Ecological and evolutionary impacts of urbanization: applying a causal modeling framework

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Abstract

Urbanization, as the fastest growing land use type, shapes biodiversity through a suite of abiotic and biotic changes driven by the profound alteration of environmental conditions in built environments. Understanding the mechanisms behind biodiversity patterns in urban areas requires disentangling the direct and indirect pathways through which urbanization impacts ecological and evolutionary dynamics. We show how a structural causal modeling framework can be used to provide insight into processes generating biodiversity patterns in urban contexts by building structural equation models to disentangle direct and indirect pathways by which urbanization affects abundance and coat color variation in eastern gray squirrels (*Sciurus carolinensis*). Integrating camera traps and point count surveys across 49 sites, we observed pronounced urban-rural gradients in squirrel abundance and color variation. Human population density affected abundance of color morphs by mediating resource availability, predator activity, habitat amount, and fragmentation. But markedly different mechanisms drove abundance of color morphs across the landscape. Our findings reveal how explicit modeling of multiple pathways of environmental change can deepen our mechanistic understanding of how urbanization alters biodiversity patterns.

Key words

Urban evolution, urbanization, causal modeling, path analyses, melanism, trait variation, urban mechanisms, gray squirrel, *Sciurus carolinensis*

Authors' contributions

Jesse B. Borden: writing - original draft (lead); conceptualization, investigation, methodology, data curation, visualization, writing - reviewing and editing (equal). **James P. Gibbs:** conceptualization, funding acquisition, investigation, methodology, writing- reviewing and editing (equal). **John P. Vanek:** conceptualization, investigation, methodology, writing – review and editing. **Bradley J. Cosentino:** conceptualization, funding acquisition, investigation, methodology, formal analysis, project administrator, supervision, writing – review and revision (lead)

1. Introduction

Urbanization represents the fastest growing land use type and poses formidable challenges to biodiversity (Aronson et al., 2014; Ritchie & Roser, 2018; Szabó et al., 2023). At a fundamental level, urbanization consists of a suite of abiotic and biotic changes driven by high concentrations of people and the physical environment they build (Ritchie & Roser, 2018) (Fig. 1a). The ecological and evolutionary consequences of urbanization are often studied using the urban-rural gradient approach in which components of biodiversity are compared along a landscape-scale sampling area from the urban center to rural environments (Mcdonnell & Hahs, 2008; McDonnell & Pickett, 1990). This approach has been used to document associations of population size, species distributions, community composition, and genetic and phenotypic trait variation with urbanization. Although the urban-rural gradient approach has been helpful to clarify spatial patterns of biodiversity associated with urbanization, reliance on coarse metrics of urbanization (e.g., distance to city center, human population density, impervious cover; Moll et al. 2019) provides little insight into the underlying mechanisms driving urbanization effects on biodiversity.

To understand the mechanisms underlying biodiversity patterns in urban areas, it is helpful to consider that changes associated with urbanization cascade through multiple pathways, impacting biodiversity in complex ways (Alberti et al., 2020). For example, road networks, which are most dense in urban centers with high human settlement densities, can directly affect biodiversity through vehicular collisions and noise pollution (Bennett, 2017; Francis et al., 2012; Kok et al., 2023). Road networks can also *indirectly* affect biodiversity in multiple ways—through increasing habitat fragmentation and pollution runoff, altering predator-prey dynamics, constraining space use through habitat loss, or facilitating the spread of invasive species

(Bennett, 2017; Bowman et al., 2010; Cerqueira et al., 2021; Mumma et al., 2019). As such, axes of environmental change along urbanization gradients are composed of a system of interacting and cascading effects which directly and indirectly drive ecological and evolutionary patterns (Fig. 1). Understanding the mechanisms generating spatial patterns of biodiversity along urban-rural gradients requires approaches that disentangle the direct and indirect causal pathways linking biodiversity to people.

