	Yes
	<i>T. h. abieticola</i>	930552	Yes
	<i>T. h. baileyi</i>	930553	Yes
	<i>T. h. columbiensis</i>	931268	Yes
	<i>T. h. dakotensis</i>	930554	Yes
	<i>T. h. dixiensis</i>	930555	Yes
	<i>T. h. fremonti</i>	930556	Yes
	<i>T. h. grahamensis</i>	202353	Yes
	<i>T. h. gymnicus</i>	930557	Yes
	<i>T. h. kenaiensis</i>	930558	Yes
	<i>T. h. lanuginosus</i>	930559	Yes
	<i>T. h. laurentianus</i>	930560	Yes
	<i>T. h. loquax</i>	930561	Yes
	<i>T. h. lychnuchus</i>	930562	Yes
	<i>T. h. minnesota</i>	930563	Yes
	<i>T. h. mogollonensis</i>	930564	Yes
	<i>T. h. pallescens</i>	930565	Yes
	<i>T. h. petulans</i>	930566	Yes
	<i>T. h. picatus</i>	930567	Yes
Douglas squirrel (<i>Tamiasciurus douglasii</i>)	<i>T. h. preblei</i>	930568	Yes
	<i>T. h. regalis</i>	930569	Yes
	<i>T. h. richardsoni</i>	930570	Yes
	<i>T. h. streatori</i>	930571	Yes
	<i>T. h. ungavensis</i>	930572	Yes
	<i>T. h. ventorum</i>	930573	Yes
	<i>T. d. douglasii</i>	930550	Yes
	<i>T. d. mollipilosus</i>	930551	Yes
Mearns’s squirrel (<i>Tamiasciurus mearnsi</i>)	No subspecies existing	632478	Yes

However, only *T. hudsonicus* and *T. douglasii* show this behavior, whereas *T. mearnsi* does not (Koprowski et al. 2006, 2016; Ramos-Lara 2012; Ramos-Lara et al. 2013; Hope et al. 2016), making the nomenclatural association with *Tamiasciurus* faulty.

This hoarding behavior has strong influences on hibernation methods, nesting, and feeding, therefore changing the lifestyle of this species. This difference in behavior is caused by the adaptation of the species to its unique climate (Koprowski et al. 2006). Figure 2 shows this typical midden creation from *T. hudsonicus* and *T. douglasii*.

Measures of time spent at midden and visits to midden by *T. h. grahamensis*

According to Sanderson and Koprowski (2009), the main observations for *T. hudsonicus* deal with nesting and feeding activities. This species spends 50–60% of its daytime on and around their midden, excluding resource gathering (for nest maintenance or construction). This adds another approximately 5% and underlines the abundant time spent on the ground, on and around the midden. It is assumed that *T. douglasii* shows equal behavior characteristics, based on the identical midden construction. However, no data for the species’ time budget has been found in our search. Considering this time budget for *T. hudsonicus* and *T. douglasii*, the current classification for the tree squirrel seems inappropriate. This further justifies the proposal to update the *Tamiasciurus* genus description from tree squirrel to semi tree-ground squirrel.

2.1.6 Behavioral description of *T. mearnsi*. Compared to *T. hudsonicus*, *T. mearnsi* shows a very different behavior pattern. This species’ natural habitat (Figure 1) is respectively xeric and mild (shown in Section 4.3, in the presented boxplots for the species-specific climate niche of the *T. mearnsi* and elaborated by Ramos-Lara 2012), which leads to snow and ice-free winters with abundant resources and does not require the creation and maintenance of a midden by this squirrel species.

As shown by Ramos-Lara (2012) *T. mearnsi* spends its time significantly different than its congeners. As previously seen, its congeners spend over 50–60% time on or around their midden (cavity), whereas *T. mearnsi* only spends around 1–8% in its cavity and not having middens, fully supporting our proposal of a reclassification.

2.2 Hunting situation and threats of the *Tamiasciurus* squirrels

2.2.1 Hunting situation and conservation management regulations for all congeners. *T. hudsonicus* is not federally protected throughout most of its range, the species’

Table IV. Morphology comparison within the genus *Tamiasciurus*.

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Morphometrics	Average body mass: Female = 213 g, Male = 194 g (Thorington et al. 2012). Average body length (head - body): 187–190 mm (Thorington et al. 2012).	Average body mass: 200–243 g (Thorington et al. 2012). Average body length (head - body): 181–190 mm (Thorington et al. 2012).	Average body mass: 271 g (Ramos-Lara et al. 2013) Average body length (head - body in mm): 201.00 ± 13.22 (Ramos-Lara et al. 2013)

Figure 2. Midden creation by the *T. hudsonicus*, the photo has been taken in the Tanana forest (Alaska, US) in July 2019 by Moriz Steiner.

management is virtually unconstrained and has no rules (“*laissez-faire*”, as defined by the Cambridge dictionary as “the unwillingness to get involved in or influence other people’s activities”). Enforced law cases with convictions about this species are unknown to us. Only the endangered subspecies *T. h. grahamensis* is protected, but distinctive differences are difficult to detect in the field. *T. hudsonicus* is not found and therefore not managed in 16 U.S. states, Alabama, Arkansas, Delaware, Florida, Georgia, Hawaii, Kansas, Louisiana, Mississippi, Missouri, Nebraska, New Jersey, Oklahoma, South Carolina, Texas, and West Virginia. But in 13 states (Arizona, California, Colorado, Idaho, Iowa, Kentucky, New Mexico, North Carolina, North

Dakota, Ohio, Pennsylvania, Tennessee, and Virginia) is found and the daily bag limit and possession limits are statewide regulated. However, details vary for every state, with an average daily bag limit of 6 squirrels and a possession limit of 12. But the enforcement is very low and assigned budgets and effort estimates, e.g. manpower devoted to squirrel conservation management is virtually absent. 11 U.S. states (Alaska, Connecticut, Maine, Maryland, Massachusetts, Michigan, Montana, New York, South Dakota, Utah and Wyoming) have no limitations for the hunting of *T. hudsonicus* whatsoever. The remaining 10 states have squirrels from the genus *Tamiasciurus* occurring within their borders, however, they are not mentioned

in the state's regulations, thus they are highly marginalized. (All data regarding the state-specific hunting regulations has been obtained from the corresponding government webpages; details available on request from MS). In Canada, red squirrels are designated as fur-bearing animals in every jurisdiction and may only be harvested by licensed trappers (Obbard 1987). In 1987 the harvest density was less than 1 animal/km² (2.6/mile²). The highest harvesting rate occurred in the boreal coniferous forests of Alberta and Saskatchewan (Canada) with 1.1–10 km² per hunted individual (Obbard 1987). In Mexico, *T. hudsonicus* is not found and therefore not managed.

T. douglasii is not commercially imported for the fur trade (Obbard 1987). No hunting records are available for this species. Barely any hunting regulations are existing whatsoever, only for California (daily bag limit and possession limit: 4). In the other occurring states (Nevada, Oregon, Washington, Colombia) *T. douglasii* management is not mentioned in the governmental regulations. It is completely unmanaged but hunted, with examples shown in the upcoming paragraphs. However, according to Cassola (2016b), it is not assumed to be under threat, even though no data on the matter exists. Cassola (2016b) mentions for the conservation actions “*This species is not known to occur in any protected areas*”, however, following the known distribution of the species, it appears that several national parks are centrally located within their distribution range, such as the Yellowstone National Park (however it accounts for <1% of the range).

For *T. mearnsi*, no hunting/harvesting information is available.

All relevant hunting information regarding literature reviews has been summarized in Table V.

2.2.2 Wildlife conservation/management budgets in wealthy nations of North America. Rather large wildlife conservation budgets are designated for every U.S. State, Canadian provinces, and Mexico. Those assigned budgets are listed for every region on their corresponding governmental webpages. Taking Alaska as an example, their annual budget assigned for wildlife conservation equals approximately US \$43 million (2012, most recent available (0.1% of the state's GDP)), however only US\$384,000 (0.9%) (which is 0.0001% of the state's GDP) were assigned to Small Game conservation activities (please note, there is no specification and budgeted item list available throughout their range which depicts a budget assigned to only squirrels)). No further details are publicly available for the many species belonging to the Small Mammals (<http://www.adfg.alaska.gov/index.cfm?adfg=divisions>.

wcbudgetcorefunding171819#additionalresources). For California, approximately US\$ 195 million (0.006% state's GDP) were assigned for conservation action (no future details are publicly available; <https://nrm.dfg.ca.gov/documents/ContextDocs.aspx?cat=WCB>). On a continental scale, it is noteworthy that details about the management of single species such as squirrels as a public trust resource are not presented, and unknown to us and the vast majority of the global public. The presentation of these numbers exemplifies the marginalization and misassignments of budgets for Small Mammals. Rodents account for the largest part of the mammalian class (around 40% of all mammalian species are rodents), and still, the budget assigned for conservation activities is extremely minuscule. Additionally, it seems appropriate to underline that small mammals in general account for over 70% of the entire mammalian order species but receive only a small budget to conserve them (e.g. Alaska 0.9% from the entire budget available for wildlife conservation and management).

Known potential threats due to hunting/harvesting To our knowledge, for *T. hudsonicus* there are no active threats published, given its vast distribution and its high estimated population size. In some regions, the species is even seen as a pest (Stuart 2012) and widely used for target practice by the public (see below). Only one subspecies (*T.h. grahamensis*) (Table III) is considered threatened in its natural habitat. *T. douglasii* is thought to be hunted and harvested, however not in danger, even though population size numbers are unknown (Cassola 2016b). In contrast to its congeners, *T. mearnsi* is already severely threatened due to its small population size and its restricted habitat (Ramos-Lara 2012). Hunting or harvesting of the already small population numbers could lead to extinction (as shown for other species by Keane et al. 2005).

