Global hotspots and knowledge gaps for tree and flying squirrels

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Tree and flying squirrels are important components of forested ecosystems, and are advocated as indicators of forest health. In this global assessment of the distribution, endangerment and scientific knowledge of squirrels, we reveal trends that warrant urgent attention. The tropics, particularly the forests of south and southeast Asia, are hotspots of squirrel diversity; however, this region generates the fewest scientific publications on squirrels. Additionally, the most endangered squirrels occur in tropical countries with high deforestation rates, and flying squirrels are more at risk than tree squirrels. Given the combination of high diversity, extinction risk and lack of knowledge of sciurids in the tropics, we recommend increased effort towards understanding their occurrence and biology in the imperiled tropical forests.

Keywords: Biological diversity, ecosystem services, forest loss, indicator species, species richness, Sciuridae.

CONSERVATION of biodiversity is a major goal of ecologists as significant declines are noted for most taxa[1]. Forested ecosystems have undergone excessive levels of fragmentation[2,3] (0.2% per annum worldwide[4]) largely due to anthropogenic activities and the consequences are varied[5–10]. Habitat loss and fragmentation result in loss of genetic variation[11,12] and biodiversity[13,14] and demographic impacts include changes in density, home range, reproductive performance and survivorship[10].

The mammalian rodent family Sciuridae (squirrels) is a speciose lineage with 278 species in 51 genera[15]. Ecologically, the Sciuridae consists of ground-dwelling species, arboreal-dwelling species and flying squirrels. The flying squirrels and tree squirrels are critically dependent on mature forests that provide tree tissues and seeds for food, cavities and canopies for nest sites, and stems and canopies for launch sites[16]. They are variously adapted for arboreal life, and their dependence on forests has resulted in numerous co-evolutionary relationships with forest plants[17]. As a result, arboreal squirrels are believed to be excellent indicators of forest health[18–22].

In view of the obligatory relationship of squirrels to the rapidly vanishing forested ecosystems the world over, we assess global distribution, conservation status and the state of scientific knowledge for this key group.

Materials and methods

Data on geographic distribution of squirrels were gleaned from recent assessments of mammalian phylogenies[15,23]. Ground squirrels of the tribes Xerini and Marmotini in the subfamily Xerinae were excluded due to terrestrial and fossorial habits often in non-forested ecosystems. Species with a significant arboreal component to daily existence were included: all members of the subfamilies Ratufinae (giant tree squirrels of southeast Asia), Sciurillinae (neotropical pygmy squirrels), Sciurinae (tree and flying squirrels of Eurasia, North and South America), Callosciurinae (tree squirrels of southeast Asia) and the tribe Protoxerini (palm, giant and sun squirrels of Africa) of the subfamily Xerinae. Emphasis was placed on extant diversity – introduced species were included in species richness tallies and recently extinct species were excluded. ‘Flying’ squirrels refer to volant squirrels of the tribe Pteromyini while other arboreal squirrels are referred to as ‘tree’ squirrels.

We surveyed the literature to assess global state of knowledge of tree and flying squirrel biology using two commonly selected search engines[24], Zoological Record (Thomson Scientific, Philadelphia, USA) and Science Citation Index’s Web of Science (Thomson Scientific, Philadelphia, USA). The scientific name of each species was entered into keyword and topic searches that include literature published through 15 January 2006.

Data on conservation status of each species were obtained from the IUCN Red List (www.iucnredlist.org, accessed 23–27 January 2006) and Wilson and Reeder[15]. IUCN categories of endangerment were coded to reflect an increasing level of endangerment (low concern = 1, near threatened = 2, vulnerable = 3, endangered = 4, critically endangered = 5). Data on area (ArcGIS 9.0, ESRI, 2005), centroid and population of nations (calculated with Xtools Pro, ArcGIS 9.0, ESRI, 2005) and continental anthropogenic forest fragmentation[2] were used to assess the relationship of area and latitude to species richness and publications on each species. For anthropogenic deforestation, we entered weighted scores for forest types composing ≥10% of each continent[2]. Annual deforestation

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rates from 1990 to 2000, absolute forest cover and percentage of forest cover were included [4].

Data were transformed to meet assumptions of normality for parametric analyses (correlation and simple, multiple and stepwise linear regression analyses) or non-parametric (Mann–Whitney *U* test, Kendall's and Spearman's rank correlation) analyses.

Results

Where are the hotspots of global arboreal squirrel diversity?