Our study had two goals: first, to test hypotheses about how multiple environmental changes interact to generate spatial patterns in abundance and trait variation along urbanization gradients; and second, to illustrate how a structural causal model framework can effectively be used to do so. We use eastern gray squirrels (*Sciurus carolinensis*) as our study organism. Eastern gray squirrels are ubiquitous in urban and rural habitats across their native range of eastern North America. Previous studies have shown strong urban-rural gradients in abundance and coat color in eastern gray squirrels, with both abundance and the prevalence of melanism greater in more urban environments than adjacent rural areas (Cosentino et al., 2023; Cosentino & Gibbs, 2022; Gibbs et al., 2019). Yet, the processes generating these spatial patterns are unclear, with multiple hypotheses having been proposed. For example, a translocation experiment revealed mortality in rural areas was greater for the melanic than the gray morph, leading to the hypothesis that selection pressures on coat color differ between morphs in rural areas (Cosentino et al., 2023). Differential selection between color morphs may be due to the melanic morph being generally more visible than the gray morph, which could amplify its predation risk, but also decrease the risk of vehicular collisions due to increased visibility to vehicle drivers (Gibbs et al., 2019). Thus, evidence suggests changes in crypsis may alter predation pressure and road mortality in ways that contribute to urban-rural clines in melanism

(Cosentino & Gibbs, 2022; Gibbs et al., 2019). A mechanistic understanding of how these factors operate in concert requires a method to disentangle direct and indirect effects among predation pressure, road mortality risk, and related components of environmental change along the urbanization gradient.

Causal inference in observational designs typical of urban ecology and evolution first requires a scientific model that clearly defines hypothesized causal relationships among variables in the system based on prior knowledge (Arif & MacNeil, 2023; Arif & Massey, 2023; McElreath, 2020). Our research illustrates how directed acyclic graphs (DAG) can be used to define a scientific model based on prior knowledge of the urban system. Cities are complex systems that have a variety of interacting and covarying environmental gradients, so DAGs are essential for communicating the causal relationships assumed about the system. We apply structural equation models (Grace, 2006; Grace et al., 2012), as one possible statistical approach, to estimate the relationships (or lack thereof) among variables implied by the DAG. We think this approach can be harnessed and elaborated to better understand the mechanisms generating spatial patterns of biodiversity along urbanization gradients. Because abiotic and biotic factors are spatially heterogeneous across the urban-rural gradient, disentangling their relationships can also help elucidate the processes generating fine-scale patterns of biodiversity variation within cities.

2. Methods

2.1 Study site

This research was conducted across an urban-rural gradient surrounding Syracuse, New York, USA (43.0469° N, -76.1444° W). Syracuse has ~150,000 people and is characterized by a humid

continental climate (Koppen, 1936) with four distinct seasons, including hot summers and cold winters. Tree cover ranges from 4.5% to 47% across the city, averaging 27% (Nowak et al., 2016), and the surrounding rural landscape is a mosaic agriculture and forest (Fig. S1). .

2,2 Study species and hypothesized drivers

Eastern gray squirrels are an excellent study organism to disentangle direct and indirect paths by which urbanization impacts ecological (e.g., abundance) and evolutionary (e.g., trait variation) outcomes. Eastern gray squirrels are common across urban and rural landscapes in eastern north America, and individuals tend to have one of two common coat colors – gray or black (melanic) — inherited in a simple Mendelian fashion (H. McRobie et al., 2009; H. R. McRobie et al., 2019). Eastern gray squirrels repeatedly show clines in both abundance and prevalence of melanism across urban-rural gradients (Cosentino & Gibbs, 2022; Merrick et al., 2016), providing an excellent opportunity to disentangle mechanisms underlying such patterns. We hypothesize these patterns would be driven by multiple, covarying axes of biotic and abiotic variation. Specifically, we hypothesized human population density, building cover, forest cover, forest fragmentation, the distance to roads (road distance), and mammalian predator activity would affect squirrel abundance and patterns in trait variation across the landscape. We selected these drivers based on previous research, and hypothesized mechanisms by which they affect each other and have downstream impacts on squirrel abundance and coat color prevalence (Tab. 1). For example, human population density influences resources available to squirrels (through food provided through bird feeders and nesting sites in buildings) (Benson, 2013) and building cover can also indirectly affect squirrel abundance by reducing forest cover. Forest cover and fragmentation are linked to nesting availability, food resources and habitat connectivity (Merrick