While hunting and harvesting for fur-bearing purposes are managed in some states and provinces of the North American continent, the number of poached animals is unknown. It cannot be excluded that the species, such as *T. douglasii*, get “harvested down” (see public postings in social media using squirrels for target practice etc.: <https://www.facebook.com/extremesquirrelhunting/> and <https://www.youtube.com/watch?v=zTiv3xuj7Io>). This can lead to critical conservation situations for marginalized small population subspecies in certain regions (Sanderson & Koprowski 2009) and stand opposite of a concept of science-based management using defendable numbers and policy (as promoted by Silvy 2020).

2.2.3 Other threats in the Anthropocene, Ecology of Fear, and Disease contamination. Possible threats for

Table V Hunting situation for the *Tamiasciurus* genus.

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Conservation status	Least concern (population trend: stable) (IUCN-T. <i>hudsonicus</i>). Only one subspecies (<i>T. h. grahamensis</i>), a population portion in Arizona, is endangered (AGFD 2003).	This species is considered to be common. Densities of up to 7–8 individuals per hectare have been reported (Rusch & Reeder 1978), however in most of the states the density rate lies within 0.4 and 1.0 individuals per hectare (Obbard 1987). Population densities depend on their natural habitat - composition of the forest and food availability are the determining factors.	This species has a small population due to restricted distribution and specific habitat needs (Ramos-Lara 2012). Exact population size or estimations are unknown.
Population size	Widespread in North America and Canada, abundant in many areas. Populations fluctuate with variations in food supply. Densities range from 0.2–0.5 per hectare (IUCN-T. <i>douglasii</i>). Experimental work of Sullivan and Sullivan (1982) indicated that densities of Douglas squirrels can increase five- to tenfold under a supplemental feeding regime.	This species is considered to be common. Populations fluctuate with variations in food supply. Densities range from 0.2–0.5 per hectare (IUCN-T. <i>douglasii</i>). Experimental work of Sullivan and Sullivan (1982) indicated that densities of Douglas squirrels can increase five- to tenfold under a supplemental feeding regime.	This species has a small population due to restricted distribution and specific habitat needs (Ramos-Lara 2012). Exact population size or estimations are unknown.
Hunting situation and regulations	Only the endangered subspecies <i>T. h. grahamensis</i> is protected, but distinctive differences are difficult to detect in the field. <i>T. hudsonicus</i> is not found and therefore not managed in 16 U.S. states, Alabama, Arkansas, Delaware, Florida, Georgia, Hawaii, Kansas, Louisiana, Mississippi, Missouri, Nebraska, New Jersey, Oklahoma, South Carolina, Texas and West Virginia. But in 13 states (Arizona, California, Colorado, Idaho, Iowa, Kentucky, New Mexico, North Carolina, North Dakota, Ohio, Pennsylvania, Tennessee, and Virginia) the daily bag limit and possession limits are statewide regulated. However, details vary for every state, with an average daily bag limit of 6 squirrels and a possession limit of 12. But the enforcement is very low. And 11 states of the U.S. (Alaska, Connecticut, Maine, Maryland, Massachusetts, Michigan, Montana, New York, South Dakota, Utah and Wyoming) have no limitations for the hunting of <i>T. hudsonicus</i> whatsoever. The remaining 10 states have squirrels from the genus <i>Tamiasciurus</i> occurring within their borders, however, they are not mentioned in the state's regulations, thus, highly marginalized! (The entire data regarding the state-specific hunting regulations has been obtained from the corresponding government webpages; details available on request from MS). In Canada, red squirrels are designated as fur-bearing animals in every jurisdiction and may only be harvested by licensed trappers (Obbard 1987). In 1987 the harvest density was less than 1 animal/km ² (2.6/mile ²). The highest harvesting rate occurred in the boreal coniferous forests of Alberta and Saskatchewan (Canada) with 1.1–10 km ² per hunted individual (Obbard 1987). In Mexico, <i>T. hudsonicus</i> is not found and therefore not managed.	<i>T. douglasii</i> is not commercially imported for the fur trade (Obbard 1987). No hunting records are publicly available. Barely any hunting regulations are existing, only for California (daily bag limit and possession limit: 4 squirrels. In the other occurring States (Nevada, Oregon, Washington, Colombia) <i>T. douglasii</i> 's management is not mentioned in the governmental regulations.	<i>T. mearnsi</i> is not commercially imported for the fur trade (Obbard 1987). No hunting records are publicly available and no hunting regulations existing; however, it is not a hunted species in its natural distributed habitat. Part of the population is located within the National Park Sierra de San Pedro Martir and therefore protected from hunting, however, not the entire population.

(Continued)

Table V. (Continued).

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Possible threats due to hunting/ harvesting	The harvesting rate of <i>T. hudsonicus</i> is much lower (< 1%) than the estimated density of red squirrel populations in this habitat, so it is doubtful whether trapping exerts significant pressure on local populations (COBBARD 1987).	Hunting records are widely absent for <i>T. douglasii</i> . Additionally, their population of adults is considered “stable”, therefore there is apparently no major threat coming from the hunting sector.	<i>T. mearnsi</i> is a threatened species within its restrict habitat, with a declining population trend and small population size. Hunting, already the a few adults, can lead to rapid population declines and possible extinction. it is highly advised not to hunt this species.
Budget assigned	No assigned budgets for hunting available	No assigned budgets for hunting available	No assigned budgets for hunting available

each species of the genus *Tamiasciurus* depend on the species or subspecies' habitat. Since the *Tamiasciurus* squirrels are distributed across wide parts of the North American continent, the threats are diverse. Range-wide, *T. hudsonicus* is not said to suffer under any relevant threats because of its enormous population size (Cassola 2016a), distribution (see Figure 1) and subspecies diversity (Table III). However, similar conservation cases have resulted in extinctions, e.g. Passenger pigeon (*Ectopistes migratorius*), Bison (*Bison*) or Beaver (*Castor*) (Taber & Payne 2003). Considering a finite set of global resources, promotion of economic growth has resulted in habitat loss for wildlife (for instance the population decline of Boreal Caribou (*Rangifer tarandus caribou*; Boan et al. 2018) and influences on wildlife by an inherently unsustainable economic growth (Czech & Daly 2004).

In addition to the Anthropogenic pressures, natural predators of *Tamiasciurus* include many raptors such as the Northern goshawk (*Accipiter gentilis*), Cooper's Hawk (*Accipiter cooperii*), Sharp-shinned Hawk (*Accipiter striatus*), Red-tailed Hawk (*Buteo jamaicensis*), Mexican spotted Owl (*Strix occidentalis lucida*), Great-horned Owl (*Bubo virginianus*). Further, several mammal predators such as Coyote (*Canis latrans*), Wolf (*C. lupus*), Lynx (*Lynx canadensis*), Bobcat (*L. rufus*), Gray Fox (*Urocyon cinereoargenteus*) (Schauffert et al. 2002) as well as Wild Boar (*Sus scrofa*) (Keuling et al. 2018), stray cats (Bertram & Moltu 1986) and dogs (Benson 2013) are known to prey on squirrels. Even though many predators show interest in *T. hudsonicus*, it does not seem they are severely threatening the species, as confirmed by the IUCN Red list which describes their population trend as “stable” (Cassola 2016a). However, these estimates are done in the absence of proper population numbers, harvest rates, and plans. Two core predators of *T. douglasii* are the Northern goshawk (*Accipiter gentilis*) and Northern spotted owl (*Strix occidentalis caurina* (XANTUS)) (Carey 1995).

T. mearnsi is anthropologically threatened by timber removal, grazing, wildfires, competition with the newly introduced Eastern Grey Squirrel (*Sciurus carolinensis*), generic deforestation, and natural habitat repression (De Grammont & Cuarón 2018). Shown by Mooring et al. (2004) extinction through predation can occur for this squirrel and has to be prevented.

The ecology of fear -according to Zanette and Clinchy (2019)- “refers to the total impact of predators on prey populations and communities.” This affects squirrels since they are commonly seen as mesopredators, being the prey from several large vertebrates and also functioning as predators for many small vertebrates such as

Songbirds (Passeriformes), Hares (*Lepus*), Chipmunks (*Tamias*), Lizards (*Lacertilia*), Mice (*Mus*), Rats (*Rattus*), Turkeys (*Meleagris*), Snakes (*Serpentes*), Crabs (*Brachyura*), Frogs (*Anura*), Salamanders (*Urodeda*) and conspecifics (Squirrels (*Sciuridae*)) (Callahan 1993). Additionally, it has been shown that squirrels specifically learn to prey on avian nests (Pelech et al. 2010), and Lemmings (*Dicrostonyx kilangmiutak*), studied as far back as 30 years ago (Boonstra et al. 1990), which further underlines their status and conservation importance as mesopredators. “Ecology of fear” also includes infanticide (killing of the newborn(s) from the mother), which occurs in many squirrel species (Michener 1982), and underlines the importance of future investigations to study the prey-predator relations of squirrels, thus, reducing marginalization and the “laissez-faire”-approach. Thus far, none of these effects are well known but likely play a large role on a continental scale for squirrel conservation.

Despite squirrels relying on mature trees (Holloway et al. 2012), the effects of commercial forestry as an anthropological threat on their short-time dynamics are not well studied and largely unknown (Ransome & Sullivan 2002; Cassola 2016b).

Some squirrels, however, also benefit from the Anthropocene. It is broadly known that squirrels directly benefit from provided food sources meant for other animals (aka “*subsidized predators*”), such as bird feeders. It easily acts on a continental scale. An overview of feeding location densities for the North American continent can be found in Figure 3 (data has been obtained from www.feederwatch.org and represents reported feeding locations in 2019).

