Journal of Mammalogy, 2026, **00**, 1–13
https://doi.org/10.1093/jmammal/gyag061
Research Article

Melanism dynamics in the Eastern Gray Squirrel (*Sciurus carolinensis*) over four centuries

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Abstract

The spatial patterning of gray-melanic color polymorphism of the Eastern Gray Squirrel (*Sciurus carolinensis*) has captivated naturalists for more than a century. We synthesized 400 years of historical records of occurrences, morph prevalence, and relative abundance of eastern gray squirrels to reconstruct the spatiotemporal dynamics of melanism and thereby provide insight into factors that shaped patterns of melanism observed today. Melanism declined from near fixation in the early 1800s in the Great Lakes–Northeast core area to <25% today, with the steepest losses tracking regional conversion of primary forest to cropland; later, secondary-forest recovery has not reversed these declines. Melanism occurrence has now expanded from its original Great Lakes–Northeast core area to multiple urban hotspots outside the original primary range of the melanic morph. Harvest rate analyses revealed dramatic declines in harvestable abundance for both morphs, with melanistic individuals declining 3 times faster than grays. A network was documented of 184 historical translocations of melanistic individuals mostly into cities (1900 to 1930 peak), with introduction sites associated with higher incidence of contemporary melanism. Through deforestation, intensive harvest, hunter selectivity, and widespread translocations into urban areas, humans have dramatically reshaped the evolutionary landscape of this prominent color polymorphism in eastern gray squirrels. These influences are likely to persist, with melanism potentially rebounding as hunting pressure declines and urbanization expands across the range of the species.

Keywords contemporary evolution, Eastern Gray Squirrel, historical ecology, land-use change, melanism, *Sciurus carolinensis*, urban ecology, translocation

The Eastern Gray Squirrel (*Sciurus carolinensis* Gmelin 1788) is a common North American tree squirrel of eastern and midwestern forests, suburban areas, and urban parks. Color polymorphism is conspicuous in many populations, particularly across the northern half of the species' range (Robertson 1973). Two discrete morphs predominate (Fig. 1), one gray (nonmelanic) and the other melanic, commonly called "black squirrels."

For almost a century, natural historians have noted the spatial patterns in the distribution of gray and melanic morphs (Fenner 1931; Allen 1943; Schorger 1949). Two general patterns are evident. First, a strong latitudinal cline occurs with the frequency of melanistic individuals increasing toward the northern range limit (historically and today) in southern Canada (Robertson 1973) where melanic morphs are disproportionately common in colder, moister climates (Schorger 1949), perhaps because melanistic individuals are efficient at producing and retaining heat in cold (Ducharme et al. 1989), reducing energetic costs of thermoregulation. A second general pattern is an urban–rural contrast. In contemporary populations melanism often declines with distance from the urban core, with some populations showing sharp declines from high urban frequencies to near-zero within 5 to 15 km, while others have broad or weak clines extending 30 to 50 km (a few reverse clines occur in northern parts of their range; Cosentino and Gibbs 2022) creating a patchwork of nearby but distinct melanism gradients.

Mechanisms producing and sustaining the spatial distribution of melanism among Eastern Gray Squirrel populations remain unresolved, stemming from 2 causes. First, hypotheses about potential controls on melanism have been considered in isolation, rather than as parts of an integrated biogeographic phenomenon. Second, historical records of melanism, which are copious, have not been compiled and synthesized since a first attempt by Fenner (1931). Here, we develop a granular timeline of the dynamics in melanism across the northeastern portion of the native range of the species by compiling archival records of occurrence, prevalence, and relative abundance of the melanic morph over the last 4 centuries. We then link patterns observed in melanism with trajectories of land use situated within a climatic and biogeographic context to test multiple hypotheses about selective factors that may have generated patterns of melanism

Associate Editor: John Scheibe
Received: December 13, 2025. **Accepted:** June 18, 2026

Fig. 1 Color polymorphism in the Eastern Gray Squirrel (*Sciurus carolinensis*). Image source: Elizabeth A. Hunter.

observed in contemporary Eastern Gray Squirrel populations. Specifically, we evaluated whether spatiotemporal variation in melanism can be accounted for by: (i) abiotic gradients (solar radiation/temperature, elevation, and water body proximity); (ii) land-use and forest-cover change, evaluated by modeling melanism occurrence against changing land use through time; (iii) exploitation pressure, evaluated by comparing long-term harvest rate trajectories of melanistic versus gray individuals; (iv) human-mediated translocations, evaluated by testing whether contemporary melanism is associated with proximity to documented introduction sites; and (v) urbanization, evaluated by assessing whether urban habitat associations and geographic distribution of melanistic individuals differ between historical and modern periods. Based on factors observed driving historical changes in melanism in eastern gray squirrels, we then project forward likely future trends in melanism across the northeastern portion of their range.

Methods

Reconstructing melanism dynamics

To reconstruct historical patterns in melanism, we conducted a comprehensive review of published and archival records within the native range of the Eastern Gray Squirrel in eastern North America (25 to 55°N, 90 to 60°W; Koprowski 1994). Sources of historic reports of melanistic individuals included scientific literature, published theses, state and provincial game records, newspaper reports, and museum records (sourced from the Global Biodiversity Information Facility; Telenius 2011). Year of each report was recorded and each was assessed for a mappable location to which the finest spatial resolution of observation was noted (locale, county, state/province) and an associated latitude and longitude assigned. We merged the historical dataset with community science observations derived from the SquirrelMapper project (Cosentino and Gibbs 2022) that provided an extensive assemblage of contemporary occurrences of the melanic morph. All analyses were conducted in R (R Core Team 2021).

Drivers of melanism occurrence

To visualize spatial and temporal change in the occurrence of melanism, 2D density estimation (using MASS: kde2d; Ripley et al. 2013) was applied to all occurrence records with spatial resolution of locale, with records spatially thinned to a resolution of 1 km. Reports were summarized over 4 periods that coincided with critical events in contemporary evolution of eastern gray squirrels: Exploitation (before 1875) when original forest cover was largely intact but harvest pressure was intense and unregulated; Protection (1875 to 1924) when forest cover fell to its nadir and the first game protections were enacted that limited squirrel harvest (Lawyer and Earnshaw 1919); Conservation (1925 to 1974) when forest cover began recovering and squirrel populations rebounded due to game protections within the forests that remained; and Modern (1975 to 2025) when forest cover recovery largely ceased in the face of expanding urbanization throughout the range of the species and while squirrel harvest remained regulated (Drummond and Loveland 2010). Although we compiled records across their native range, we restricted analyses to the northeastern portion (Fig. 2) where eastern gray squirrels predominate and sympatry with fox squirrels (*S. niger*) is limited, thereby minimizing misclassification of historically reported "black squirrels" that were melanistic fox squirrels. The northern boundary was defined empirically by the extent of confirmed records of melanistic individuals.

To describe the association between squirrel melanism and habitat change, climate, and geography, each local occurrence record of a melanistic individual was linked with a suite of static (elevation, distance to inland water, and average annual solar radiation) and dynamic (period-specific) environmental variables as well as proportions of primary forest, secondary forest, and urban land cover (Table 1). The suite of variables was chosen because each was linked to a hypothesis about factors that shape the distribution of melanism. Urban extent was used as a sole urbanization metric in lieu of human population density and road density, which are both highly collinear with urban extent. Solar radiation was treated as a static variable as it has not undergone any substantial temporal trend over the last century (Stanhill and Cohen 2005). Given that it was also highly correlated with average temperature ($r > 0.95$ across periods), we used solar radiation in lieu of temperature because of the documented association between solar radiation levels and occurrence of melanism in mammals and birds (Clusella-Trullas et al. 2008) as well as the known benefit to melanistic squirrels under cloudy conditions (Ciurej et al. 2019).