One hundred and thirty-six of 180 arboreal species are considered non-volant tree squirrels, whereas 44 species are flying squirrels. A latitudinal cline exists among all squirrels with diversity greatest in tropical latitudes (Figure 1; $r = -0.38$, $df = 126$, $P < 0.001$) for both tree ($r = -0.5$, $df = 126$, $P < 0.001$) and flying ($r = -0.47$, $df = 30$, $P < 0.007$) squirrels. Area of a nation marginally influences species richness for tree squirrels ($r = 0.159$, $df = 126$, $P = 0.078$) but not flying squirrels ($r = 0.056$, $df = 30$, $P = 0.760$). Endemism in tree ($r = -0.21$, $df = 128$, $P = 0.014$) and flying squirrels ($r = -0.35$, $df = 32$, $P = 0.042$) also exhibits a latitudinal cline. Diversity of arboreal squirrels in a country was predicted by three variables entering ($\alpha = 0.15$) a stepwise regression: absolute value of latitude ($P < 0.0001$), elevation range in meters ($P < 0.0001$) and percentage of forested land ($P = 0.084$). The model was of predictive value ($F_{3,127} = 15.07$, $P < 0.0001$, $r^2 = 27.2\%$): Total species richness = 3.5603–0.1295 absolute value of latitude +0.0012 elevation range +0.0462 percentage of forested land. Equatorial countries with significant topographic relief and forest cover serve as global hotspots of diversity and endemism of tree and flying squirrels as evidenced in Asia, Africa, North and South America.

What is the state of knowledge of tree and flying squirrels?

Our search for the 180 arboreal squirrels yielded 2537 publications using Zoological Record and 1218 publications using Web of Science. On only one occasion (*Sciurus richmondi*) did Web of Science find more records, whereas Zoological Record yielded more publications for 106 species and similar numbers for 73 species ($\chi^2 = 103.37$, $df = 1$, $p < 0.001$). We only use results obtained through Zoological Record from here forward.

Surprisingly, the modal number of publications for tree and flying squirrels was 0 (Figure 2), and the number of publications did not differ between tree (mean = 14.92 ± 5.45 SE, median = 1) and flying (mean = 11.55 ± 4.38 SE, median = 2) squirrels ($U_{136,44} = 2705.5$, $P = 0.34$). These median values suggest a significant dearth of data for tree and flying squirrels. In fact, mean values are highly biased by positively skewed distributions that result from nine species with ≥50 publications. These nine species occur in the northernmost latitudes of Europe, Asia and North America, and include *Sciurus carolinensis* (*n* = 489 publications), *S. vulgaris* (*n* = 461), *Tamiasciurus hudsonicus* (*n* = 265), *S. niger* (*n* = 192), *Glaucomys sabrinus* (*n* = 141), *G. volans* (*n* = 124), *Callosciurus erythraeus* (*n* = 65), *Pteromys volans* (*n* = 60) and *S. aberti* (*n* = 60).