However, squirrels cannot solely rely on the food from feeders and require natural food sources as the basis of their nutrition. Therefore, the loss of old-growth forests cannot be beneficial for most squirrels (Laurance et al. 2000). Additionally, luring animals, in this case squirrels, in urban areas with feeders comes with downsides such as disease transmission from squirrels to other animals and even humans (Stitt 2006). This fact has been shown for a long time already, the most recent example for such a case being the 2019 and 2020 Covid-19 or SARS CoV epidemic (Tracing map available here: <https://coronavirus.jhu.edu/map.html>). Other examples include rabies, the Creutzfeldt-Jakob disease (Kamin & Patten 1984), and the bubonic plague for rodents (Benedict 1996). Having squirrels present in urban areas, interacting with humans (see Figure 3) can consequently lead to such transmissions. Subsequently, it should not be forgotten that squirrels are never risk-free when it comes to transmissible diseases and contact with them should, therefore, be limited as far as possible.

3. Methods on additional Taxonomic Niche Descriptions

3.1 Ecological niche literature review

Ecological niche presentations have already been conducted in the past, however not to this extent nor on the North American continent. Examples are existing for the Red squirrel (*Sciurus vulgaris*) in England (Gurnell & Pepper 1991). However, a comparison between all the species from the



Figure 3. Bird feeder locations from the North American continent.

genus *Tamiasciurus* has never been presented, especially not with all the metrics we include here. We performed this literature review using www.google.scholar.com and other internet search engines using the keywords “ecological niche squirrel”, “ecology niche identification rodents” and similar.

3.2 Habitat/climatic niche identification

We extracted and synchronized climate niche information with geographic areas and species distribution information. Therefore, it was possible to identify in which climatic niche a certain species is living and what the descriptive factors of this niche habitat consist of (García 2006; Huang et al. 2010). An ecological niche is an “n-dimensional hypervolume”, where the dimensions are environmental conditions and resources that define the requirements of an individual or a species to practice its way of life, more specifically, for its population to persist (Schoener 2009). Hutchinson (1957) defines the hypervolume as the resources (e.g. light, nutrients, structure, etc.) available to (and specifically used by) organisms, and “all species other than those under consideration are regarded as part of the coordinate system”.

Based on the Hutchinson niche concept we exemplified, quantified, and synthesized the presented differences between the three genetically related squirrel species (*T. hudsonicus*, *T. douglasii* and *T. mearnsi*) in order to explain the differences in hibernating, feeding, and nesting behavior.

3.2.1 Adding GIS mapping to the known ecological niche information for *Tamiasciurus* squirrels. To create representative distribution maps, we downloaded a USGS (U.S. Geological Survey) data set (Appendix A). This data was visualized with a projected GIS map from the North American continent (Figure 1), created with ArcGIS and OpenGIS (QGIS).

In this study, we overlaid a Digital Elevation Model (DEM) with the distribution points of the three study species, downloaded from USGS to identify the range distribution of the *Tamiasciurus* squirrels (Figure 1). To compare the actual distribution of the squirrels with the ideal free distribution (Fretwell & Lucas 1970; Křivan et al. 2008), we created a 1,632 randomized point distribution across the North American continent (map and details can be obtained on request from the authors).

Every location of the distribution point data (in Figure 1) lies within the overall climate niche, each with a pixel size of 900 × 900 m (downloaded from the Worldclim data set CRU-TS 4.03 (Harris et al. 2014; Fick & Hijmans 2017). We associated the

location of each data point with a specific climatic niche. These climate niche pixels contain long-term mean temperature and mean precipitation for summer (April-September) and winter (October-March) months, as well as altitude. We exported the resulting data cube as text (ASCII) files into Excel and R for further analysis and processing described below.

3.2.2 Boxplots for climate niche comparison. After importing this data into R, we plotted the three study species (*T. hudsonicus*, *T. douglasii* and *T. mearnsi*) as well as the computed average of the randomly distributed landscape background data points across the North American continent, against their descriptive metrics for the occurrence. The metrics include the mean values of the temperature in winter (October-March), temperature in summer (April-September), precipitation in winter, precipitation in summer, as well as actual altitude. We used the R package ‘ggplot2’ and used commands “aes” and “geom_violin” to compute the plots. The results are shown in sequence in Section 4.

3.3 Obtaining climate niche metrics and effects on their hibernation, nesting and feeding behavior.

The reason to identify the unique climate niche for each *Tamiasciurus* squirrel species is to investigate the hypotheses for why *T. mearnsi* does not create middens, but its congeners do create middens. Adding GIS mapping and statistical (R) software for solving behavioral questions is crucial for species conservation and survival and is here emphasized by us.

4. Results

4.1 Findings from the literature review

All the findings presented in the introduction section have been summarized in Table VI. This includes the importance of our study, squirrel’s descriptive metrics, squirrel’s evolutionary history, conservation status, population metrics, habitat and behavior descriptions, hunting regulations, threat identification, and ecological conservation focus areas. The information in this table also provides a summary of our literature review.

4.2 GIS mapping and Ecological niche analysis

Figure 1 illustrates the distribution of the species *T. hudsonicus*, *T. douglasii* and *T. mearnsi* across the North American continent (as occurrence points – downloaded from USGS (Hope et al. 2016). It

Table VI. Summary of the literature reviews.

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Importance of research investigation	Much research has been carried out in the last centuries to study this species with continuously new technologies and approaches, making it a well understood and well-studied species. Its broad distribution contributed to the high research effort investigating this species. Even though the research effort has been particularly high for this species compared to its congeners, their conservation management is still low.	<i>T. douglasii</i> is compared to <i>T. hudsonicus</i> less well studied, however it is still under the best studied rodent species in North America.	<i>T. mearnsi</i> is an extremely poor studied species, with very little knowledge about population size and few confirmed location detections. Future investigations are highly requested to guarantee the continuous existence of this species, with correct up-to-date taxonomy as crucial basis.
Importance of Epigenetics in taxonomy	Epigenetics describes heritable phenotype changes that do not involve alterations in the DNA sequence (Dupont et al. 2009). Modern taxonomy has to include many aspects of epigenetics to ensure all species-influencing factors such as the behavior, appearance and evolution of the respective species. <i>T. mearnsi</i> represents many epigenetic discrepancies with the description of the corresponding genus. Mainly its behavior, habitat niche, and conservation status, differ from the current taxonomic description. Leading to possible mismanagement and conservation and therefore to extinction of the species. This can be changed with an update in taxonomy, underlining its unique behavior and habitat niche (which influenced the species to change nesting, feeding and hibernation behavior).		
Morphometrics	Average body mass: Female = 213 g, Male = 194 g (Thorington et al. 2012). Average body length (head - body): 187–190 mm (Thorington et al. 2012).	Average body mass: 200–243 g (Thorington et al. 2012). Average body length (head - body): 181–190 mm (Thorington et al. 2012).	Average body mass: 271 g (Ramos-Lara et al. 2013) Average body length (head - body in mm): 201.00 ± 13.22 (Ramos-Lara et al. 2013)
Vocalizations	<i>T. hudsonicus</i> uses 6 distinct vocalizations (e.g. territorial rattle)	<i>T. douglasii</i> uses 6 distinct vocalizations (e.g. territorial rattle)	Vocalizations show similarities, but on seemingly higher pitch (Smith 1978).
History	<i>T. hudsonicus</i> has been suspected to be first migrated on the continent of North America over Beringia, from there onwards, the species has chosen to establish itself in different habitats next to its congener <i>T. douglasii</i> .	<i>T. douglasii</i> has started to establish itself next to its congener <i>T. hudsonicus</i> probably soon after their migration onto the North American continent.	The ancestral from <i>T. mearnsi</i> (with high probability the <i>T. douglasii</i>) presumably moved into Baja California along a corridor between the Sierra Nevada and Sierra San Pedro Martir. Such a dispersal route could have opened first about 2 million years B. P. with the onset of the Nebraskan glacial (Stephen & Lindsay 1981). Since its isolation, the body size increased, and litter size and number changed as well.
Conservation status	Least concern (population trend: stable) (Cassola 2016b). Only one subspecies (<i>T. h. grahamensis</i>), a population portion in Arizona, is endangered (Arizona Game and Fish Department 2003).	Least concern (population trend: stable) (Cassola 2016)	Endangered (population trend: decreasing), endemic and threatened in its habitat (De Grammont & Cuarón 2018)
Population size	Widespread in North America and Canada, abundant in many areas. Densities of up to 7–8 individuals per hectare have been reported (Rusch & Reeder 1978), however in most of the states the density rate lies within 0.4 and 1.0 individuals per hectare (Obbard 1987). Population densities depend on their natural habitat - composition of the forest is the determining factor.	This species is considered to be common. Densities range from 0.2–0.5 per hectare (Cassola 2016a). Populations fluctuate with variations in food supply. Experimental work of Sullivan and Sullivan (1982) indicated that densities of Douglas squirrels can increase five- to tenfold under a supplemental feeding regime.	This species has a tiny population due to restricted distribution and specific habitat needs (Ramos-Lara 2012). Exact population size or estimations are unknown.

(Continued)

Table VI. (Continued).