Values for each environmental variable were extracted and assigned to each occurrence record. Each dynamic environmental variable was averaged within its respective historical period and joined to squirrel occurrences in that period. Because of the unknown precision of many historical occurrences, values extracted from each environmental variable and assigned to each occurrence record represented the "neighborhood" value, that is, average value within 5 km of each occurrence record. We then fit presence-only species distribution models for the 4 periods trained on period-specific occurrences using Maxent (Phillips et al. 2017) with default features/regularization, 1 replicate (500 iterations), 10,000 random background points per period, and each predictor raster clamped to its 1st to 99th percentile

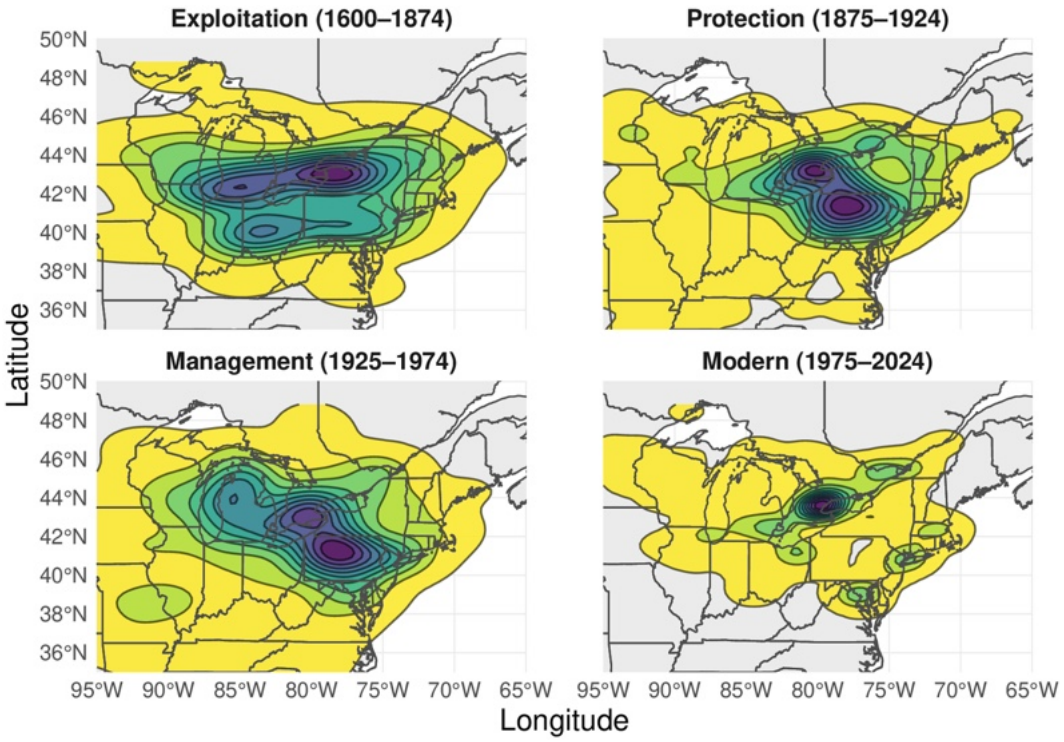

Fig. 2 Occurrences of melanistic eastern gray squirrels from 1600 to 2025 throughout their native range in eastern North America by historical period. Contours depict isopleths of kernel density estimates (0.01 to 1.00) generated from occurrence records spatially thinned to 1 km and generalized using 2D kernel density estimation.

Table 1 Suite of static and dynamic environmental variables used to evaluate hypothesized drivers of melanism dynamics of the Eastern Gray Squirrel.

Variable	Description	Data source	Citation
Elevation	Land surface elevation (m above sea level)	Global Multi-resolution Terrain Elevation Data 2010	Danielson and Gesch (2011)
Temperature	Mean annual air temperature (°C)	Berkeley Earth, 1850–2015	Rohde and Hausfather (2020)
Solar radiation	Mean kJ m^{-2} day^{-1}	WorldClim 1 (1970–2000)	Fick and Hijmans (2017)
Proximity to inland water	Euclidean distance to nearest major inland waterbody (km)	HydroLAKES	Messager et al. (2016)
Primary and secondary forest cover and urban land cover	Proportion of grid cell covered	Global Historical Land-Cover Change and Land-Use Conversion, ESA CCI, 1770–2010	Meiyappan and Jain (2012)

All variables were continuous and re-scaled to a spatial resolution of 1 km.

range to limit outliers, implemented via the "dismo" R interface to Maxent (Hijmans et al. 2017).

Changes in melanism prevalence

To examine trends in fraction of eastern gray squirrels reported as melanic (i.e., melanic prevalence) we extracted year-anchored counts with $n \geq 3$ squirrels that included melanistic and gray individuals from unified reports of both made at a specific locale. We noted whether a given count was associated with a hunting-derived report or part of a systematic observation (a census, survey, or expert estimate) enabling evaluation of bias in melanic prevalence associated with report type, i.e., whether hunters disproportionately targeted melanistic individuals (Creed and Sharp 1958). We integrated the historical dataset with estimates of contemporary (1975 to 2025) melanism prevalence derived from SquirrelMapper observations (Gibbs et al. 2019; Cosentino and Gibbs 2022), summarized on 1° × 1° latitude–longitude grids, i.e., approximately the area of 3 to 4 counties in the eastern United States.

Historical trends in morph prevalence across the historical and contemporary dataset were assessed using generalized linear models with binomial error structures. Predation/harvest and hunter selectivity was assessed by modeling Year and report Type (hunting vs systematic) with a Type × Year interaction. We also modeled region-specific trends in melanic prevalence in a generalized linear mixed model with logit link, including random intercepts and random Year slopes by Region: Great Lakes Canada = Ontario and Quebec, (95.2°W, 41.6°N, 57.1°W, 62.6°N); Northeast/New England = New York, Vermont, New Hampshire, Massachusetts, Connecticut, Rhode Island, and Maine (79.8°W, 40.5°N, 67.0°W, 47.5°N); Upper Midwest/Great

Lakes U.S. = Michigan, Wisconsin, Minnesota, Illinois, Indiana, and Ohio (97.2°W, 37.0°N, 80.5°W, 49.4°N); and Mid-Atlantic/Appalachia = Pennsylvania, Tennessee, and Washington, D.C. (90.3°W, 35.0°N, 74.7°W, 42.3°N).

Changes in abundance

As an index of relative abundance of each morph at a given site and year, we calculated harvest rate from all reports of the number of melanic and gray individuals taken by hunters at the same site that also included the number of hunters and duration of hunt. Hunter-harvest data are abundant in historical sources and government reports, with local newspaper accounts typically reporting 0 to 20 squirrels per day for small parties, earlier community-wide hunts in the 1700s to 1800s reporting 10^2 to 10^3 squirrels per hunt, and game-management-era county-wide totals reaching 10^3 to 10^4 squirrels annually; all were standardized by harvest rate = squirrels taken/hunter/day. Historical trends in harvest rates of eastern gray squirrels in aggregate as well as by morph were evaluated using generalized linear models with Gaussian error structures. Harvest rates are widely used as an index of relative abundance albeit one subject to many biases (Skalski et al. 2007). To validate harvest rate as an index of actual squirrel abundance, we related squirrels killed/hunter/day to estimates of Eastern Gray Squirrel density (individuals/hectare) obtained from all studies we were able to identify in the published literature that presented paired harvest rate-density estimates from the same sites in the same year, e.g., 3 studies across 3 study areas for 17 site-years in total (Dennett and Kidd 1960; Kidd 1969; Nixon et al. 1975).

Patterns of translocation

Historical reports of squirrels translocated between sites were compiled, recording the year of translocation as well as source, destination, and (where provided) number of individuals translocated. We modeled translocations as a directed, weighted network among the United States and Canadian states/provinces, aggregating records to edge counts (source to destination) using the package "igraph" (Csárdi et al. 2025). Hub sources were identified as nodes in the top 10% of output. To quantify the legacy effects of melanistic squirrel translocations on contemporary local patterns of melanism, we paired each documented introduction site with the fraction of melanistic individuals recorded within 50 km during the modern period (1975 to 2025) and compared these values with those from 500 randomly selected SquirrelMapper locations. We evaluated these legacy effects by modeling contemporary melanism counts at documented introduction versus random sites via a quasi-binomial GAM in "mgcv" (Wood and Wood 2015), controlling for latitude and longitude.

Reconstruction of range-wide melanism dynamics and projection of future trends

We reconstructed range-wide melanism dynamics in eastern gray squirrels by first extracting time-varying habitat extent of forest (primary plus secondary, including all types of deciduous and conifer forest) and urban areas, obtained from the Historical Land-Cover Change and Land-Use Conversions Global Dataset (NOAA NCEI DSI 9821_01; spatial scale = 1 km^2; Meiyappan and Jain 2012). Second, we estimated habitat-specific temporal trends in melanism prevalence estimated from locality- and county-level records (p, weighted by n). Each observation was linked to the nearest land-cover year and fit with a weighted binomial GAM including a habitat factor (proportion Urban or Forest within a 5 × 5 pixel window or ca. 25 km^2 area surrounding each observation), with a Year smooth and a group-specific spatial smooth for latitude/longitude, yielding annual predictions of morph prevalence at the median latitude/longitude by habitat type. Last, year- and habitat-specific gray squirrel harvest rates were converted to population densities via a linear relationship identified between the 17 paired harvest rate-density estimates (Fig. 6C). To hind-cast habitat-, year-, and morph-specific population sizes, for each year t, habitat h, and habitat- and year-specific melanism prevalence estimate m, we estimated the total number of melanistic and gray individuals range-wide as:

$$\text{Population}_{m,h,t} = \text{Area}_{h,t} \times \text{Destiny}_{h,t} \times \text{Prevalance}_{m,h,t}$$

summed across habitats. Forward projections to 2100 were then undertaken using recent land-use forecasts for forested and urban areas from Chen et al. (2022) (RCP45 scenario) while holding 2025 estimated densities and habitat-specific melanism prevalence estimates constant.