et al., 2016; Parker & Nilon, 2008). Proximity to roads increases road mortality risk, which plays an important role in squirrel mortality in urban environments (Gibbs et al., 2019). Lastly, mammalian predator activity drives predation risk and influences the landscape of fear, potentially altering squirrel behavior and distribution (Gaynor et al., 2019).

2.3 Camera trapping and point count surveys

We used camera traps and point count surveys to estimate the abundance of gray squirrel color morphs at 49 sites between 16 September 2021 and 13 October 2022 (Cosentino et al., 2023). Because squirrel populations are limited by tree cover, sites were selected in urban greenspaces and rural woodlots with mature deciduous trees (Merrick et al., 2016; Parker & Nilon, 2008). Site locations were chosen to span the urban-rural gradient ranging 1.3–23.7 km from the city center (median = 9.3 km), and separated by at least 1 km. At each site we deployed a single camera trap (Browning Strikeforce Pro XD) between September 2021 and March 2022, fastening the camera to a tree 30-50 cm off the ground. Cameras were active for 46-379 days (median = 263 days), with daily detection histories generated for each color morph by a single observer. We also conducted visual point count surveys at each site between October 2021 and October 2022. During each survey, a single observer recorded the number of squirrels seen of each color morph during a 3-min period. Sites were surveyed 2-7 times each (median = 5).

2.4 Environmental covariates

The environmental covariates selected for our analyses (Tab.1) were measured using the *raster* and *exactextractr* packages in R (Baston et al., 2022; Hijmans et al., 2023). We used a 300-m buffer to summarize environmental covariates around each site to encompass a typical

home range size of gray squirrels (<5 ha) (Koprowski et al., 2016). Human population density was calculated using NASA's CIESIN gridded human population dataset (Center For International Earth Science Information Network-CIESIN-Columbia University, 2017). Building cover was calculated using the building footprint dataset from Cornell University Geospatial Information Repository. Road distance was taken by measuring the distance to the nearest road with a speed limit greater than 30 mph and measured using the NYS GIS Resources repository for public data (https://data.gis.ny.gov). We isolated roads with high-speed limits because vehicular collisions are rare on roads with speed limits <30 mph (unpublished data). Forest cover was measured using the tree cover band from ESA WoldCover dataset derived from Sentinel-1 and Sentinel-2 satellite imagery (Zanaga et al., 2022). We quantified forest fragmentation using the WoldCover dataset by calculating the number of disjunct cores within a 1-km radius of each site using the *landscapemetrics* package in R (Hesselbarth et al., 2019). We used a 1-km radius to represent potential fragmentation effects as this scale is sufficient to capture fragmentation (a landscape-scale process) and it encompasses possible long distance dispersal events typical of males during mating seasons (Cosentino & Gibbs, 2022). Mammalian predator activity was indexed using our camera trap imagery and calculated as the percentage of camera trap days mammalian predators were detected at each site (Bu et al., 2016). Predators detected by camera trap included coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus)*, red fox (*Vulpes vulpes*), fisher (*Pekania pennanti*), domestic dog (*Canis familiaris*) and domestic cat (*Felis catus*).