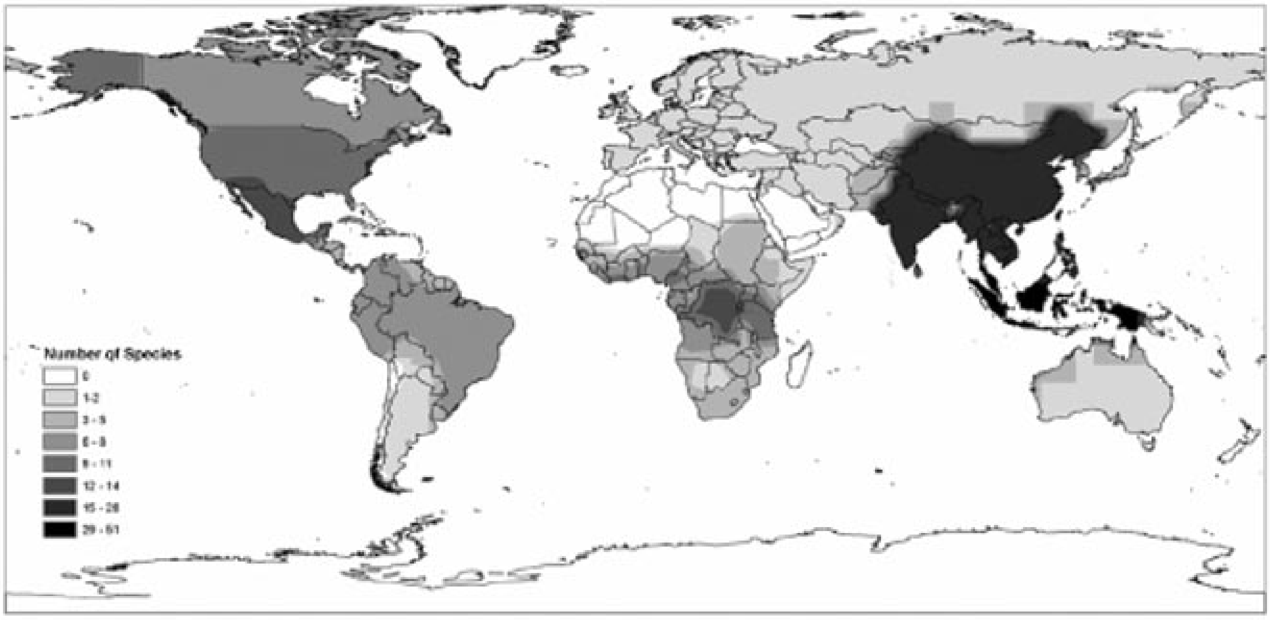

Figure 1. Interpolation of species richness for all arboreal squirrels in the family Sciuridae demonstrating latitudinal cline in diversity. Darkest colours correspond to areas of greatest squirrel diversity per nation.

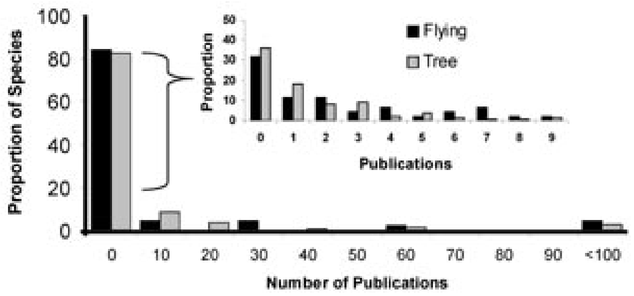

Figure 2. Frequency histogram of number of publications for species of tree and flying squirrels. The values on the abscissa refer to the lowest number of publications in a grouping by units of 10; 0, for example, is equivalent to 0–9 publications.

A reversed cline with latitude occurred relative to the cline observed for diversity ($r = 0.823$, $df = 126$, $P < 0.0001$) with publications more likely for species in higher latitudes for tree ($r = 0.864$, $df = 125$, $P = 0.0001$) and marginally so for flying ($r = 0.304$, $df = 30$, $P = 0.091$) squirrels (Figure 3). Clearly, we have much to learn about squirrels in tropical forests.

Conservation status of tree and flying squirrels

One hundred and twenty-nine (72.9%; 104 tree, 25 flying) of 176 squirrels were in the lowest risk category of the IUCN, whereas the remaining 47 (30 tree, 17 flying) species (27.1%) were of elevated extinction risk (Table 1). The majority of these species are endemics, with 52.9% of 17 flying (71.4% endemics of seven species designated as vulnerable, endangered and critically endangered) and 70.0% of 30 tree squirrels (75.0% endemics of 16 species designated as vulnerable, endangered, and critically endangered) range-restricted. At lower levels of taxonomy, such as for subspecies, levels of concern may be even greater than at the species-level. For instance, among the tree and flying squirrels of North America, 81.2% of species in the genera *Sciurus* (five of six species), *Tamiasciurus* (two of three species), and *Glaucomys* (two of two species) receive legal protection due to concerns about their long-term persistence in at least some portion of their range[21]. Overall, tree squirrels were less likely to be of conservation concern (mean = 1.37 ± 0.07 SE, median = 1) than flying squirrels (mean = 1.76 ± 0.18 SE, median = 1: $U_{134, 42} = 2296$, $P = 0.02$).

Our knowledge of species as indicated by the number of publications is negatively related to an increased risk of extinction for tree (Kendall's rank $r = -0.142$, $df = 134$, $P = 0.05$) but not flying squirrels (Kendall's rank $r = -0.043$, $df = 42$, $P > 0.74$). Highest levels of endangerment (vulnerable, endangered and critically endangered) tend to be the subject of fewer publications (mean = 2.96 ± 1.19 SE, median = 0) than low concern and near threatened species (mean = 15.07 ± 4.57 SE, median = 1: $U_{167,23} = 2318.5$, $P = 0.09$).