Results

Melanic occurrence and distribution

We acquired 2,529 observations of occurrence of melanic individuals from between 1600 and 1995 with spatial resolution determined as "locale." These were integrated with 27,416 site-level observations of melanic individuals in contemporary populations captured between 1975 and 2025 via the SquirrelMapper project. Melanism occurred broadly across all historical periods (Fig. 2) albeit shifting from an initial broad, continuous core in the southern Great Lakes–Northeastern U.S.—St. Lawrence River Lowlands corridor to a patchier, mostly city-centered pattern in more recent decades. More specifically, during the Exploitation era (1600 to 1874), observations were concentrated in a band from southern Ontario through western/central New York and Pennsylvania into Ohio, suggesting a historical concentration around the Great Lakes–Allegheny region. In the Protection era (1875 to 1924), melanic density became more restricted within this same corridor, especially around Ohio–western Pennsylvania–southern Ontario, while largely disappearing from the New England states. Through the Management era (1925 to 1974), the kernel centered on southern Ontario through western/central New York and Pennsylvania became less dense. By the Modern era (1975 to 2024), the distribution of reports of melanistic individuals resolved into discrete hotspots mostly aligned with metropolitan areas along the Great Lakes and Atlantic seaboard, while persistence across intervening rural areas diminished, notably disappearing from former core areas of western/central New York and Pennsylvania.

Habitat suitability over time

Across the 4 period-specific Maxent models (6 predictors; n = 2,863 background points each), discrimination increased through time with AUC of 0.777 (1600 to 1874; n = 201 occurrences), 0.819 (1875 to 1924; n = 703 occurrences), 0.824 (1925 to 1974; n = 573 occurrences), and 0.903 (1975 to 2025; n = 4,897 occurrences), likely associated with the greater sample size of occurrences of melanistic individuals during more recent periods. Solar radiation dominated during all periods (60% to 80% contribution) with urban land cover increasing in importance during each successive period (0% to 20%). Forest cover, of both primary and secondary forest, maintained a steady contribution with combined contribution of ca. 40%. Elevation and distance to

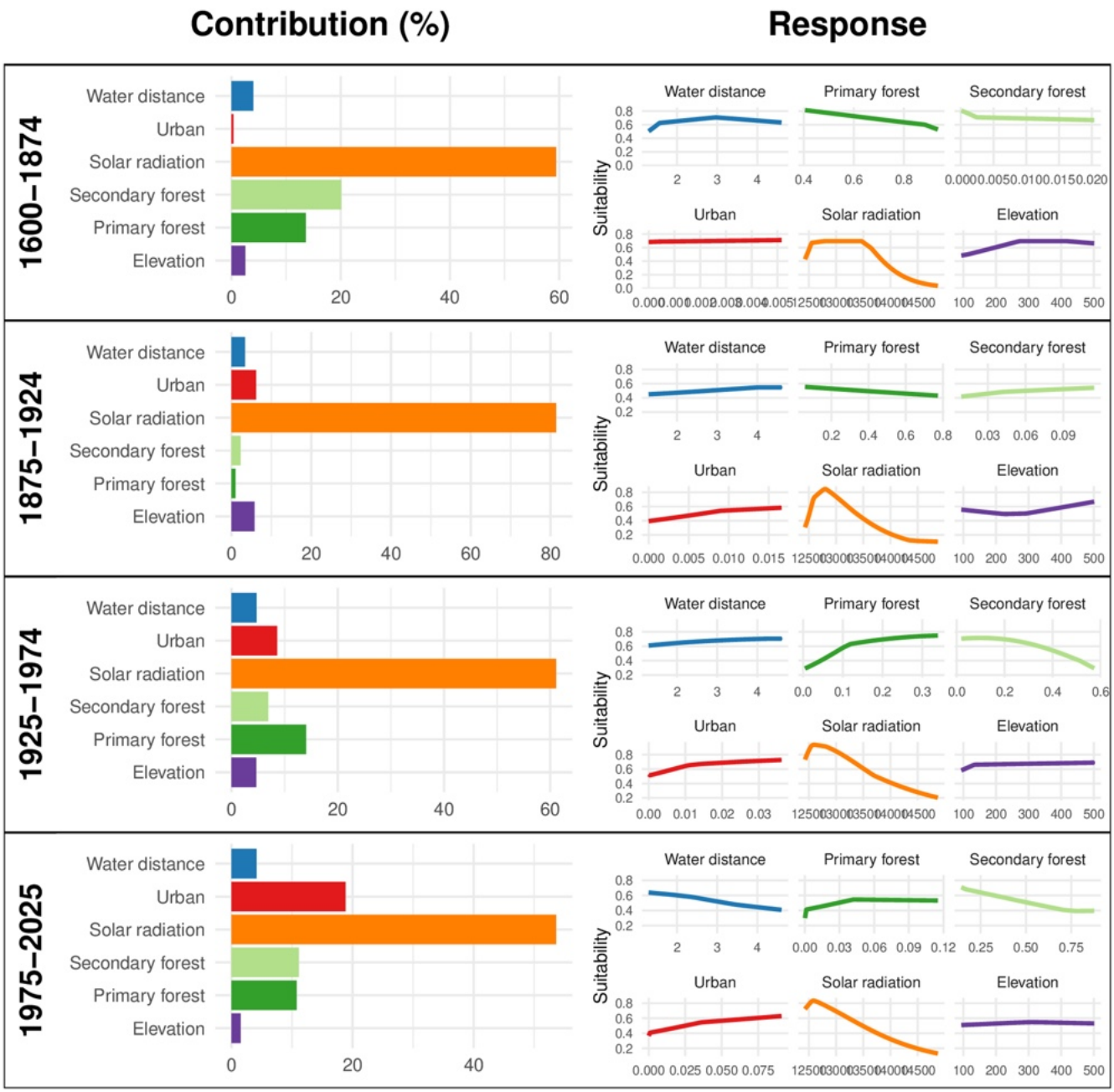

Fig. 3 Variable contributions (left) and response curves (right) for predicted habitat suitability models for melanistic eastern gray squirrels across four time historical periods.

nearest large waterbody were minor (<10%) contributors during all periods. Response curves were stable: suitability generally increased with urban cover, decreased with increasing solar radiation, and exhibited inconsistent effects for forest cover, elevation, and distance to water.

Melanism prevalence

We acquired 625 unified, site-specific counts of melanic and gray morphs each with $n \geq 3$ squirrels dating between 1600 and 1995. Counts totaled 482,831 melanic and 6,414,087 gray morph individuals gleaned from reports valid at the "locale" or "county" scale. These were combined with 27,416 observations of melanistic individuals and 189,924 observations of gray individuals reported between 1975 and 2025 to the SquirrelMapper project (Cosentino and Gibbs 2022) aggregated on a 1° × 1° latitude–longitude grid. A quasibinomial GLM indicated a strong overall decline in melanism over time ($\beta_{year} = -0.0153 \pm 0.0010$, $t = -15.76$, $P < 0.001$; 1,046 df), from near fixation in early records from 1600 to the early 1800s then dropping to <25% in more recent decades (Fig. 4A). A Report_type × Year interaction ($\beta = 0.0164 \pm 0.00405$, $t = 4.05$, $P < 0.001$; 1,044 df) revealed a flatter temporal trend for observational records and stronger declines for hunting-derived reports (Fig. 4B). Our archival search uncovered 1 extended, systematically collected time series of melanism prevalence in eastern gray squirrels in the historical core region of melanism worth highlighting as a regional case study. Harvest data of hunter-killed squirrels gathered between 1918 and 1947 for the State of New York (derived from annual reports of the New York State Conservation Department) revealed that over this 30-year-long span, melanic prevalence among the 5,136,656 hunter-killed

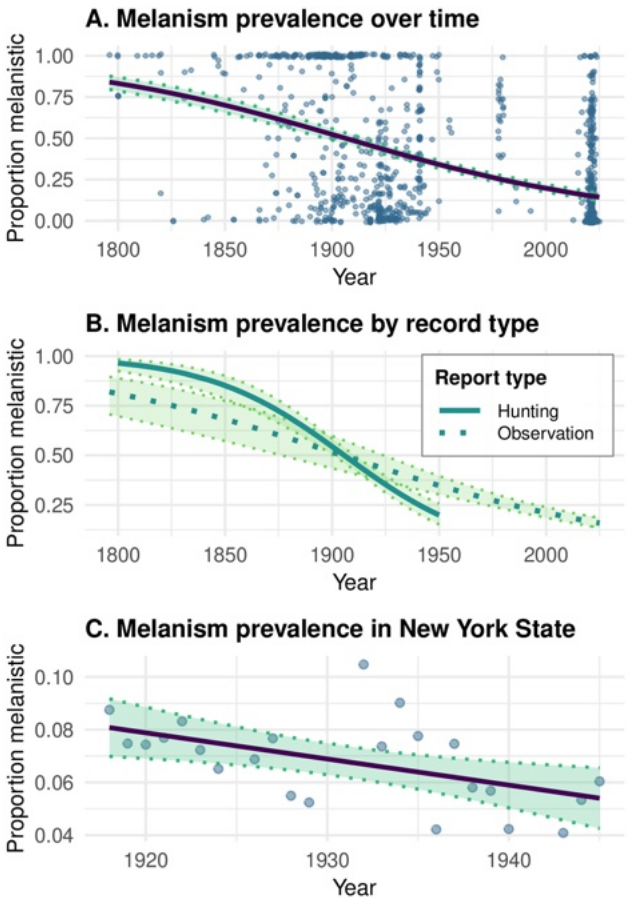

Fig. 4 (A) Temporal trend in incidence of melanism of eastern gray squirrels throughout the northeastern portion of their native range controlling for latitude and longitude of report site; (B) temporal trend in melanic incidence estimated from hunting reports versus expert reports separately, controlling for latitude and longitude of report site; (C) melanic prevalence in harvest data of eastern gray squirrels killed by hunters across New York State between 1918 and 1948. Trend lines bounded by 95% confidence intervals.

squirrels reported declined linearly over time (linear regression: R^2=0.415, F 1,24 = 17.0, P < 0.001) from ca. 8% in the late 1910s to ca. 3% by 1950 (Fig. 4C).