2.5 Modeling framework

We built a structural equation model (SEM; Grace, 2006) to test how urbanization affects color morph prevalence and squirrel abundance via multiple direct and indirect pathways. We generally followed the guidelines for graph-theoretic implementation of SEM with local estimation (Grace et al., 2012), including development of a metamodel (Fig. 1), a causal graph represented as a DAG (Fig. 2), and assessment of causal assumptions by testing the model for missing links (Fig. 2), followed by re-specification and final model estimation (Fig. 3 & 4). Our SEM consisted of two submodels. The first submodel (our "urbanization" submodel) included direct and indirect pathways linking biotic and abiotic covariates that could affect squirrel abundance (Fig. 2). The second submodel consisted of an integrated hierarchical model combining camera detection data and visual point counts to estimate squirrel abundances by color morph at each site (Cosentino et al., 2023; Kéry & Royle, 2020). This model included an observation model to estimate detection probability of squirrels during surveys, and an ecological process model to test how abundance of each color morph was related to each environmental covariate. Integrating the urbanization and the hierarchical model allowed us to quantify direct and indirect pathways by which urbanization drives color morph frequencies while accounting for imperfect detection of individual squirrels at sampled sites.

2.5.1 Urbanization submodel

The urbanization submodel consisted of linear regressions with identity-link functions to estimate the hypothesized causal relationships among human population density, building cover, road distance, percent forest cover, forest fragmentation, and predator activity (Fig. 2). Although many of these variables have been used as indices of urbanization either alone or as part of a composite index, we developed a model to represent hypothesized relationships linking these

variables. The foundation of our urbanization submodel was human population density, operating on the assumption that environmental change along urbanization gradients ultimately is driven by people. We included direct effects of human population density on building cover and road distance, assuming that buildings and roads are primarily infrastructure used by people. Because roads are the main way to access buildings, we included a direct effect of building cover on road distance. Because buildings and roads require tree removal, we included direct effects of building cover and road distance on forest cover. Forest fragmentation has a known negative relationship with forest cover (Fahrig, 2003, 2017), so we included a direct effect of forest cover on fragmentation. We also included direct effects of building cover and road distance on forest fragmentation, under the assumption that these landscape elements should cause discontinuities in forest cover, irrespective of their effects on absolute forest cover. Each environmental variable was included as a direct effect on predator activity as urbanization can have profound effects on mammalian predator activity (Bateman et al., 2012; Ordeñana et al., 2010).

Urban systems are characterized by many covarying environmental gradients, which creates high potential for confounding variables. Unobserved confounders can cause spurious relationships between the environmental variables in our model and squirrel abundances. To mitigate this concern, we included distance to city center as an additional covariate in the model, with a direct effect on human population density. Including distance to city center allowed us to estimate residual spatial variation in squirrel abundance and morph frequencies along the urbanization gradient. This variable was intended to index axes of environmental variation along the urbanization gradient that were not included in our model, controlling for possible unobserved confounders (Cosentino et al., 2023; Dee et al., 2023).

2.5.2 Squirrel abundance submodel

Our integrated hierarchical model of squirrel abundance consisted of an ecological process submodel to estimate the abundance of each color morph (N_{ik}, where $k = 1$ for the melanic morph and $k = 2$ for the gray morph), and an observation process submodel to estimate individual detection probabilities (p_{ijk}) based on repeated surveys j of color morph k at each location i. For the observation process, we modeled the counts y_{ijk} of each morph from point count surveys as $y_{ijk}|N_{ik} \sim Binomial(N_{ik}, p_{ijk})$ (Royle, 2004), and we modeled the binary detections y_{ijk} of each morph from trail cameras as $y_{ijk}|N_{ik} \sim Bernoulli(P^*_{ijk})$, where $P^*_{ijk} = 1 - (1 - p_{ijk})^{Nik}$ (Royle and Nichols 2003). Because squirrel activity is influenced by ambient temperatures, we modeled individual detection probability as a function of daily ambient temperature (Cosentino et al., 2023; Wassmer & Refinetti, 2019):

$$\text{logit}(p_{ijk}) = a0_k + a1_k*\text{temperature}_{ij} + a2_k*\text{temperature}^2_{ij},$$

where for each color morph k, $a0_k$ represents the intercept, $a1_k$ represents a linear effect of daily temperature, and $a2_k$ represents a quadratic effect of temperature. A quadratic effect was included as squirrel activity peaks with the intermediate temperatures observed during fall and spring (Cosentino et al., 2023).