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Geographic faunal realms	Holarctic	Holarctic	Neotropical
Habitat	Northern boreal coniferous forests, temperate and polar environments, found in a mixed variety of forests including coniferous, deciduous, and mixed forests, they are also able to thrive in suburban and urban settings (Taylor et al. 1999; Steele 1998).	Northern boreal coniferous forests, temperate and polar environments, found in a mixed variety of forests including coniferous, deciduous, mixed forests and they are also able to thrive in suburban and urban settings (Taylor et al. 1999; Steele 1998).	Xeric and hot conditions with extremely restricted habitat. Presence of different coniferous species (predominately pines (<i>Pinus jeffreyi</i> , <i>P. lambertiana</i> , <i>P. contorta</i> and <i>Abies concolor</i>) are crucial for their optimum habitat (Ramos-Lara et al. 2013).
Temperature distribution - natural habitat	Detected from Northern Alaska, southwards until Arizona, eastwards until the west coast of North America (e.g. Virginia, North and South Carolina). Species can be found in many north continental parts of America and has, therefore, also adapted to various habitat types with their macro/microclimatic deviations. Adaptations have led to the differentiation of subspecies for each macro climate type (Table III and Wei et al. 2015).	Detected from Canada (British Columbia), southwards until California, Washington, Oregon, Nevada (United States). Most of their habitat is located in the pacific northwest with mean annual Temperature of 12°C (TaD)	Only detected in xeric and hot conditions with habitat restricted to the forests and mountains of Sierra de San Pedro Martir in Baja California, Mexico. Natural habitat extremely restricted to local climate. Climate Baja California: mean annual temperature 19.6 °C (INEGI, 2010).
Precipitation distribution - natural habitat	The species' adaptation to precipitation differences is similar to temperature deviations in different habitat types and can therefore strongly vary.	Likewise, the temperature, also the precipitation in the species' habitat is characterized by Pacific northwest climate. Annual mean precipitation: 219.1 mm (TaD)	Species highly restrictions to its small habitat and therefore its precipitation. Climate Baja California: mean annual precipitation 169.4 mm (INEGI, 2010).
Altitude distribution - natural habitat	Highest detections reach up to 2,500 ft (762 m) in the Rocky Mountains - tending to remain lower (0–762 m) (Taylor et al. 1999; Steele 1998)	Since the Pacific northwest borders to the Pacific Ocean and includes the Coast - and Cascade Mountain Range, the distribution of <i>T. douglasii</i> is broadly distributed from 0 up to 3300 m asl (Pfau 2004).	Species detected between 2,100 m and 2,400 m asl (Ceballos & Oliva 2005). Baja California mean altitude: 1555 m (INEGI, 2010). <i>T. mearnsi</i> pushed back to the mountain regions of Baja California (INEGI, 2010).
Climate relationships	<i>T. hudsonicus'</i> habitat shows differences in its climatic characteristics compared to <i>T. douglasii</i> ; however, the major proprieties remain similar (as freezing winters with snow coverage, as well as the presence of a snow melting period, thus, a higher water availability, but restricts the squirrel to create middens and stick with the typical nesting behavior established from the genus <i>Tamiasciurus</i>).	<i>T. douglasii's</i> habitat shows differences in its climatic characteristics compared to <i>T. hudsonicus</i> , however the major proprieties remain similar (as freezing winters with snow coverage, as well as the presence of a snow melting period, delivering together a higher water availability but restricts the squirrel to create middens and stick with the typical nesting behavior established from the genus <i>Tamiasciurus</i>).	Compared to the other species, <i>T. mearnsi</i> occupies a habitat with barely freezing winters, water remains in its liquid state, even in winter at an altitude of over 2400 m asl (previous table). This confirms the xeric and hot conditions of its habitat, allowing the species to avoid spending efforts in creating middens (since food is year-round available and not covered by snow or ice like for the other congeners).
Nesting behavior	Nesting occurs mainly on the ground, in their middens (additionally to nutrition storage)	Nesting occurs mainly on the ground, in their middens (additionally to nutrition storage)	Nesting occurs mainly in tree branchings and not on the ground.
Hibernation nutrition method	Nutrition sources are similar to the ones described for <i>T. mearnsi</i> . Storage occurs in larderhoards of cones known as middens (Finley 1969) with a size up to 12 meters in diameter (Huettmann & Steiner 2019 - unpublished).	Nutrition sources are similar to the ones described for <i>T. mearnsi</i> . Storage occurs in larderhoards of cones known as middens (Finley 1969) with a size up to 12 meters in diameter (Huettmann & Steiner 2019 - unpublished).	Food (fungi, conifer seed, and conifer branch tips during spring and early summer (Taylor et al. 1999; Steele 1998)) is year around available, therefore there is no need for special storage creation/ maintenance efforts (middens).
DNA	<i>T. mearnsi</i> is highly related to <i>T. douglasii</i> , closely with <i>T. hudsonicus</i>		(Continued)

Table VI. (Continued).

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Hunting situation and regulations	Only the endangered subspecies <i>T. h. grahamensis</i> is protected, but distinctive differences are difficult to detect in the field. <i>T. hudsonicus</i> is not found and therefore not managed in 16 U.S. states, Alabama, Arkansas, Delaware, Florida, Georgia, Hawaii, Kansas, Louisiana, Mississippi, Missouri, Nebraska, New Jersey, Oklahoma, South Carolina, Texas and West Virginia. But in 13 states (Arizona, California, Colorado, Idaho, Iowa, Kentucky, New Mexico, North Carolina, North Dakota, Ohio, Pennsylvania, Tennessee, and Virginia) the daily bag limit and possession limits are statewide regulated. However, details vary for every state, with an average daily bag limit of 6 squirrels and a possession limit of 12. But the enforcement is very low. And 11 states of the U.S. (Alaska, Connecticut, Maine, Maryland, Massachusetts, Michigan, Montana, New York, South Dakota, Utah and Wyoming) have no limitations for the hunting of <i>T. hudsonicus</i> whatsoever. The remaining 10 states have squirrels from the genus <i>Tamiasciurus</i> occurring within their borders, however, they are not mentioned in the state's regulations, thus, highly marginalized! (The entire data regarding the state-specific hunting regulations has been obtained from the corresponding government webpages; details available on request from MS). In Canada, red squirrels are designated as fur-bearing animals in every jurisdiction and may only be harvested by licensed trappers (Obbard 1987). In 1987 the harvest density was less than 1 animal/km ² (2.6/mile ²). The highest harvesting rate occurred in the boreal coniferous forests of Alberta and Saskatchewan (Canada) with 1.1–10 km ² per hunted individual (Obbard 1987). In Mexico, <i>T. hudsonicus</i> is not found and therefore not managed.	<i>T. douglasii</i> is not commercially imported for the fur trade (Obbard 1987). No hunting records available. Barely any hunting regulations are existing, only for California (daily bag limit and possession limit: 4). In the other occurring States (Nevada, Oregon, Washington, Colombia) <i>T. douglasii</i> 's management is not mentioned in the governmental regulations.	<i>T. mearnsi</i> is not commercially imported for the fur trade (Obbard 1987). No hunting are records available. No hunting regulations existing; however, it is not a hunted species in its natural distributed habitat. Part of the population is located within the National Park Sierra de San Pedro Martir and therefore protected from hunting, however, not the entire population.
Budget assigned for hunting	No assigned budgets for hunting available	No assigned budgets for hunting available	No assigned budgets for hunting available

(Continued)

Table VI. (Continued).

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Possible threats due to hunting/ harvesting	The harvesting rate of <i>T. hudsonicus</i> is much lower (< 1 %) than the estimated density of red squirrel populations in this habitat, so it is doubtful whether trapping exerts significant pressure on local populations (CObbard 1987).	Hunting records are widely absent for <i>T. douglasii</i> . Additionally, their population of adults is considered “stable”, therefore there is apparently no major threat coming from the hunting sector.	<i>T. mearnsi</i> is a threatened species within its restrict habitat, with a declining population trend and small population size. Hunting, already the a few adults, can lead to rapid population declines and possible extinction. it is highly advised not to hunt this species.
Other threats	Species often seen more as pest than as species with high importance of conservation. <i>T. hudsonicus</i> is not threatened by any anthropogenic activity which could severely threaten the population. Only threats concerning this species have been indicated for isolated population groups or the subspecies <i>T. h. grahamensis</i> , which is well protected in its habitat (Pinaleño Mountains of Graham County, southeastern Arizona). (Sanderson & Koprowski 2009)	Most of the population of <i>T. douglasii</i> is protected by several different National Parks in northwestern America (e.g. Yellowstone, Yosemite, Greater Lake, Mount Rainier, Olympic National Park etc.). Therefore, no major threats are considered to exist for the population of this species.	Threats to the population of <i>T. mearnsi</i> , which could negatively interfere with the already decreasing population, are timber removal, grazing, wildfire, and competition with introduced <i>Sciurus carolinensis</i> (since the 1940s). This species' biggest threat is loss of biological diversity due to anthropogenic activities such as deforestation and restricted habitat (Ramos-Lara 2012), additionally to habitat loss.
Ecological conservation focus	Suggested conservation action: conserve as many old-growth coniferous forests as possible since <i>Tamiasciurus</i> squirrels are indicators for longevity and great health of the forest. Presence of these squirrels indicates the forest's natural climax and an intact ecosystem.	Suggested conservation action: conserve as many old-growth coniferous forests as possible since <i>Tamiasciurus</i> squirrels are indicators for longevity and great health of the forest. Presence of these squirrels indicates the forest's natural climax and an intact ecosystem.	Maintaining the threatened endemic species population size (achievable with selected tree cutting and by providing their natural habitat with the characteristics for their survival (specific pines and conifers for their nutrition and nesting habits)) and keeping the population as strong as possible against the habitat fight with the newly introduced eastern gray squirrels (<i>Sciurus carolinensis</i>) by not favoring their spreading.
Tree squirrel relation	Mainly observed on the ground with nesting and nutrition storage in middens on the ground. Mainly detected in the trees when hiding from predators. Therefore, not correctly described in taxonomy (as tree squirrel), rather semi tree-ground squirrel.	Mainly observed in tree canopies and on branches, nesting and hiding occur in trees as well, therefore is the taxonomic description as tree squirrel more appropriate.	Mainly observed on the ground with nesting and nutrition storage in middens on the ground. Mainly detected in the trees when hiding from predators. Therefore, not correctly described in taxonomy (as tree squirrel), rather semi tree-ground squirrel.