Across all 4 macro-regions within the range of eastern gray squirrels in eastern North America, the melanic morph declined in prevalence over time, but with magnitude and timing differing among regions (Fig. 5A). A mixed-effects beta-binomial GLMM revealed an overall decline in melanism prevalence through time across regions (β_{year} = −0.0146 ± 0.0035 SE, z = −4.16, P < 0.001) with regions differing in baseline melanism prevalence ($SD_{intercept}$ = 1.30), but not temporal slopes (SD_{slope} = 0.0067). In the Great Lakes Canada core (ON/QC), melanism began near fixation in the 1800s and then trended downward in the 20th century to 50% by the 2000s, still the highest prevalence among regions. The Mid-Atlantic/Appalachian region showed a steadier, moderate decline from roughly two-thirds in early records to about one-quarter to one-third in recent decades. The Upper Midwest/Great Lakes U.S. exhibited a long, gradual decline from 70% to 75% in the 1800s to 20% to 30% in contemporary populations. In contrast, the Northeast/New England region experienced the sharpest decline: frequencies near 50% in the 1800s declined to near zero by the early 1900s.

In the context of contemporaneous, regional land use trends (Fig. 5B) across all regions, melanism declined as primary forest was lost, with the timing and strength of decline tracking deforestation and cropland expansion in each region. Notably, subsequent secondary-forest recovery that occurred in most regions did not reverse the range-wide decline in melanism. Specifically, Great Lakes Canada showed a late, steep drop in melanism prevalence (ca. 100% to ca. 50%) mirroring primary forest decline after ca. 1800; Mid-Atlantic/Appalachia declined gradually (ca. 70% to ca. 20% to 30%) with early primary forest loss and a cropland peak around 1900; Northeast/New England fell sharply early (ca. 50% to ca. 10% to 15%) alongside mid-1800s deforestation and cropland surge and remained low despite a large 20th-century rebound in secondary forest; and Upper Midwest/Great Lakes U.S. dropped (ca. 75% to ca. 25%) as primary forest collapsed and cropland rose in the late-1800s/early-1900s with little secondary forest replacement of primary forest lost such that limited forest cover here continues to restrict Eastern Gray Squirrel distribution broadly (of both morphs) (Nupp and Swihart 2000).

Abundance

We acquired 376 records from between 1800 and 1950 of Eastern Gray Squirrel harvest indicating substantial declines in harvest rates for both morphs (Fig. 6A and B) with harvest rates for melanistic individuals declining about 3 × faster than those for gray individuals. More specifically, harvest rates of melanistic individuals declined over time (β_{year} = −0.00496 ± 0.00113 SE, t = −4.40, P < 0.001), were higher at higher latitudes (β_{lat} = 0.08164 ± 0.01613, t = 5.06, $P \leq$ 0.001), and lower farther west (β_{long} = −0.02807 ± 0.00895, t = −3.14, P = 0.002), whereas elevation had no effect (P = 0.326). In contrast, squirrel harvest rates showed no temporal trend (β_{year} = 0.00007 ± 0.00095, t = 0.07, P = 0.944), but were lower at higher latitudes (β_{lat} = −0.05556 ± 0.01363, t = −4.08, P < 0.001), slightly higher farther east (β_{long} = 0.01841 ± 0.00756, t = 2.43, P = 0.0156), and lower at higher elevations (β_{elev} = −0.00045 ± 0.00017, t = −2.62, P = 0.0092). Total harvest rates also declined strongly through time (β_{year} = −0.00823 ± 0.00068, t = −12.07, P < 0.001), were lower farther west (β_{long} = −0.02657 ± 0.00613, t = −4.34, P < 0.001) and at higher elevations (β_{elev} = −0.00043 ± 0.00016, t = −2.71, P = 0.007), but showed no latitudinal pattern (P = 0.565).

The mixed-effects model corroborated an overall regional decline in total harvest rate through time (β_{year_c} = −0.01485) but with moderate among-region variation in baseline harvest rates (SD intercept = 0.318) and weaker variation in slopes (SD slope = 0.010), suggesting that regional harvest dynamics differed even as the general trend was downward. More specifically, across all 4 macro-regions (Fig. 6C), the Mid-Atlantic/Appalachian and Upper Midwest/Great Lakes U.S. regions began with the highest harvest rates, occasionally exceeding 100 squirrels/day/hunter, and then underwent an exponential decline. Harvest rates in the Northeast/New England region started lower (ca. 45 squirrels/day/hunter) but followed the same downward trajectory, reaching near zero by the early 1900s. Harvest rates in Great Lakes Canada remained low over time at ca. 8 squirrels/day/hunter.

Evaluation of the validity of the harvest rate as an index of local abundance of eastern gray squirrels indicated that across the 3 studies that we located with site-paired and year-coincident harvest rate-density estimates there was a strong positive relationship across the 17 site-years between estimates of harvest rates and squirrel density at those same sites (Fig. 6D, β = 0.838 ± 0.091 SE, t = 9.24, P < 0.001).

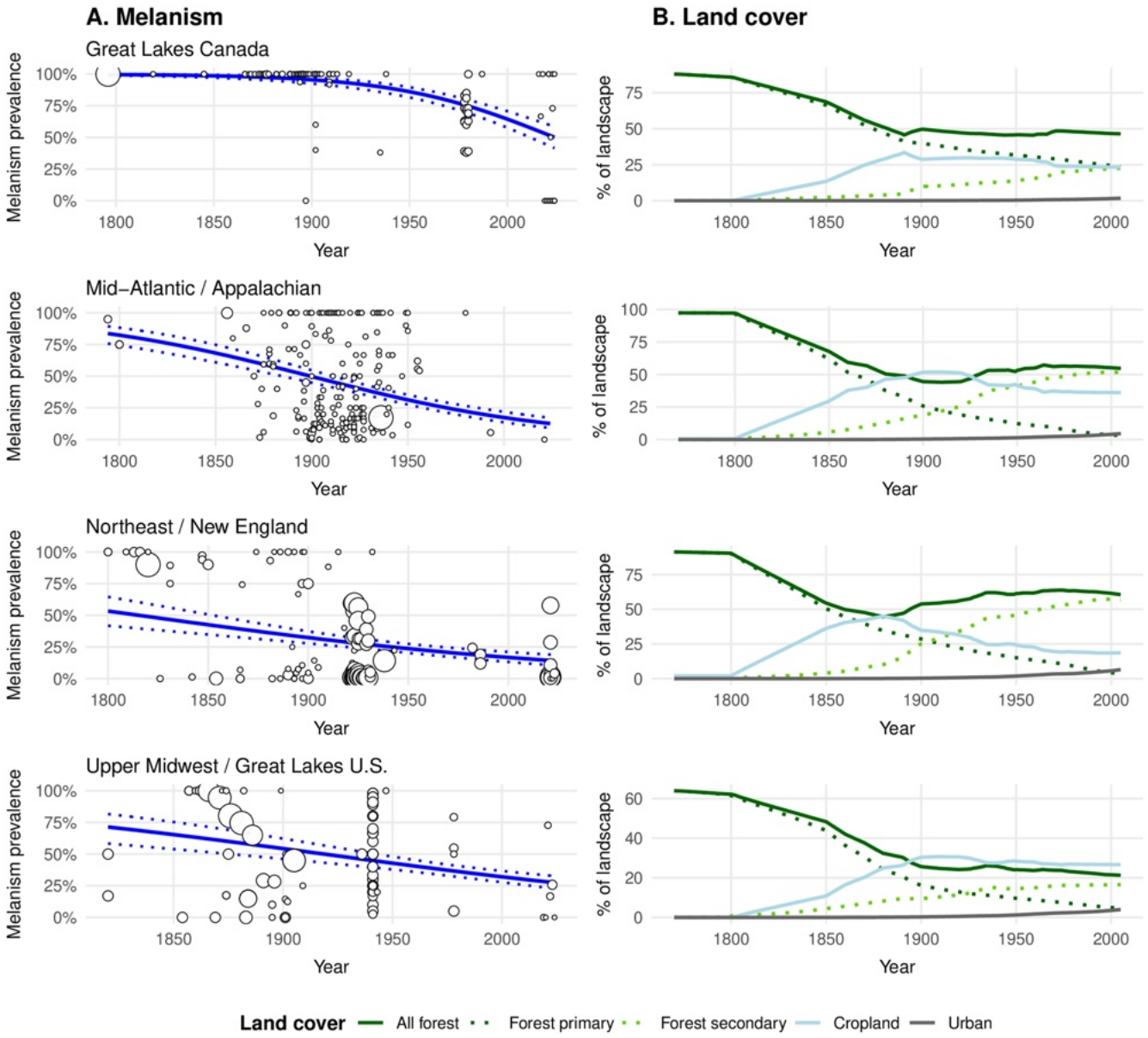

Fig. 5 (A) Melanism prevalence in eastern gray squirrels versus year by region: Great Lakes Canada = ON and QC; Northeast/New England = NY, VT, NH, MA, CT, RI, and ME; Upper Midwest/Great Lakes U.S. = MI, WI, MN, IL, IN, and OH; and Mid-Atlantic/Appalachia = PA, DC, and TN. Point size proportional to sample size. Trend lines bounded by 95% confidence intervals. (B) Change in land use (from Meiyappan and Jain 2012) contemporaneous to regional changes in melanism.