For the ecological process submodel, we described the abundance of each color morph as $N_{ik} \sim Poisson(\lambda_{ik})$, where λ_{ik} is the expected total abundance of squirrels of each color morph k at location i. We modeled the expected abundance of each color morph as:

$$\log(\lambda_{ik}) = \beta0_k + \beta1_k*\text{distance}_i + \beta2_k*\text{population}_i + \beta3_k*\text{building}_i + \beta4_k*\text{road}_i + \beta5_k*\text{forest}_i + \beta6_k*\text{frag}_i + \beta7_k*\text{predator}_i,$$

where for each color morph k, $\beta 0$ represents the intercept and $\beta 1$- $\beta 7$ represent slopes for effects of distance to city center, human population density, building cover, road distance, forest cover, forest fragmentation, and predator activity.

2.5.3 Model estimation process

We used Bayesian estimation to fit the SEM with JAGS 4.3.0 (Plummer, 2017) and the package *jagsUI* (Kellner & Meredith, 2024) in R (Version 4.2.3, R Core Team 2023). We generally used noninformative prior distributions for intercept and slope parameters (Gelman & Hill, 2007). An informative prior was specified for intercepts for individual detection probability and abundance of each color morph because we had prior knowledge of mean detection probability and squirrel abundance (Cosentino et al., 2023; Lemoine, 2019). Half-Cauchy priors were used for variance parameters, as they are appropriate when setting parameters for variance in hierarchical models (Gelman, 2006). We applied log transformations to population density, road distance, and fragmentation, and we applied a logit transformation to building cover. All environmental covariates were standardized to zero mean and unit standard deviation. For each step of the estimation process (see below), we ran three chains with 20,000 adaptation iterations followed by 4000 iterations, discarding the first 1000 iterations as burn-in and thinning the remaining iterations by three. This resulted in 3000 iterations to describe posterior distributions. Convergence of parameter estimates was confirmed with the Gelman-Rubin statistic (R-hat < 1.1; (Gelman & Hill, 2007).

Model fitting occurred in multiple steps, starting with fitting the initial urbanization submodel. We applied d-separation tests to examine the urbanization submodel for missing links

(Shipley, 2009). These tests consisted of a linear regression between each pair of variables X_i and X_j that were not directly connected in the initial model. Other variables $\{Z\}$ that were direct effects on X_i or X_j were included as covariates in each regression. We tested each independence claim (X_i and X_j)|$\{Z\}$ by examining whether a 90% credible interval for the slope relating X_i and X_j included 0. If the 90% CI excluded 0, we added a direct path between X_i and X_j to the urbanization submodel. After all missing links were added based on the d-separation tests, we refit the urbanization submodel (Fig. 3). We examined 90% CIs for each slope term in the refit model, and we dropped terms when the 90% CI included 0. We used a 90% threshold to err on the side of caution and including possibly important links in the final model. The final SEM consisted of fitting the final urbanization submodel (Fig. 3) together with the squirrel abundance submodel (Fig. 4, Fig. S2). We used 95% CIs to guide interpretation of the final SEM. Model residuals were visually inspected at each step of the estimation process to confirm regression assumptions were met.

For each response variable in the final SEM, we quantified explanatory power (R^2) for Bayesian regression models as the variance of the predicted values divided by the sum of the variance of the predicted values and variance of the residuals (Fig. S2; Gelman et al., 2019). Residuals for each linear regression in the urbanization submodel were quantified as $y_i - \hat{y}_i$, where y_i is the observed value and $\hat{y}_i$ is the predicted value at each site i. For squirrel abundances, we defined residuals as $N_{ik} - \lambda_{ik}$ for each color morph k (Wright et al., 2019).