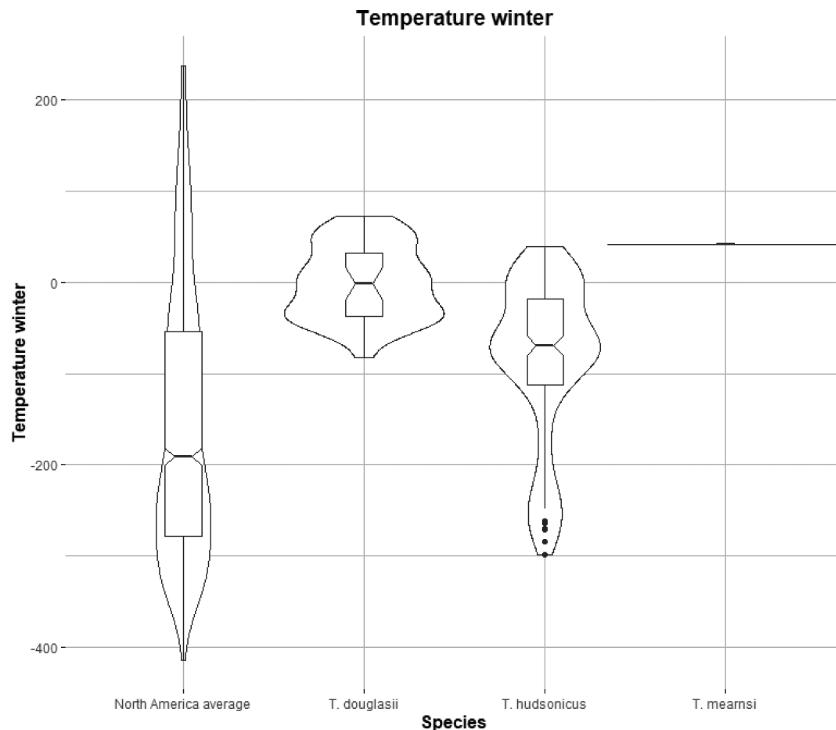


Figure 4. Ecological niches with the focus on the winter temperature.

indicates where the optimal ecologic niche for each species is geographically located and distributed.

4.3 Boxplots for climate niche comparison

The most significant differences we identified between the climate niches were for the winter temperatures (October–March), which influence the hibernation method of the squirrels. This significant finding allows for the first time to offer a hypothesis, supported by statistical data, why *T. mearnsi* does not create middens.

4.3.1 Ecological niches of studied squirrels based on mean winter temperature. The mean winter (October–March) temperature for *T. mearnsi* is above 0°C, resulting in liquid precipitation and virtually no snow or ice coverage during the cold periods, thus, food is available year-round. We think this climatic difference may explain the subsequent difference in behavior from the *T. mearnsi* compared to its congeners (where mean winter temperature is below 0°C) (Figure 4).

4.3.2 Ecological niches of *Tamiasciurus* squirrels based on the mean summer temperature. Overall, all three species inhabit ecologic niches which do not differ drastically from each other with respect to the North American summer (April–September) temperature

average (Figure 5). However, for *T. mearnsi*, altitude must be underlined since the mean altitude of *T. mearnsi* is around 2,400 asl. (Figure 8), which is 95% greater than the other species' altitudinal distribution and, as commonly known, temperatures decline as inversely with altitude.

4.3.3 Ecological niche properties with the focus on the winter precipitation. The two closely related species *T. douglasii* and *T. mearnsi* show a significant difference in the amount and type of winter precipitation (Figure 6). This is a significant habitat difference which supports the suggested reclassification of *T. mearnsi*. The shown aridity for the habitat of *T. mearnsi* is enforced not only by the low precipitation but also by the form of precipitation. Throughout the year temperatures stay above 0°C (Figure 4) and water is rapidly lost into the ground in *T. mearnsi*'s habitat. This water loss is additionally enforced by the soil type of the habitat region of *T. mearnsi*, as squirrels rely on the ground conditions, fungi, insects, and the associated soil community (Loeb et al. 2000). According to a World Soil Information map (Batjes 2012; GIS data not publicly provided), the habitat of *T. mearnsi* is characterized by mainly Leptosol soil type, mixed with Arenosol. Arenosol mainly consists of sand with a coarser texture, mixed with Leptosol which possesses a very shallow texture with mostly rocky components above hard rock (IUSS 2015). This soil combination strongly facilitates the loss

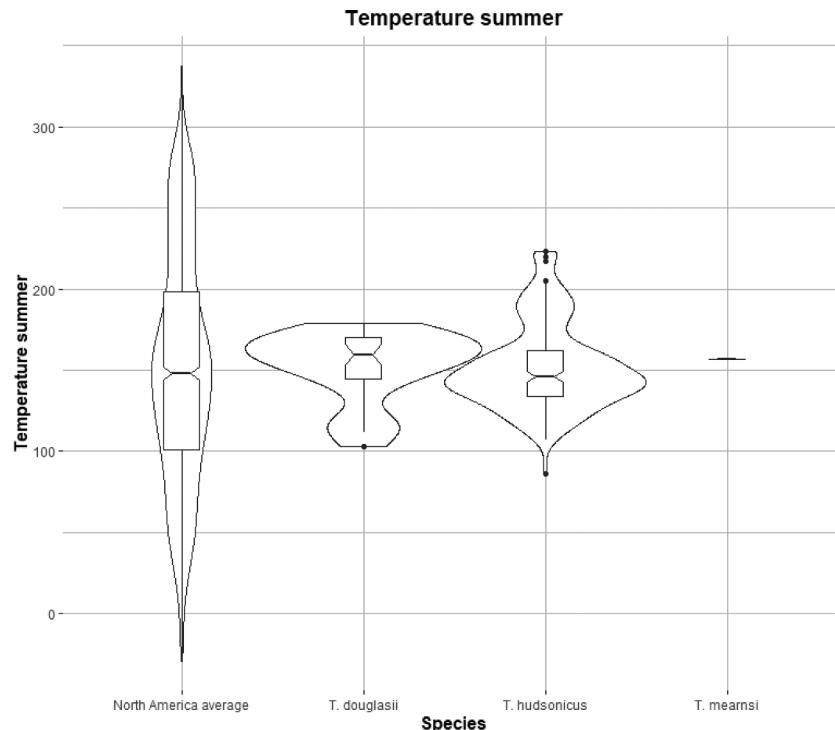


Figure 5. Ecological niches with the focus on the summer temperature.

of the water into the ground and underlines the extremely xeric conditions and the low water availability of *T. mearnsi*'s climate niche.

4.3.4 Ecological niche identification for each studied squirrel, with a focus on the summer precipitation. Important to outline here is the summer precipitation (April -September) for *T. mearnsi* as it is not significantly different than that of the other two species (*T. hudsonicus* and *T. douglasii*) (Figure 7). However, temperatures are high which facilitates water loss in air and soil (see Figure 5).

4.3.5 Ecological niches of studied squirrels based on altitude. The mean altitude for *T. mearnsi* is significantly greater than the other species' averages, underlining their unique habitat niche (average 2,400 above sea level) (Figure 8).

4.3.6 Summary of the Ecological Niche Analysis. As taken from the boxplot in Figure 5, outlining our most significant finding, the winter temperature difference between the three species appears to be a likely driver of the observed difference in hibernation methods. The average winter temperature is above 0°C, resulting in liquid precipitation and no snow or ice coverage, thus food is available year-round, and hibernation (in the form of creating middens) is not necessarily required. This climatic difference likely explains the difference in expressed behavior of *T. mearnsi*

compared to its congeners (where mean winter temperature is below 0°C and food would be buried under snow and ice during the winter season). Other habitat characteristics (xeric, mild, high in altitude) from *T. mearnsi* are also likely causes of their evolutionary behavior development. Figure 9 summarizes all presented boxplots for a better overview.

We conclude from our data that an epigenetic approach to species' taxonomy differed from a solely genetic one, providing a more robust analysis. Our approach uniquely incorporates an identification of the climate niche in which each species lives, supporting a reclassification for and within *Tamiasciurus*. The genus *Tamiasciurus*' description should be updated from tree squirrel to semi tree-ground squirrel. *T. mearnsi* should be reclassified within the genus *Tamiasciurus*, by proposing a new subgenus (*pseudotamias*) to improve conservation management decisions. By stating that this particular species does not participate in hoarding behavior, conservationists know not to make decisions targeted at squirrels that do hoard.

5. Discussion

5.1 Major findings of this study

The main focus of this study is to compile the best available data and to offer solutions that address the

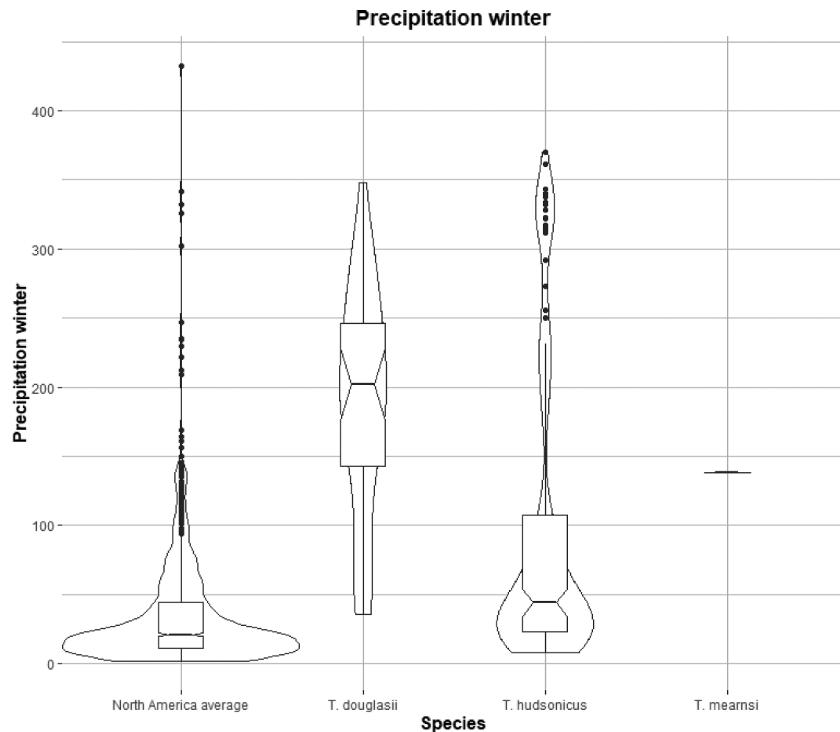


Figure 6. Ecological niches with the focus on the winter precipitation.