Translocations

We located records of 184 different translocation events of melanistic individuals occurring between 1862 and 1970, with most occurring between 1900 and 1930 (Fig. 7A and B). Primary donor sites were Michigan and Ontario (Fig. 7C), which each sent about half of their translocated melanistic individuals internally and remaining squirrels to New York, Tennessee, Ohio, Virginia, Arkansas, and others. A small cluster of Minnesota donating to Manitoba and Oregon was unconnected to the main translocation network. Overall, the pattern suggests introductions concentrated along a Great Lakes–Mid-Atlantic corridor, with a few repeated cases and many one-time translocations, but also cases of secondary and even tertiary translocations (Fig. 7C). Most translocation destinations (92%) were urban areas; the remainder were rural sites. A binomial GAM showed that introduction history was a predictor of contemporary melanism in a given area: each additional documented introduction increased the log-odds of contemporary melanism by 0.058 ($\beta = 0.058 \pm 0.009$ SE; $z = 6.38$, $P < 0.001$), equivalent to ca. 6% higher odds per introduction.

Historical reconstruction and future projection of melanism dynamics

Historical reconstruction of the Eastern Gray Squirrel population in the eastern United States and Canada (Fig. 8A) estimated it to have declined from just under 1 billion individuals in 1700 to around 100 million today, with the forest-associated subpopulation of melanistic individuals estimated to have declined by 2 to 3 orders of magnitude from the 1800s to the late 1900s, then leveling off as forest extent began to recover. The estimated urban component of melanistic

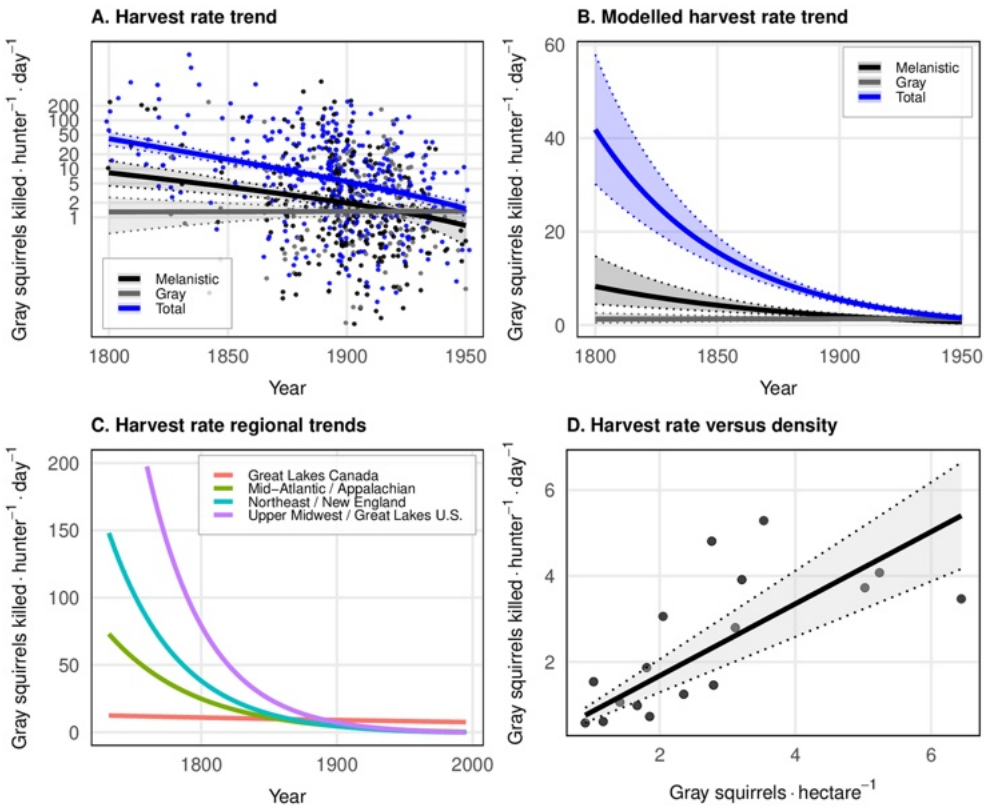

Fig. 6 Observed (A) and modeled (B) trends in 376 harvest rates of eastern gray squirrels (squirrels killed hunter^{-1} day^{-1}) from 1800 to 2000, by morph and for total squirrels (blue). Harvest rates for total squirrels will not necessarily be the sum of gray and melanic individuals because some early harvest rates records were undifferentiated to morph. (C) Region-specific trends in harvest rates of hunted eastern gray squirrels, 1800 to 2000. (D) Relationship between harvest and density estimates in contemporary populations of eastern gray squirrels across 17 site-years. Trend lines bounded by 95% confidence intervals.

individuals increased monotonically to become comparable at present to the contemporary prevalence of melanism in the rural forests that remain. A slight reversal of long-term decline in melanism prevalence was projected to be occurring at present (Fig. 8B) as urbanization expands.

Discussion

This reconstruction of melanism dynamics in eastern gray squirrels shows that melanism has undergone a pronounced spatiotemporal reorganization over the last 4 centuries. We observed a strong transition from an historically widespread Great Lakes-Northeast nucleus to modern, urban-dominated pockets embedded in a landscape sparse with melanistic individuals. Recent historical urban expansion may have produced a rebound in melanic frequency, which will likely continue over the next 100 yrs given projected changes in land use.

A decrease in prevalence of squirrel melanism coincident with the multi-century period of European colonization of eastern North America has been suggested from anecdotal observations (Fenner 1931) but not heretofore documented. This change has been conjectured to be associated with land-use change and patterns of exploitation unfavorable to melanic forms. More specifically, forest clearing combined with reversion to younger age classes in the forests that remained may have increased visual conspicuousness against melanic morphs amid more open forests in rural areas (Allen 1943), where hunting of eastern gray squirrels for food and crop protection was intense (Schorger 1949) and remains so. In such areas, hunters evidenced selectivity for the melanic morph (Fig. 6C), a mechanism first suggested by Creed and Sharp (1958) to promote the gray morph. Notably, in all contemporary environments where gray squirrels occur the melanic morph is more conspicuous than the gray morph to potential predators (Proctor et al. 2025).

These results refine the climate-based hypotheses for both spatial and temporal declines in melanism prevalence. Solar radiation was a predictor of melanism across periods, with melanism persisting more often in areas with lower incoming solar radiation that would also be cooler in lowlands near water. Multiple mechanisms for climate-mediated selection on coat color have been proposed. Ducharme et al. (1989) showed that melanistic individuals have greater nonshivering thermogenesis and heat retention than the gray morph at cold temperatures. Furthermore, the thermal melanism hypothesis predicts that dark coat color is beneficial in cold climates due to greater potential for radiant heating, a prediction supported in fox squirrels where melanistic individuals heat more efficiently than agouti morphs on cloudy days (Ciurej et al. 2019). The loss of cooler, forested wetlands historically associated with melanic forms (e.g., Comstock 1894) likely drove declines in melanism in central and western New York, northwestern Ohio, northern Indiana, and eastern Illinois, where extensive wetland forests were lost. In addition, logging, structural simplification, and fragmentation of upland forests across the region may have increased temperatures in remaining habitats, reducing their suitability for melanic squirrels.