Not only is our knowledge of tree and flying squirrels, in particular within tropical forests, poor relative to their conservation status, but forested environments are rapidly disappearing. Annual deforestation rates (Spearman's rank $r_{126} = 0.53$, $P < 0.001$) and anthropogenic fragmentation ($r_{128} = 0.15$, $P < 0.08$) are highest in countries with the greatest number of flying and tree squirrels within the global hotspots. Average IUCN status for a species in each country was predicted by three variables that entered a stepwise regression: absolute value of latitude ($p < 0.0001$), area of a country ($P < 0.001$), and annual rate of deforestation ($P = 0.045$). The model was of significant predictive value ($F_{3,127} = 83.10$, $P < 0.0001$, $r^2 = 66.00\%$): Average IUCN status = 1.069 + 0.0178 absolute value of latitude $- 4.35 \times 10^{-8}$ country area in km^2 + 0.0372 annual deforestation rate. The entrance of latitude as the initial variable may be perplexing because it denotes a positive relationship between latitude and level of endangerment. This results because of the low species richness at high latitudes and the fact that the two widest ranging Palearctic squirrels (*S. vulgaris* and *P. volans*) are of elevated IUCN status and often the only two species present. The next two variables that entered indicate that small countries are more likely to have high levels of imperillment and high rates of deforestation.

Conclusions

The Sciuridae likely originated in the Northern Hemisphere, perhaps in the Nearctic[25] and spread to its current distribution[23]. The tropical forests of Asia, Africa, Central and South America are the current centres of tree and flying squirrel diversity and endemism. Species richness exceeds 50 in southeast Asia and is typically 6–10 species with substantial endemism in most tropical forests (Figure 1). Our analysis revealed that latitude, elevation gradient and amount of forested land accounted for significant amounts of variation in species richness; structural and topographic complexity may promote diversity. The values that can be assigned to the tree and flying squirrels are myriad. Whereas tree and flying squirrels can cause tree damage[26–28], depredate crops[29], damage property[30], and serve as disease vectors[31,32], their significance in forest ecosystems far outweighs potential costs. Squirrels perform considerable ecosystem services[33] such as seed planting and dispersal[34], pollination[35], influencing plant form and function[16,17], and fungal spore dispersal[36] and may serve as indicator species in some forest types[18–22]. Both tree and flying squirrels also form a significant prey base for a multitude of species in tropical[37,38,39] and temperate forests[40]. Squirrels are hunted for subsistence[41–43] and sport as well as trapped for pelts[44]. Additionally, squirrel by-products are collected for potential medicinal

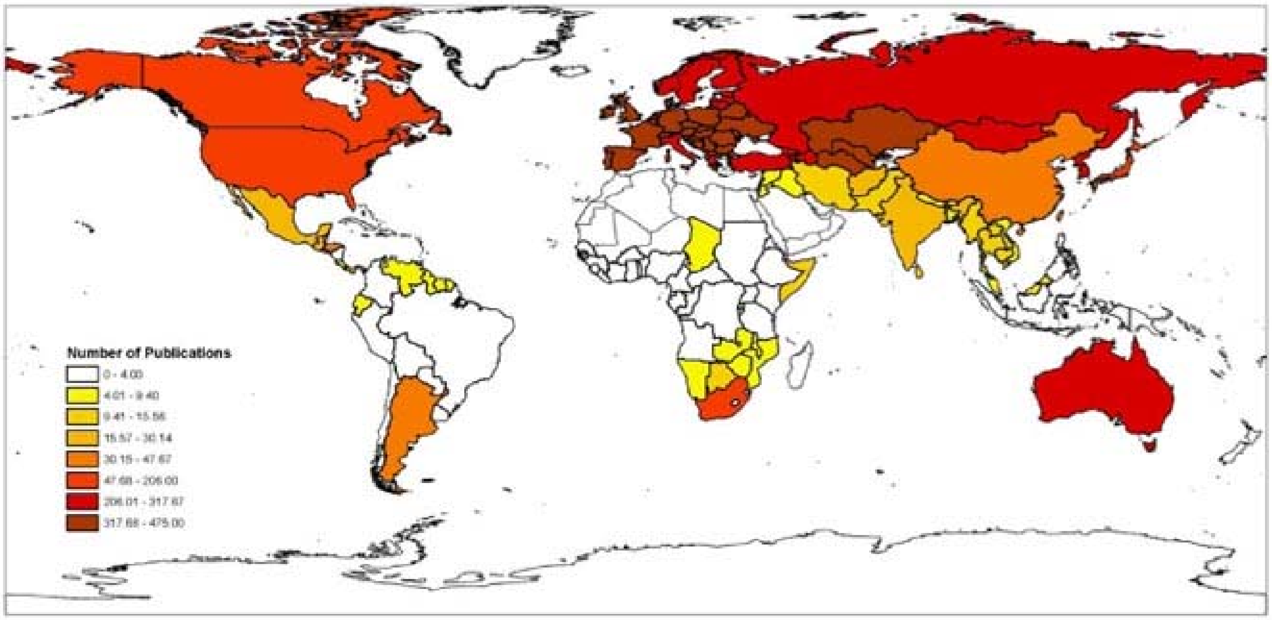

Figure 3. Mean number of publications per species of all arboreal squirrels in the family Sciuridae, demonstrating a reversed latitudinal cline. Darkest colours correspond to areas of greatest mean number of publications per species.