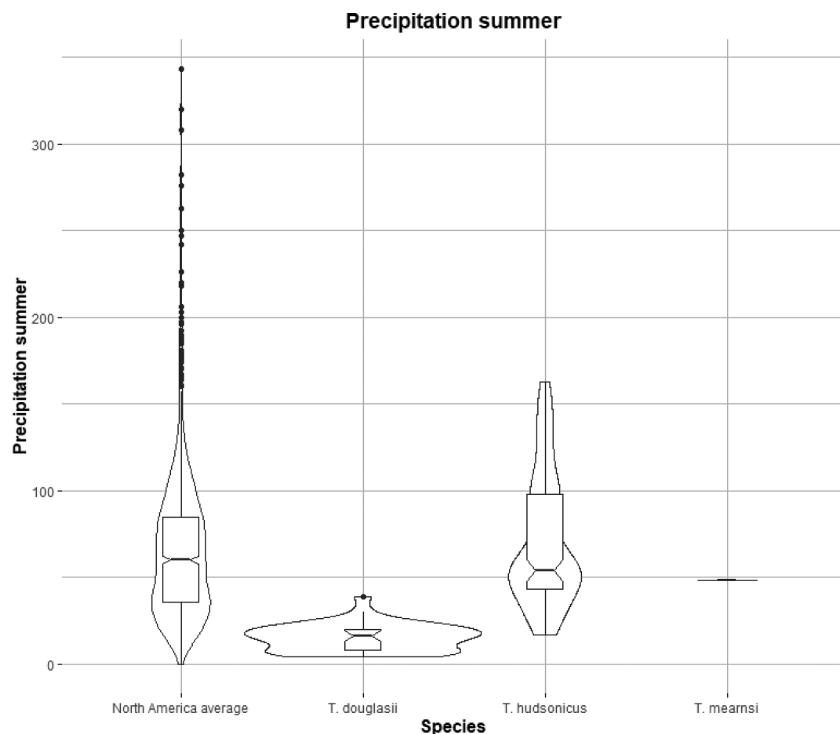


Figure 7. Ecological niches with the focus on the summer precipitation.

pervasive taxonomic confusion affecting conservation management of the animal kingdom. Here we focus on an ubiquitous and relatively simple species group,

Tamiasciurus squirrels, in order to show that this problem is pervasive within human-animal study and conservation management, even in wealthy nations

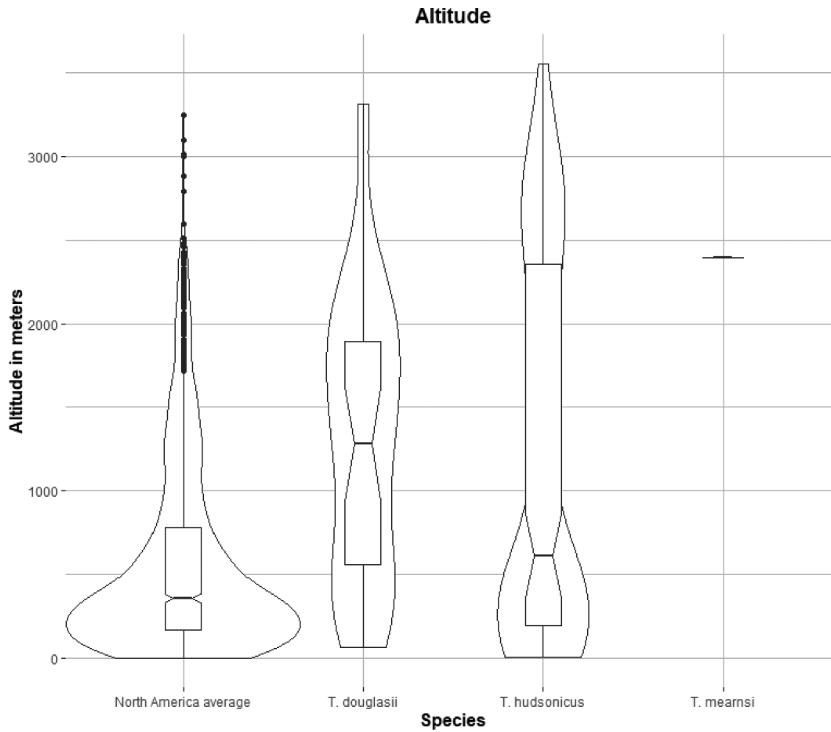
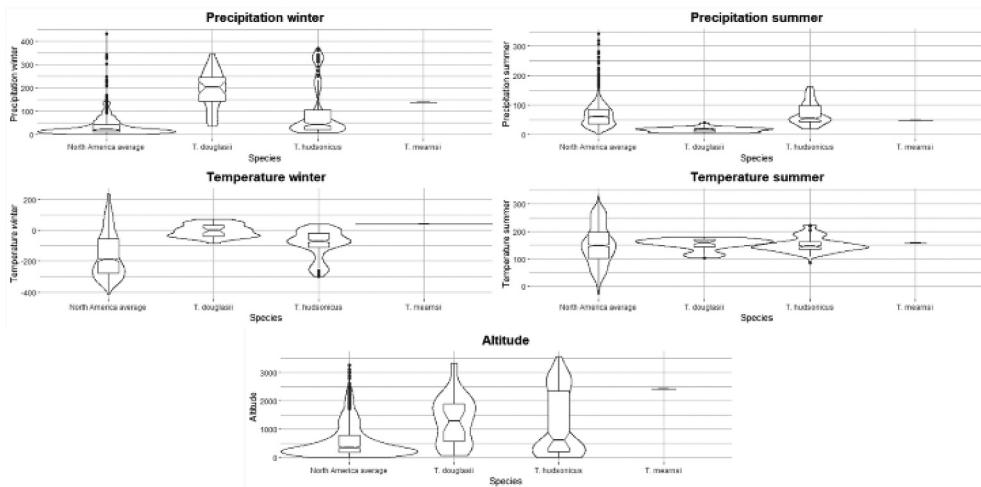


Figure 8. Ecological niches with the focus on the altitude.

Figure 9. Summary of the ecological niche descriptions of the genus *Tamiasciurus*.

(see details in Section 5.8). In response, we present for the first-time a more holistic, balanced, and less biased assessment method using publicly available data, aiming for solutions to misclassifications. Using mainly an epigenetic approach and synergetic analysis, we focused here on an improved perspective, correction, and conservation management success for the genus. This method helps to avoid conservation management failures resulting in mislabeling, wrong

perceptions, mismanagement, and possible extinction of species. Many aspects of our work are not particularly new but have never been summarized as done here. For instance, our literature review adds to findings from the climate niche identification. Due to the evolution of the species' in different ecologic and climatic niches, their behavior changed in order to adapt; likely that increases their fitness. The differentiation of the squirrel's behavior is a great example

that phylogenetic plasticity of individual animals could lead to behavioral evolution with the well-known goal of improving fitness. Creating middens requires a lot of energy (Larsen & Boutin 1994). It usually involves hibernation (food caches required). Middens also require good handling of predators for survival on the ground. Avoiding this specific behavior, originally evolved in regions with great snow coverages and cold winters, *T. mearnsi* can use the time and energy normally required for midden construction and maintenance differently. This time is spent on additional food gathering or other resource acquisition, which creates a benefit for this species in their specific climate niche compared to its congeners. It leads to higher survival rates and therefore to increased fitness.

5.2 Differences among the distinctive climatic niches of the congeners

We found that climate niches with unique characteristics (temperature, precipitation, altitude, and soil) host species with different behaviors from the same genus. Most importantly, the presented figures indicate that the combination of different metrics describing a climate niche may cause species to respond differently to their environment. Therefore, species adjust their behavior to maximize their fitness (summarized in Table VII).

5.3 Assumed species-specific evolution within their respective climate/habitat niche

Between *T. hudsonicus* and *T. douglasii*, there is little interaction. We found that only a small area of their distribution overlaps. *T. mearnsi* has been completely isolated for more than 12,000 years (Lindsay 1981). The occurrence of genetic hybrids is little known (Hope et al. 2016), but should deserve more attention in this context and our wider research. This topic has not been broadly discussed in our work, and it requires future research efforts.

Clearly, all of the mentioned species established in different climate niches, which in the case of *T. mearnsi* may have led to its distinctive behavior compared to its congeners.

5.4 Similar cases on mammals with taxonomy conservation problems

For wider applicability, and as shown in Table I, what we found is not particularly unique and can be observed in many other species. *Tamiasciurus* is not the only case where taxonomic misclassifications

occur and await resolution for conservation gain. There are many other species, certainly small mammals, with similar problems. Some examples are compiled in Tables I and VIII. They represent research and conservation needs, where future investigations are highly requested and necessary.

The problems of taxonomic misclassification, lack of data availability, squirrels as a relevant but under-studied mesopredators, the lack of conservation interest by wealthy nations, and more, demand all further discussion and research. The results of our case study on the *Tamiasciurus* genus have widespread applications in these areas and beyond, which we will briefly outline below.