Climate warming cannot be discounted as a driver of declining melanism in eastern gray squirrels. The northern portion of their

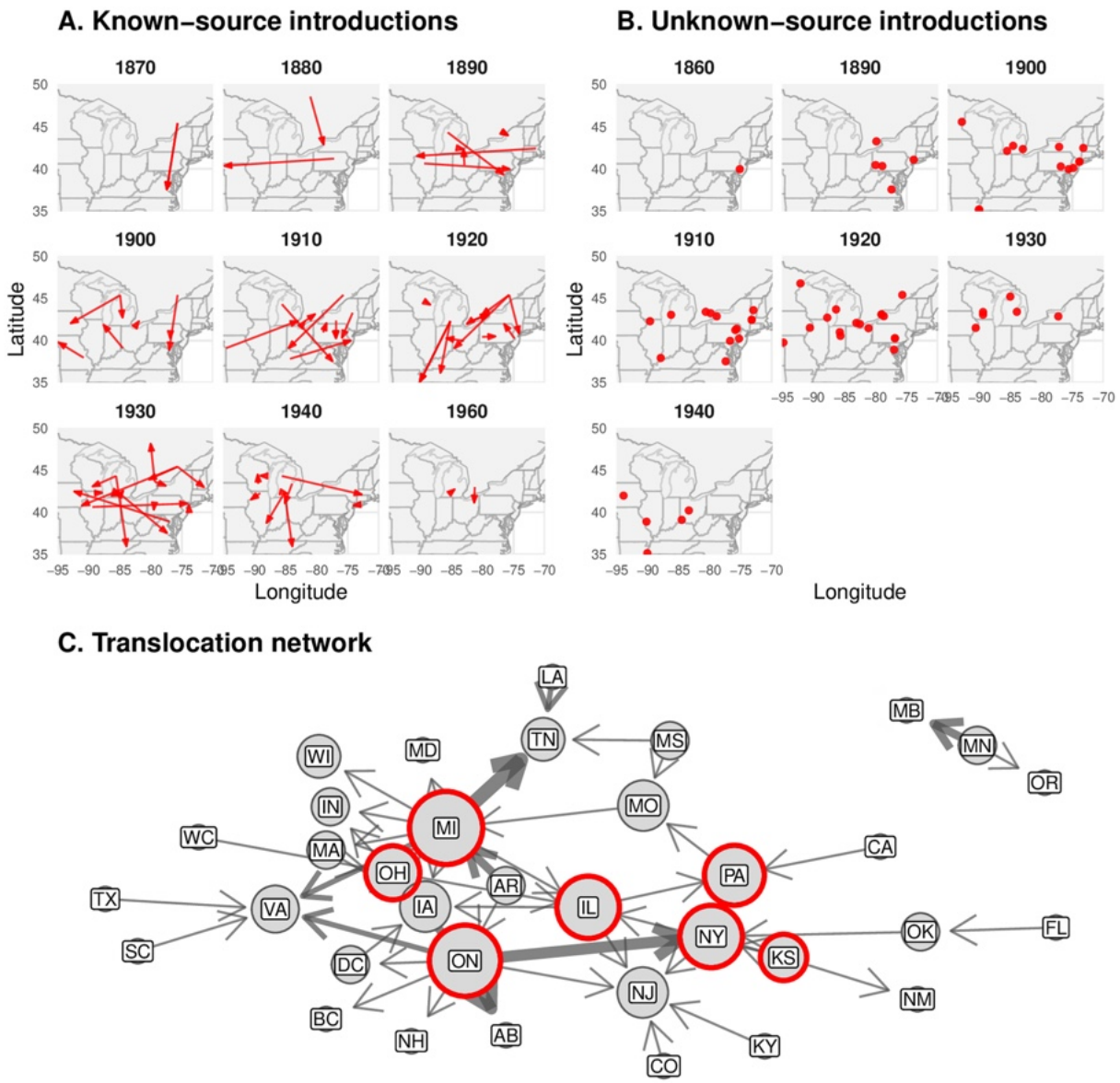

Fig. 7 Documented historic translocations of melanistic eastern gray squirrels from known sources (A, red arrows point from source origin to introduction site) and unknown sources (B, red dots indicate introduction sites). Translocation connectivity diagram (C): node names are state/province postal abbreviations; and node size is proportional to total incoming, internal, and outgoing translocations, with arrows pointing from source to destination and arrow width proportional to the number of translocations documented (thinnest = 1 translocation, thickest = 5 translocations,). Top 10% of nodes in outgoing connections bordered in red.

range, where melanistic individuals were historically concentrated, has warmed by ~1.5 °C over the last century, with greater increases during winter (Hayhoe et al. 2008). This warming represents roughly half the temperature difference between the isotherms that historically delineated the upper and lower limits of melanism in the species, suggesting that recent regional climate warming has been of a sufficient magnitude to potentially play a role in melanism declines.

Several factors may reconcile why the melanic morph remains common in many cities despite urban heat islands that might disfavor darker pelage thermally, as well as why the proportion of melanistic individuals rarely rises above 50% in all but the most northern, coldest cities (Cosentino et al. 2023). These factors include altered predator guilds and predation risks, reduced harvest pressure due to prohibition of hunting squirrels in cities, supplemental resources, and substrate/background effects that could change detection and mortality risk (Proctor et al. 2025). Moreover, the microclimates occupied by squirrels in urban areas may be colder than indicated by regional ambient temperatures. For example, increased snowmelt in warmer cities may reduce ground temperatures, while limited canopy cover and greater wind exposure can exacerbate local cooling. Notably, incoming solar radiation is lower in cities than adjacent rural areas because of scattering and absorption caused by air pollution (Alpert et al. 2005). Any costs of melanism in a warming environment (both in urban areas due to urban heat islands and range-wide due to regional climate warming) may also be balanced by the selective benefits of reduced roadkill risk of melanistic individuals (Parlin et al. 2025).

The results of the relative abundance analysis indicate a collapse in harvestable gray squirrel abundance over the last century, with a broadly consistent decline, except for in Great Lakes Canada (Ontario, Quebec) where relative abundances have remained stable. This

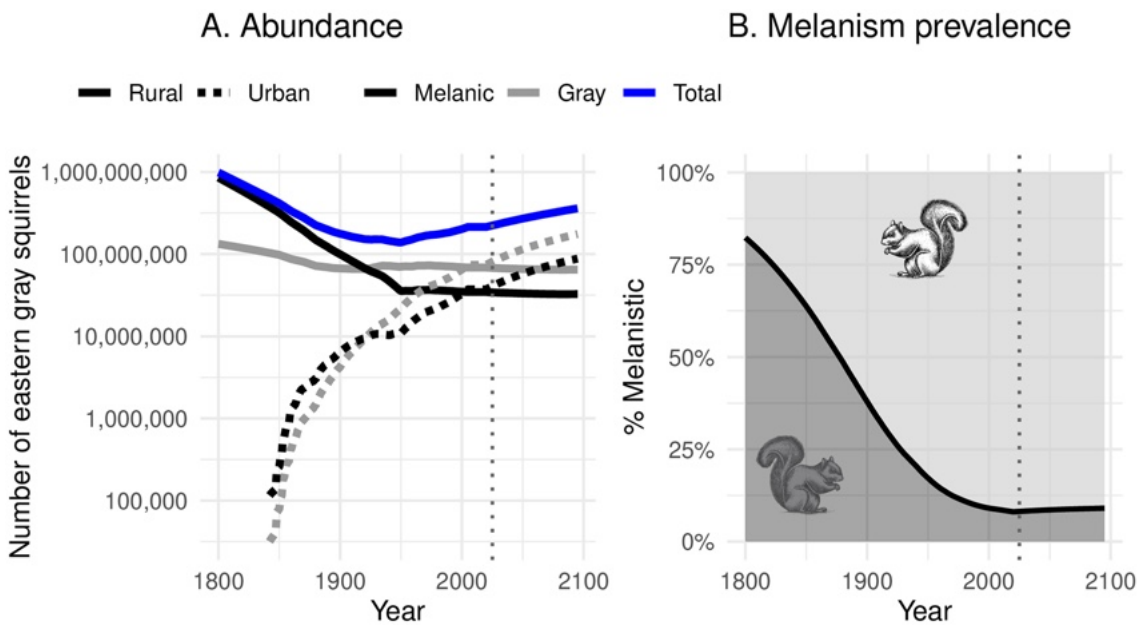

Fig. 8 Reconstructed dynamics and future projections of habitats, abundance, and melanism prevalence in eastern gray squirrels from 1800 to 2100. (A) Estimated aggregate population size by morph (melanic, gray, total) and habitat type (rural forest, urban areas). (B) Hind- and fore-casted melanism prevalence. In both graphs vertical dashed line = present (ca. 2025).

pattern coincides with a reduction of squirrel numbers about the year 1900 reported earlier (Cahalane 1961), which at the time raised the specter of impending extinction of the Eastern Gray Squirrel (Osborne 1923). These widespread site-level reductions in squirrel abundance were likely due to a combination of factors. Clearly, overharvest played a role, with imposition of limits on squirrel harvest in the form of hunting regulations undertaken in response to collapse of Eastern Gray Squirrel populations, starting uniformly across most states and provinces by 1915 to 1925, often with daily limits on take of 5 squirrels or less, reducing harvest rates to the low levels seen in the modern period. Notably, harvest rates realized by hunters typically have remained well below permitted harvest limits (Dennett and Kidd 1960; Kidd 1969; Nixon et al. 1975), which themselves are far below historical harvest rates (Fig. 6B), suggesting that Eastern Gray Squirrel densities in the forest remaining have not recovered to historical levels.