Table 1. Conservation status of tree and flying squirrels according to the IUCN categories

Conservation status	Tree squirrels (no. of species)	Flying squirrels (no. of species)	All arboreal squirrels (%)
Critically endangered	1	2	1.7
Endangered	1	4	2.8
Vulnerable	14	1	8.5
Near threatened	14	10	14.1
Least concern	104	25	72.9

value[45] and seed sources[46]. Tree squirrels may serve as models for human function, pathology[47] and disease[48], and as examples for environmental education[49]. In temperate countries, recreational observations also generated a lucrative industry (e.g. nest boxes, squirrel feeders and binoculars) with economic impact[50]. As a result, arboreal squirrels are integral members of forested ecosystems that perform important ecosystem services[27] and can have significant economic impacts.

Given the importance and numerous values ascribed to arboreal squirrels, the complete lack of scientific knowledge for so many species is disheartening. Perhaps most telling is the reversed latitudinal cline between arboreal species richness and frequency of publications, and despite the tropics function as epicentres of diversity, our knowledge of squirrels in these latitudes is limited. Most publications from the tropics pertain to distributional records, species descriptions and basic community surveys; there is a noticeable lack of intensive research that translates clearly to management and conservation actions. Flying squirrels are particularly understudied given their elevated risk of extinction. The application of management strategies to reverse trends in imperillment is compounded by the fact that flying squirrels are less researched. Flying squirrels, as well as other small cryptic and nocturnal mammals, are often forgotten in conservation and management plans, and the application of management strategies to reverse trends in imperillment is further impeded by lack of scientific information.

Eastern gray squirrels ($n = 489$), Eurasian red squirrels ($n = 461$) and red squirrels of North America ($n = 265$) tally more publications than the sum of nearly all tropical tree squirrels combined. The three most widely studied flying squirrels (*G. sabrinus*, $n = 141$, *G. volans*, $n = 124$, *P. volans*, $n = 60$) are also the three most northerly distributed species of the Pteromyini. As a result, much of what we know about arboreal squirrels originates with an extremely small subset of Holarctic tree and flying squirrels. The response of arboreal squirrels to anthropogenic disturbances is known to be species-specific[10], and the wisdom and appropriateness of the application of this knowledge towards conservation solutions for other species are not known. Numerous differences between tropical and temperate forest ecosystem functions also caution against direct application; nevertheless, results of temperate studies can generate testable hypotheses for lesser-studied species in the tropics. Our dearth of knowledge of these key indicators of forest health may be an extreme liability given the ecosystem services rendered by this diverse and widespread mammalian taxa, whose members may serve as harbingers of global climate change[23,51,52] and trends in forest health[18–22].

This pattern is even more alarming in light of current worldwide trends in deforestation and habitat fragmentation[4]. Much study is needed to fully assess the ecological relationships and functions of squirrels within forested environments. More effective inventory and monitoring techniques must be developed to assist with rapid assessments of tree and flying squirrel presence and population status. These techniques will address the lack of data on individual species, in addition to providing critical data on forest health for long-term monitoring efforts and instigate forestry and development practices that are sustainable and minimize impacts on native fauna. While community inventories and population monitoring programmes are needed for conservation, we believe that it is imperative to conduct studies that extend our knowledge through basic research. Efforts that investigate foraging behaviour, social and mating systems, and ecological interactions show promise to inform our conservation and management efforts and can be applied to understand the significance of counts and surveys. In this way, the wealth of studies on more temperate species can provide a foundation for hypothesis testing and comparative analyses.

Such strategies will be necessary to save the loss of tree and flying squirrels along with forests that are disappearing at a rate of 0.2% per annum worldwide[4]. Perhaps of greatest concern, forest loss rates are highest in the hotspots of arboreal squirrel diversity such as 1.0% in southern and southeast Asia, 0.4% in South America, 0.6% in Africa, and in countries with the greatest tree and flying squirrel diversity to include a 2.0% loss in Indonesia (51 species) and 0.7% in Malaysia (40 species) (regions of highest squirrel diversity worldwide), and a 0.4% loss in Mexico (14 species – greatest diversity in the New World). Development of local and worldwide strategies of conservation and management of these important forest dwellers is critical. Meetings such as the Fourth International Tree Squirrel Colloquium and First International Flying Squirrel Colloquium that bring researchers, conservationists and land managers together to focus on common problems and solutions are necessary[53]; however, efforts must be continued to use the wealth of expertise and sustain interactions that occur.

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