5.5 General issue on the taxonomic structure and the inappropriate approach of subspecies

As shown in Tables I and VIII, the examining species are not the only ones with taxonomic issues, and many other genera, species and subspecies suffer similarly. The concept of understanding species correctly – including subspecies – sits at the core of many taxonomic misclassifications. Misclassification negatively affects wildlife conservation status and how humans understand, interact with, and manage species – the living world. Therefore, we appeal to the best practice, which is to always keep the greater intention of species conservation in mind (e.g. Naess & Drengson 2008; Silvy 2020). Taking the Snow Petrel as an example (as mentioned in Table I), conservation effort should focus on an entire species and its habitat, without subdividing the effort into the existing subspecies, for a higher conservation success. Talking about the concept of subspecies, in this study we want to underline the approach from Haig and Winker (2010), which highlights that for birds and mammals, including humans, subspecies are not scientifically and mutually accepted and therefore, such divisions and classifications should not be made. With few exceptions perhaps, e.g. Orcas (*Orcinus orca*) where the specific culture of subgroups (pods) facilitates the identification of conservation priorities (Hauser et al. 2007), special avoidance for the creation of a species or sub-species hierarchy has to be sought, where no species or “sub”-species should be placed over another (Wodak & Reisigl 1999).

5.6 Squirrel's as mesopredators and the effect of their marginalization on the ecosystem and subsequent conservation of their prey and ecological services

As summarized by Callahan (1993), several squirrel species function as active predators for small

Table VII. Comparison of the different climatic niches of the three squirrel species.

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Temperature distribution - natural habitat	Detected from Northern Alaska, southwards until Arizona, eastwards until the west coast of North America (e.g. Virginia, North and South Carolina). Species can be found in many north continental parts of America and has, therefore, also adapted to various habitat types with their macro/microclimatic deviations. Adaptations have led to the differentiation of subspecies for each macro climate type (Wei et al. 2015).	Detected from Canada (British Columbia), southwards until California, Washington, Oregon, Nevada, (United States). Most of their habitat is located in the pacific northwest with mean annual Temperature of 12°C (TaD) (INEGI 2010).	Only detected in xeric and hot conditions with habitat restricted to the forests and mountains of Sierra de San Pedro Martir in Baja California, Mexico. Natural habitat extremely restricted to local climate. The climate in Baja California has a mean annual temperature of 19.6 °C (INEGI, 2010).
Precipitation distribution - natural habitat	The species' adaptation to precipitation differences is similar to temperature deviations in different habitat types and can therefore strongly vary.	Likewise, the temperature, also the precipitation in the species' habitat is characterized by Pacific northwest climate. The annual mean precipitation equals 219.1 mm (TaD)	The species is highly restricted to its small habitat and therefore its precipitation. The climate in Baja California has a mean annual precipitation of 169.4 mm (INEGI 2010).
Altitude distribution - natural habitat	The highest detections reach up to 2,500 ft (762 m) in the Rocky Mountains - tending to remain lower (0–762 m) (Taylor et al. 1999; Steele 1998)	Since the Pacific northwest borders to the Pacific Ocean and includes the Coast - and Cascade Mountain Range, the distribution of <i>T. douglasii</i> is broadly distributed from 0 up to 3300 m asl (Pau 2004).	The species is solely detected between 2,100 m and 2,400 m asl (Ceballos & Oliva 2005). Baja California's mean altitude equals approximately 1555 m (INEGI 2010). <i>T. mearnsi</i> was pushed in the mountain regions of Baja California, following its natural distribution while escaping from human interactions in the nature (INEGI, 2010).
Climate relationships	<i>T. hudsonicus'</i> habitat shows differences in its climatic characteristics compared to <i>T. douglasii</i> , however, the major proprieties remain similar (as freezing winters with snow coverage, as well as the presence of a snow melting period, delivering together a higher water availability but constrains the squirrel to create middens and stick with the typical nesting behavior established from the genus <i>Tamiasciurus</i>).	<i>T. douglasii'</i> habitat shows differences in its climatic characteristics compared to <i>T. hudsonicus</i> , however, the major proprieties remain similar (as freezing winters with snow coverage, as well as the presence of a snow melting period, delivering together a higher water availability but constrains the squirrel to create middens and stick with the typical nesting behavior established from the genus <i>Tamiasciurus</i>).	Compared to the other species, <i>T. mearnsi</i> occupies a habitat with barely freezing winters, precipitation remains in its liquid state even in winter at an altitude of over 2400 m asl (Figure 8). This confirms the xeric and hot conditions of its habitat, allowing the species to avoid spending efforts in creating middens (since food is year-round available and not covered by snow or ice like for its congeners).

Table VIII. Cases in the small mammal family where taxonomy and classification disputes exist and affect conservation efficiency, similar to the *Tamiasciurus* genus.

Order/family/ genus/species	Short order/family/genus/species description	Description of the misclassification/taxonomic chaos
Small mammals in general	Mammals under a certain weight (varying between 1–5 kg) are often described as small mammals. Some main orders are Rodentia, Soricomorpha and Erinaceomorpha (Bertolino et al. 2015)	Due to still heavily debated, obsolete and outdated taxonomy linked to several species in the mentioned orders is often unbeneficial for their conservation when species get e.g. split. It is often pretended that the conservation issues are thereby resolved, when they are in fact worsened. This trend is also notable in the classification of their conservation status (Bertolino et al. 2015).
<i>Rodentia</i> (entire order)	About 40% of all mammal species are rodents (2,277 species), this impressive number can lead easily to confusion in the classification.	Underlined by Wood (1955), the Rodentia's taxonomy is misleading and obsolete. Several attempts have been made to update and simplify this confessional classification. However, without much success, and entire families, genera and species remain misclassified. The order's size is apparently too great for a single person to obtain enough knowledge of all containing species. Consequently, all the species within the order <i>Rodentia</i> are affected by confusing and obsolete classifications with the immediate need of a taxonomic revolution for these small mammals.
Ground Squirrels (<i>Marmotini</i>)	The ground squirrels are members of the rodent squirrel family (Sciuridae), which generally live on or in the ground, rather than trees.	Obsolete taxonomy and disagreement between taxonomists have created confusion and misclassifications within this family and its species for centuries already (Kryštufek & Vohralík 2013).
Prairie Dogs (<i>Cynomys</i>)	They are herbivorous rodents native to the grasslands of North America and are part of the Ground squirrels.	Unreasoned subspecies classification by using only a genetic approach or only a morphologic one instead of combining both approaches, creating taxonomic confusion and can be hampered for their study and conservation (Sackett et al. 2014).
Shrews (<i>Soricidae</i>)	Its external appearance is similar to the one of long-nosed mice, however, a shrew is not a rodent, as mice are. It is, in fact, a much closer relative of hedgehogs and moles. Shrews are distributed almost worldwide.	Different subspecies are linked to several different species and appear multiple times under different species (Vogel et al. 1986, Bertolino et al. 2015).
Alaska tiny shrew (<i>Sorex</i> <i>yukonicus</i>)	This species is endemic to Alaska (Cassola 2017), however not much is known about it.	This species was originally described as Eurasian least shrew (<i>S. minutissimus</i>), however was then declared as new species in 1997 (Dokuchaev 1997). However, until this day this new speciation is not commonly accepted and many disagreements rooting to this recent taxonomy update.
Tenrec/Tailless tenrec (<i>Tenrec</i> <i>ecaudatus</i>)	Tenrecs are widely diverse; as a result of convergent evolution, some resemble hedgehogs, shrews, opossums or mice (Olson 2013). They occupy aquatic, arboreal, terrestrial and fossorial environments, endemic in Madagascar.	Within the endemic family Tenrecidae, there is uncertainty over the taxonomy of the largest genus, <i>Microgale</i> . The number of species recognized in this genus ranges from 10 to 21 depending on the source (Stephenson 1995).

vertebrae (e.g. songbirds, hares, chipmunks, lizards, mice, rats, turkeys, snakes, crabs, frogs, salamanders and conspecifics (squirrels)). *T. douglasii* is known for its predation of Ground squirrels (*Marmotini*) (Roest 1951), and *T. hudsonicus* is well known for its predation of chipmunks, other tree squirrels, cottontail (*Sylvilagus*), snowshoe hare (*Lepus americanus*), mourning dove (*Zenaida macroura*) and several other birds (O-Donoghue 1991; Hatt 1929; Seton 1929; Hamilton 1934; Nero 1987; Taylor 1988). These well-known predator-prey relationships occur around the globe for many different

squirrel species (Thorington et al. 2012), and are a valuable ecological service. Regardless of the squirrel's influence in the larger ecosystem (especially to songbirds and other birds (Callahan 1993), there is little management of hunting or habitat loss for economic development, and there is very low conservation budgeting. A lack of regulations and management result in unknown current population sizes (Cassola 2016a, 2016b), and therefore unknown predation rates and mortality estimates for squirrels and the species with which they interact. All the while the conservation status of squirrels is stated

as “stable” by the International Union for Conservation of Nature Red List for *T. hudsonicus* and *T. douglasii* (IUCN Red list (Cassola 2016a, 2016b)), ignoring the many regulatory and management issues surrounding “squirrels” and other “stable” animal populations. Such assessments cannot be defended with real data (Silvy 2020). Additionally, the context of infanticide should not be left out, especially as a major contributor to the ecology of fear (Michener 1982). Conclusively, increased management efforts for squirrels will result in better knowledge about their soil ecosystem, interactions with fungi, predator-prey relationships with vertebrates such as songbirds, and wider ecosystem services, resulting in increased conservation success.

5.7 Data availability, lack of transparent data, the importance of open access data and metadata

Two of the most common scientific values are transparency and replicability (Aguinis & Solarino 2019). Many relevant data for squirrels are absent, such as harvest data, poaching information, population sizes and forest inventory data. The importance of this topic is emphasized by the lack of available data for our discussion of soil composition and its influence on squirrel’s behavior. The essential habitat data set from the referred source (WRB) and range distribution maps from “Squirrels of the World” (Thorington et al. 2012) could not be traced down and could not be replicated for our purposes. Therefore, to comply with the most modern scientific standards,

we strongly encourage an open access data sharing mindset from any modern publication, especially for species conservation questions. This certainly must apply to squirrels.