In addition to harvest pressure, declines in Eastern Gray Squirrel abundance may also have been driven by reduction in habitat quality due to the disappearance from eastern deciduous forests of the American Chestnut (*Castanea dentata*), a prominent mast-bearing tree species (Landon 1941), and strong declines in abundance of others, notably oaks (*Quercus* spp.) as well as American Beech (*Fagus grandifolia*), which have been replaced by early successional species that produce lower frequency or abundance of seed (Thompson et al. 2013). All regions showed large variability in relative abundance estimates of squirrels in early years, perhaps due to production cycles in mast-bearing trees known to trigger population irruptions (Nixon et al. 1975) but that no longer occur (Schorger 1949). Forest loss has also been accompanied by strong spatial fragmentation of the forests that remain, which also reduces habitat suitability for eastern gray squirrels (Nupp and Swihart 2000).

Changes in populations of natural predators are not likely to have played a role, as those collapsed historically to an even greater extent than have Eastern Gray Squirrel populations, including those of carnivorous mammals (Laliberte and Ripple 2004; Ray 2010), predatory reptiles, e.g., timber rattlesnakes (*Crotalus horridus*; Babcock 1925, 1929; Furman 2007), and raptors (Bednarz et al. 1990), although populations of the raptor species that are primary predators upon eastern gray squirrels—Red-tailed Hawk (*Buteo jamaicensis*), Broad-winged Hawk (*B. platypterus*), and Red-shouldered Hawk (*B. lineatus*)—have recovered in the post-organochlorine era (Sauer et al. 2017; Rosenberg et al. 2019).

Human-mediated translocations of melanistic individuals may have helped establish, and in some cases amplify, urban loci of melanistic individuals that later persisted via local demographic and selective forces. We documented that melanistic eastern gray squirrels were translocated heavily around 1900 to 1930, in a network far larger and more extensive than previously understood. The translocations documented are likely only a fraction of those that occurred and do not include commercial transactions that our archival searches indicated were also rampant (i.e., transport and sale of "black squirrels" as pets, many of which became escapees). These extensive translocations left a measurable imprint on present-day melanism, with sites of documented introductions showing elevated odds of melanic occurrence.

Several biases in reconstruction of the distribution of melanic individuals with the archival research methods used in this study warrant caution. Archival reports may vary in detectability and interest for unusual morphs, perhaps favoring reporting of melanic forms. Harvest rate as an index of relative abundance is also subject to bias. Harvest rates integrate hunter skill and preference as well as local squirrel abundance. An important potential bias includes hunter efficiency, which has likely increased due to advances in weaponry used for hunting squirrels, but this factor would have favored an increase in catch-per-unit-effort, not the dramatic decline observed.

There is also potential bias in noting occurrence of "black squirrels" in regions of sympatry of gray squirrels with other Sciurids; more specifically, melanic forms of both fox squirrels (Kiltie 1992) and American red squirrels (*Tamiasciurus hudsonicus*; Benton 1958) have been termed "black squirrels." We were careful to only include records of "black squirrels" that included a reference to eastern gray

squirrels but some reports of melanic fox squirrels (in southern and western portions of the study area where both *S. carolinensis* and *S. niger* overlap) may have been included. Melanism in American red squirrels is much more rare (Benton 1958) but does occur, including in the New England states, where melanistic red squirrels have been historically called "black squirrels."

Urban bias in reporting frequency also remains a concern. Most contemporary observations in this study were likely made by casual observers who disproportionately report from where they live in cities, near roads, and in parks, while rural and remote areas are under-sampled (Geldmann et al. 2016). Clearly, melanism in eastern gray squirrels is promoted in urban areas as revealed by systematic studies that do not rely on crowd-sourced observations (e.g., Cosentino et al. 2023), but in this study that relied on such observations, urban bias in reporting may have overstated urban occurrence and distorted range maps by conflating observer effort with morph occurrence. Spatial thinning of observations employed in this study would have partially mitigated any urban reporting bias.

Further unknowns temper future projections of melanism prevalence due to uncertainty around shifts in the relative importance of current selective factors. At least 1 major selective factor, hunting pressure, is in long-term decline and unlikely to rebound (Grandy et al. 2003). Also, in urbanizing areas, road network densities and traffic volume and speed are increasing (Burghardt et al. 2022) and represent the primary mortality source for tree squirrels (McCleery et al. 2008; Simpson et al. 2013) and a selective factor favoring melanistic individuals (Parlin et al. 2025). We speculate that the combined effects of decreasing hunting pressures and increasing road mortality could expand future prevalence of melanism in eastern gray squirrels over that projected based on habitat trends alone.

Targeted manipulations and natural experiments could clarify mechanisms underpinning the melanism dynamics observed in this otherwise correlational study. Replicated transplants (e.g., Cosentino et al. 2023) and seminatural enclosure/common-garden experiments across multiple urban–rural pairs could quantify environment-dependent survival, reproduction, and thermoregulatory costs of melanic versus gray individuals. Quasi-experimental designs around changes in forest cover, road infrastructure, and squirrel harvest management practices could isolate anthropogenic drivers of differential mortality or dispersal. Genomic time series working with museum specimens, combined with documented translocation histories, could help distinguish contemporary selection from legacy introductions (e.g., Bonar et al. 2026).

Taken together, this synthesis indicates that over the last 400 years melanism in eastern gray squirrels has been shaped by stable abiotic constraints (mainly solar radiation) with a modern overlay driven by anthropogenic forces, especially forest extent and urbanization as well as legacies of translocation by humans and harvest pressures. The contemporary mosaic of urban strongholds amid broader rural declines illustrates how humans have restructured the evolutionary landscape of this prominent polymorphism in the Eastern Gray Squirrel. Melanism in eastern gray squirrels will likely remain dynamic into the future as climate, land-use, and hunting patterns continue to change throughout the species' native range.

Author contributions

James Peter Gibbs (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing—original draft, Writing—review & editing) and Bradley Cosentino (Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Writing—review & editing)

Funding

This research was supported by the U.S. National Science Foundation (DEB-2018140, DEB-2018249).

Conflict of interest

None declared.

Data availability

All data used in this study, as well as a sample of historical narratives documenting melanism decline, are available here: https://blacksquirrel.shinyapps.io/data_app/

References

Allen DL. 1943. Michigan fox squirrel management. Game Division, Michigan Department of Conservation.

Alpert P, Kishcha P, Kaufman YJ, Schwarzbard R. 2005. Global dimming or local dimming?: effect of urbanization on sunlight availability. Geophysical Research Letters 32(17):L17802. https://doi.org/10.1029/2005GL023320

Babcock H. 1925. Rattlesnakes in Massachusetts. Boston Society of Natural History 35:5–10.

Babcock H. 1929. The snakes of New England. Boston Society of Natural History 1:1–31.

Bednarz JC, Klem D, Goodrich LJ, Senner SE. 1990. Migration counts of raptors at Hawk Mountain, Pennsylvania, as indicators of population trends, 1934. Auk 107(1986):96–109. https://doi.org/10.1093/auk/107.1.96

Benton AH. 1958. Melanistic red squirrels from Cayuga County, New York. Journal of Mammalogy 39(3):445. https://doi.org/10.2307/1376166

Bonar M, Blumenfeld A, Fusco N, Campagna L, Timpson A, Thomas M, Cosentino B, Gibbs JP, Caccone A. 2026. Cities as genetic refugia: rural selection maintains Mc1R pigmentation cline in squirrels despite an urban bottleneck. Proceedings of the Royal Society B 293(2069):20253278. https://doi.org/10.1098/rspb.2025.3278

Burghardt K, Uhl JH, Lerman K, Leyk S. 2022. Road network evolution in the urban and rural United States since 1900. Computers, Environment and Urban Systems 95:101803. https://10.1016/j.compenvurbsys.2022.101803

Cahalane VH. 1961. Mammals of North America. New York (NY, USA): The Macmillan Company.

Chen G, Li X, Liu X. 2022. Global land projection based on plant functional types with a 1-km resolution under socio-climatic scenarios. Scientific Data 9(1):125. https://doi.org/10.1038/s41597-022-01208-6

Ciurej A, Oblander A, Swift AW, Wilson JA. 2019. Melanism as a potential thermal benefit in eastern fox squirrels (*Sciurus Niger*). European Journal of Ecology 5(2):79–87. https://doi.org/10.2478/eje-2019-0013

Clusella-Trullas S, Terblanche JS, Blackburn TM, Chown SL. 2008. Testing the thermal melanism hypothesis: a macrophysiological approach. Functional Ecology 22(2):232–238. https://doi.org/10.1111/j.1365-2435.2007.01377.x

Comstock FM. 1894. Color variations of the gray squirrel. Forest and Stream, 1894:399–400.