Because all urbanization covariates were standardized for analysis, regression coefficients in the urbanization submodel represent standardized coefficients (Tab. S1), whereas the raw regression coefficients in the squirrel abundance submodel were unstandardized (Tab. S2). We used the observation-empirical approach to quantify standardized regression coefficients

in the squirrel abundance submodel (Lefcheck et al., 2018). We used the standardized coefficients to quantify direct, indirect, and total effects of predictors on each response variable.

2.5.4 Residual spatial variation in proportion melanic and total abundance

Using the model estimates for each morph abundance, we derived total squirrel abundance ($N_\text{total}_i = N_{i1} + N_{i2}$) and the proportion of melanic squirrels (N_{i1}/N_total_i). We then compared the direct and total effects of distance to city center on morph abundance, total abundance, and proportion melanic. The direct effect of distance to city center represents residual spatial variation along the urbanization gradient unexplained by explanatory variables in our urbanization submodel, whereas the total effect represents residual spatial variance plus variation explained by the urbanization submodel (i.e., indirect effects of distance to city center mediated by covariates in the urbanization submodule). The difference between the direct and total effect isolates variation explained by the urbanization submodel (Fig. 5).

2.5.5 Comparison of effects between morphs

To compare the direct effects of each explanatory variable on abundance between color morphs, we derived the posterior distribution of the difference in unstandardized regression coefficients between morphs for each predictor. We used unstandardized coefficients to compare direct effects between morphs because standardized coefficients were conflated by differences in variance in abundance for each morph. Thus, we used standardized coefficients to compare the

relative strength of pathways *within* each morph abundance model (Fig. 4a & 4b), whereas unstandardized coefficients to compare effects *between* morphs (Fig. 4c).

3. Results

3.1 Urbanization submodel

Our urbanization submodel demonstrated how human population density affects abiotic and biotic factors through multiple causal pathways (Fig. 3). Human population density directly increased building cover, which subsequently decreased forest cover. When forest cover decreased, forest fragmentation increased. Thus, population density indirectly decreased forest cover and increased forest fragmentation through its effect on building cover. We also found evidence for a direct positive effect of population density on forest fragmentation that was not included in our initial model (Fig. 2; Tab. S1). Mammalian predator activity was positively related to human population density, independent of effects of population density on building cover, forest cover, and fragmentation. Population density was negatively related to distance to city center as expected, and d-separation tests identified a residual negative relationship between forest fragmentation and distance to city center. None of the variables in our model predicted distance to high-speed roads.

3.2 Morph abundances

Our model revealed markedly different pathways by which urbanization affects color morph abundances of gray squirrels (Fig. 4, Tab. S2). Human population density had a strong direct effect on abundance of the gray morph, with abundance higher in more densely populated areas. In contrast, there was no direct effect of human population density on melanic abundance.

342 Both gray and melanic abundances were indirectly related to human population density via its
343 cascading effects on building cover, forest cover, forest fragmentation, and predator activity.
344 Forest cover, fragmentation, and predator activity all had direct effects on each morph, but the
345 nature and magnitude of these effects varied between morphs. For example, forest cover had a
346 negative direct effect on gray abundance but a positive direct effect on melanic abundance.
347 Fragmentation had a negative direct effect on both morph abundances, but the effect was
348 stronger for the melanic than gray morph (Fig. 4c). Melanic abundance was negatively related to
349 predator activity, whereas gray abundance was *positively* related to predator activity. Road
350 distance had a positive direct effect on melanic abundance but no effect on gray abundance.
351 Building cover had no direct effect on the abundance of either morph.