5.8 Resolving Management Absurdities: The case of the Gross Domestic Product (GDP) of the North American continent countries in relationship with wildlife management and marginalized environmental issues

Squirrels happen to live in some of the richest nations of the world. The national economy of those nations is pushed for consistent growth (see Figure 10). Man-made climate change is directly linked to the industrialization and economic growth of a few major actors and nations (Newell & Paterson 2010), causing biodiversity loss and population declines for marginalized species (Johnson et al. 2017). Marginalization is a common side effect of the modern economy for small animals such as squirrels or birds (Czech & Daly 2004). Hereby, we want to draw attention to all small wildlife and recommend the approach to economy outlined at www.steadystate.org.

Figure 10 clearly illustrates that the nations of the North American continent gained increased wealth in the last 50–60 years. These nations, especially the United States and Canada, are part of the wealthiest nations in the world, with Mexico featuring some of the wealthiest individuals in the world. However, these nations do not invest proportionately in their natural resources when it comes to wildlife conservation (shown in the previous hunting section).

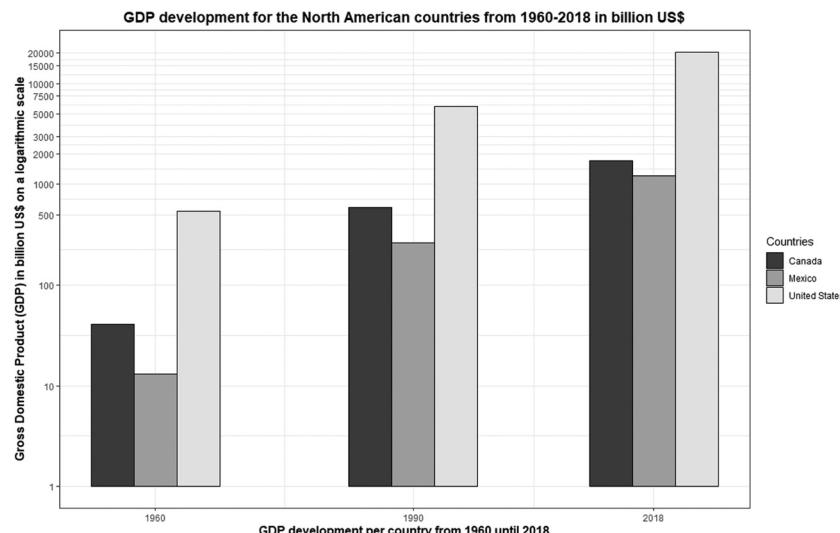


Figure 10. GDP development for the North American continents from 1960–2018 in billion US\$.

These nations have trillions of US\$, however only few hundred million US\$ are assigned to wildlife conservation, and just a few hundred thousand US \$ (less than 0.00001% of the US GDP) are assigned to small game species including squirrels, if they are even mentioned in governmental reports, which is rare (see Section 2.2.1). Consequently, we want to advocate for higher transparency in governmental reports where budget assignments are listed. Additionally, we appeal for a re-consideration of budget assignments to reduce the marginalization of small mammals and to guarantee higher conservation success.

All major discrepancies addressed in this study have been summarized in Table IX.

5.9 Suggested way forward

Our findings warrant a change. For improvement, we propose an update of the genus description *Tamiasciurus* to change it from tree squirrel to semi tree-ground squirrel. This update is mainly based on their time management/budget which depicts the species spending more than 65–70% of their observed time on the ground (Sanderson & Koprowski 2009). In addition, we propose to move *T. mearnsi* into the

Table IX. Summary of all major discrepancies addressed in this study.

Attributes	<i>Tamiasciurus hudsonicus</i>	<i>Tamiasciurus douglasii</i>	<i>Tamiasciurus mearnsi</i>
Unknown population size	Population estimates are unknown (Cassola 2016a)		Population estimates are unknown, even though the species is endangered (De Grammont & Cuarón 2018)
Habitat loss	No major threats are known to threaten the species' existence. Subspecies can be locally endangered due to anthropological influences (Sanderson & Koprowski 2009).	Subgroups are assumed to be locally threatened by deforestation and habitat fragmentation (Cassola 2016b).	Species' habitat is estimated not to exceed 266 miles ² (689 km ²) (De Grammont & Cuarón 2018), with major anthropological threats such as deforestation and restricted habitat (Ramos-Lara 2012).
Target practices and poaching	Extensively practiced, as shown here: www.facebook.com/extremesquirrelhunting/ www.youtube.com/watch?v=zTiv3xuj7Io		Practicing activities as shown for the congeners, this species would be shortly extinct.
IUCN Red List statements	Listed as stable species' population, even though no population estimates are existing whatsoever (Cassola 2016a)		Listed as endangered, with declining population trend and is strongly restricted regarding its habitat, still not fully protected in the wild (De Grammont & Cuarón 2018).
GDP comparison with wildlife conservation budget	These species occur predominately in the United States (GDP of 20.5 trillion US\$, 2018 (Figure 7)), where only 0.09% (18.870 billion US\$) are assigned to wildlife (Smith 2014) (estimated percentage lower in 2020). Taking California as example (both species occur in this state), their state GDP (3.2 trillion US\$ (2019), 15.2% of the U.S. GDP) only include 195 million US\$ (0.006%) for all wildlife conservation/management actions, no details for squirrels available (www.nrm.dfg.ca.gov/documents/ContextDocs.aspx?cat=WCB).		This species only occurs in a small area in Baja California (Mexico), therefore no other nations influences the wildlife conservation actions. Mexico accounts with 1,2 trillion US\$ (2018) to the wealthiest nations worldwide, however, assigned budget plans are not publicly available whatsoever and have not been detected online.
Marginalization of small mammals and opacity form governments	This previously presented data is only available for all wildlife conservation (including big game, small game, fisheries etc.), no subdivisions are publicly available. If the sum of all spending only accounts for 0.006% of the GDP (in California), it can only be imagined how utterly low the assigned budget for wildlife conservation/management actions is for small game (squirrels).		The opacity from the nation (Mexico), this squirrel species is endemic in, underlines the urgent need for governmental entities to be more transparent, with the effect that the public sees the urgent need to assign more budget for wildlife management to finally reach higher conservation success, to avoid the extinction of this species.
Extinction threats	These species are broadly considered as widely distributed, in high densities (even though, no actual data is available to support this).		This species requires urgently higher conservation effort since its population numbers are assumed to be small and continuously shrinking, as well as their already minuscule habitat.

newly proposed subgenus “*pseudotamias*” (translated: non-hoarding squirrel), which is urgently warranted in order to guarantee taxonomic correctness for public stakeholders. Taxonomy as a field of study is rather complex and classifications remain widely disagreed upon and unclear. Often chaotically dominated by just a few players, institutions, and mindsets, this system leaves out the wider public. It is not sustainable, hardly meaningful, and certainly not scientific or democratic. This can be resolved by a more holistic classification system, including all species-/genera-interfering characteristics rather than only single ones (morphological appearance, genetical relations etc.). Additionally, increased budget assignments for small mammals, especially squirrels, can have a major impact on their conservation success. Higher law enforcement for hunting regulations can additionally strongly contribute to science-based management for these squirrels.

5.10 Wider perspective of the current situation

As practiced, taxonomy is continuously running deeper into a global terminological and conservation crisis, – man-made – climate change and pandemics being among them. This can have severe impacts on biological and ecological conservation, institutions, the profession and its perception and society itself. The reality of “modernity” shows us no other (Alexander 2013), and as we presented here some of those aspects using *Tamiasciurus* squirrels. A higher scientific effort, a different approach and mindset – a different global framework – have to be investigated and achieved. This is required to erase and improve these incorrect classifications such as the present case of the *Tamiasciurus* genus and the *Tamiasciurus mearnsi*. We perceive squirrel management as a small and easy item to be fixable though, while others might be more complex.

Eventually, it comes down to how humans – the Anthropocene – relate to other species and life (e.g. see Regmi & Huettmann 2020 for wilderness area examples), and how it relates and interacts with them for wider well-being of the universe. There is a direct correlation between rapid economic growth and the direct impact on climate change and biodiversity loss (Rosales 2008). Chapin et al. (2011) showed an example of required earth stewardship and science for good action to sustain the human-earth system. Here we present some uncomplicated solutions easy to implement.

6. Conclusion

Based on synthesizing the taxonomic conservation status of wildlife -namely squirrels-, we conclude here that

the *Tamiasciurus* description is to be updated to (semi ground-tree squirrel). Because of their unique behavior, we also conclude that a reclassification of Mearns’s Squirrel (*Tamiasciurus mearnsi*) is needed by creating a new subgenus “*pseudotamias*” for this species. Also, a wider structural change is needed in the approach of how taxonomy, research and conservation management are done for a more sustainable human-nature interaction.

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Metadata availability

All the metadata and codes used to create the Figures within this study are freely accessible and can be obtained on request from MS.

Supplementary material

Supplemental data for this article can be accessed [here](#).

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Appendix A.

1. Raw USGS data set of the squirrel occurrence points from the genus *Tamiasciurus* across the North American continent ([10.1016/j.ympev.2016.04.014](https://doi.org/10.1016/j.ympev.2016.04.014)) (“RawUSGS_Squirrel_occurrence_data”)
2. Shapefile of the squirrel occurrence points used for the mappings in GIS. (“mmc_FH3.shp”)
3. R code for the creation of the violin boxplots to visualize the different climate niches (“R_violin_boxplots_final1.R”)
4. GIS layers (Climate, country borders, and additional files to support the mentioned ones (e.g. for the shapefile))00
5. Bird feeder location in North America from 2019 (“Birdfeeder_locations_2019.csv”)
6. *Tamiasciurus hudsonicus fremonti* climate niche boxplots (“*Tamiasciurus hudsonicus fremonti* violin climate boxplots.jpg”)