Cosentino BJ, Gibbs JP. 2022. Parallel evolution of urban–rural clines in melanism in a widespread mammal. Scientific Reports 12(1):1752. https://doi.org/10.1038/s41598-022-05746-2

Cosentino BJ, Vanek JP, Gibbs JP. 2023. Rural selection drives the evolution of an urban–rural cline in coat color in gray squirrels. Ecology and Evolution 13(10):e10544. https://doi.org/s 10.1002/ece3.10544

Creed WA, Sharp WM. 1958. Melanistic squirrels in Cameron County, Pennsylvania. Journal of Mammalogy 39(4):532–537. https://doi.org/10.2307/1376791

Csárdi G, Nepusz T, Traag V, Horvát S, Zanini F, Noom D, Müller K, Schoch D, Salmon M. 2025. igraph: network analysis and visualization in R. R package version 2.2.1. https://CRAN.R-project.org/package=igraph. https://doi.org/10.5281/zenodo.7682609

Danielson JJ, Gesch DB. 2011. Global multi-resolution terrain elevation data 2010 (GMTED2010). US Geological Survey Open-File Report 2011-1073, Reston (Virginia): U.S. Geological Survey. https://pubs.usgs.gov/of/2011/1073/

Dennett D, Kidd JB. 1960. An analysis by tag returns of three years' controlled squirrel hunting. In: Proceedings of the 14th Annual Conference of the Southeastern Association of Game and Fish Commissioners; p. 66–73.

Drummond MA, Loveland TR. 2010. Land-use pressure and a transition to forest-cover loss in the eastern United States. BioScience 60(4):286–298. https://doi.org/10.1525/bio.2010.60.4.7

Ducharme MB, Larochelle J, Richard D. 1989. Thermogenic capacity in gray and black morphs of the gray squirrel, *Sciurus carolinensis*. Physiological Zoology 62(6):1273–1292. https://www.jstor.org/stable/30156213

Fenner EA. 1931. Melanism in the northern gray squirrel [master's thesis]. [Ithaca (NY, USA)]: Cornell University.

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12):4302–4315. https://doi.org/10.1002/joc.5086

Furman J. 2007. Timber rattlesnakes in Vermont and New York. Hanover (NH, USA): University Press of New England.

Geldmann J, Heilmann-Clausen J, Holm TE, Levinsky I, Markussen BO, Olsen K, Rahbek C, Tøttrup AP. 2016. What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. Diversity and Distributions 22(11):1139–1149. https://doi.org/10.1111/ddi.12477

Gibbs JP, Buff MF, Cosentino BJ. 2019. The biological system—urban wildlife, adaptation, and evolution: urbanization as a driver of contemporary evolution in gray squirrels (*Sciurus carolinensis*). In: Hall MA, Balogh S, editors. Understanding urban ecology. Cham (Switzerland): Springer International Publishing; p. 269–286. https://doi.org/10.1007/978-3-030-11259-2_12

Grandy JW, Stallman E, Macdonald DW. 2003. The science and sociology of hunting: shifting practices and perceptions in the United States and Great Britain. In: Salem DJ, Rowan AN, editors. The state of the animals II: 2003. Washington (DC, USA): Humane Society Press; p. 107–130.

Hayhoe K, Wake C, Anderson B, Liang X-Z, Maurer E, Zhu J, Bradbury J, DeGaetano A, Stoner AM, Wuebbles D. 2008. Regional climate change projections for the Northeast USA. Mitigation and Adaptation Strategies for Global Change 13(5-6):425–436. https://doi.org/10.1007/s11027-007-9133-2

Hijmans RJ, Phillips S, Leathwick J, Elith J. 2017. dismo: species distribution modeling. R package version 1.1-4. https://CRAN.R-project.org/package=dismo

Kidd JB. 1969. Louisiana squirrels. In: Ensminger J, editor. Readings in wildlife and fish conservation, high school conservation curriculum project. North Louisiana Supplementary Education Center, ESEA Project Grant No. OEG-3-7-703577-4862.

Kiltie RA. 1992. Tests of hypotheses on predation as a factor maintaining polymorphic melanism in coastal-plain fox squirrels (*Sciurus Niger* L.). Biological Journal of the Linnean Society 45(1):17–37. https://doi.org/10.1111/j.1095-8312.1992.tb00629.x

Koprowski JL. 1994. Sciurus carolinensis. Mammalian Species 480(480):1–9. https://doi.org/10.2307/3504224

Laliberte AS, Ripple WJ. 2004. Range contractions of North American carnivores and ungulates. BioScience 54(2):123–138. https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2

Landon M. 1941. Changes in the squirrel populations of charlotteville township, Norfolk County, Ontario, 1890–1940. Canadian Field-Naturalist 55:102–103.

Lawyer GA, Earnshaw FL. 1919. Game laws for 1919: a summary of the provisions of federal, state and provincial statutes. Washington, D.C.: U.S. Department of Agriculture.

McCleery RA, Lopez RR, Silvy NJ, Gallant DL. 2008. Fox squirrel survival in urban and rural environments. Journal of Wildlife Management 72(1):133–137. https://doi.org/10.2193/2007-138

Meiyappan P, Jain AK. 2012. Three distinct global estimates of historical land-cover change and land-use conversions for over 200 years. Frontiers of Earth Science 6(2):122–139. https://doi.org/10.1007/s11707-012-0314-2

Messager ML, Lehner B, Grill G, Nedeva I, Schmitt O. 2016. Estimating the volume and age of water stored in global lakes using a geo-statistical approach. Nature Communications 7:13603. https://doi.org/10.1038/ncomms13603

Nixon CM, McClain MW, Donohoe RW. 1975. Effects of hunting and mast crops on a squirrel population. Journal of Wildlife Management 39(1):1–25. https://doi.org/10.2307/3800460

Nupp TE, Swihart RK. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. Journal of Mammalogy 81(2):512–526. https://doi.org/10.1644/1545-1542(2000)081<0512:LLCOSM>2.0.CO;2

Osborne FA. 1923. Is the gray squirrel disappearing? Nature Magazine 2:122–123.

Parlin AF, Cosentino BJ, Lehtinen RM, McDonald JE, Sinclair ECC, Gibbs JP. 2025. Road mortality contributes to the evolution of an urban–rural cline in squirrel coat color. Evolutionary Applications 18(5):e70109. https://doi.org/10.1111/eva.70109

Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME. 2017. Opening the black box: an open-source release of Maxent. Ecography 40(7):887–893. https://doi.org/10.1111/ecog.03049

Proctor J, Bryan A, Cosentino BJ, Gibbs JP. 2025. Crypsis in a polymorphic mammal along an urbanization gradient. Urban Ecosystems 28(2):94. https://doi.org/10.1007/s11252-025-01708-4

R Core Team. 2021. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. https://www.R-project.org/

Ray JC. 2010. Conservation planning with large carnivores and ungulates in eastern North America: learning from the past to plan for the future. In: Millspaugh JJ, Thompson FR III, editors. Landscape-scale conservation planning. Dordrecht (Netherlands): Springer; p. 167–204.

Ripley BD, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D. 2013. MASS: support functions and datasets for Venables and Ripley's MASS. R package version 7.3-26. https://CRAN.R-project.org/package=MASS

Robertson GI. 1973. Distribution of color morphs of *Sciurus carolinensis* in Eastern North America. [master's thesis]. [London (ON, Canada)]: University of Western Ontario.

Rohde RA, Hausfather Z. 2020. The Berkeley Earth land/ocean temperature record. Earth System Science Data 12(4):3469–3479. https://doi.org/10.5194/essd-12-3469-2020

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, Stanton JC, Panjabi A, Helft L, Parr M, et al. 2019. Decline of the North American avifauna. Science 366(6461):120–124. https://doi.org/10.1126/science.aaw1313

Sauer JR, Pardieck KL, Ziolkowski DJ, Smith AC, Hudson MAR, Rodriguez V, Berlanga H, Niven DK, Link WA. 2017. The first 50 years of the North American breeding bird survey. Condor: Ornithological Applications 119(3):576–593. https://doi.org/10.1650/CONDOR-17-83.1

Schorger AW. 1949. Squirrels in early Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 39:195–247.

Simpson VR, Hargreaves J, Butler HM, Davison NJ, Everest DJ. 2013. Causes of mortality and pathological lesions observed post-mortem in red

squirrels (*Sciurus vulgaris*) in Great Britain. BMC Veterinary Research 9:229. https://doi.org/10.1186/1746-6148-9-229

Skalski JR, Townsend RL, Gilbert BA. 2007. Calibrating statistical population reconstruction models using catch-effort and index data. Journal of Wildlife Management 71(4):1309–1316. https://doi.org/10.2193/2005-707

Stanhill G, Cohen S. 2005. Solar radiation changes in the United States during the twentieth century: evidence from sunshine duration measurements. Journal of Climate 18(10):1503–1512. https://doi.org/10.1175/JCLI3354.1

Telenius A. 2011. Biodiversity information goes public: GBIF at your service. Nordic Journal of Botany 29(3):378–381. https://doi.org/10.1111/j.1756-1051.2011.01167.x

Thompson JR, Carpenter DN, Cogbill CV, Foster DR. 2013. Four centuries of change in northeastern United States forests. PLoS One 8(9):e72540. https://doi.org/10.1371/journal.pone.0072540

Wood SN, Wood MS. 2015. mgcv: mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation. R package version 1.8-7. https://CRAN.R-project.org/package=mgcv

Journal of Mammalogy 2026 00(00) 1–13
https://doi.org/10.1093/jmammal/gyag061
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