352 In addition to direct effects, our model revealed many indirect and cascading paths by
353 which urbanization impacted each morph abundance (Tab. S2). The direction of most indirect
354 effects of urban covariates on abundance was consistent with direct effects, but in some cases the
355 direct and indirect effects were opposite. For example, forest cover and building cover had
356 different direct and total effects. Forest cover directly drove lower gray morph abundance but
357 had a weak indirect positive effect through its reducing fragmentation, resulting in no total effect
358 of forest cover on gray morph abundance (Tab. S2). Building cover had no direct effect on either
359 morph, but indirectly drove lower melanic abundance, resulting in a negative total effect of
360 building cover on melanic abundance (Tab. S2).

361 Importantly, there was no direct effect of distance to city center on gray morph
362 abundance, but there was a negative total effect (Fig. 5, Tab. S2). This indicates that the variation
363 in gray abundance along the urbanization gradient was adequately explained by variables in our
364 urbanization submodel. In contrast, we found both direct and total negative effects of distance to

city center on melanic abundance (Fig. 4 & 5, Tab. S2). The strong direct effect of distance to city center on melanic abundance indicates there was substantial residual variation in melanic abundance along the urbanization gradient that remained unexplained by the covariates in the urbanization submodel. Derived quantities (proportion melanic and total squirrel abundance) showed strong negative clines with distance to city center (Fig. 5b & 5c), outcomes that align with previous research showing this pattern across numerous cities (Cosentino et al., 2023; Cosentino & Gibbs, 2022). However, our models decompose this finding between morphs and reveal the cline in total abundance was driven largely by the decline of melanic abundance as distance to city center increased, a finding in line with previous work showing melanic survival declines further from the city center (Cosentino et al., 2023, Fig. 5).

Discussion

Our findings reveal a complex network of effects by which the urban environment alters abundance and trait variation in gray squirrels. We show markedly different mechanistic pathways driving abundance of two distinct phenotypes, and these distinct processes together determine urban-rural clines in species abundance and trait variation. Human population density impacted the two morphs in different ways, having a direct positive effect on gray morph abundance, a pattern likely facilitated by novel resources associated with people (i.e., bird feeders), but only indirectly impacted melanic morph abundance through its effect on landscape structure (i.e., through forest cover and fragmentation). For some covariates (e.g., forest fragmentation) the direction of the effect on color morph abundances was the same, but the magnitude of effect differed. But, for other covariates (e.g., predator activity and forest cover) the effects were entirely opposite (Fig. 3). Thus, our study reveals phenotypic specific

388 mechanisms and complex processes underlying known urban-rural clines in biodiversity patterns
389 (Fig. 2 & 3). Our findings also demonstrate urbanization is comprised of a network of processes
390 that should be considered in concert to understand and mitigate their impacts.

391 Developing a scientific model with hypothesized causal relationships between drivers—
392 represented in our DAG—is critical for informing appropriate statistical modeling in ecological
393 systems (Arif & MacNeil, 2023). Statistical models built from DAGs enable researchers to
394 differentiate between direct and indirect effects, control for confounders, and identify spurious or
395 masked effects to better understand the multiple causal processes at play (Grace et al., 2012;
396 McElreath, 2020). For example, our models revealed forest cover had a direct negative effect and
397 an indirect positive effect through fragmentation on gray morph abundance, leading to no total
398 effect. Without modeling the relationships between forest cover and fragmentation in our system,
399 we would have erroneously concluded that forest cover has no effect on gray morph abundance,
400 when, in fact greater forest cover on its own likely caused a decline in gray morph abundance,
401 but this effect was countered by the positive indirect effect via reduced fragmentation. Thus, our
402 work highlights how DAGs can be used in studies in urban ecology and evolution to disentangle
403 interacting mechanisms at play in each system and break down their effects into their various
404 components (Arif & MacNeil, 2023; McElreath, 2020).

405 Our results also provide important insights into how urban effects can be mediated by
406 phenotypic trait variation, with some trait variants being more sensitive to anthropogenic impacts
407 than others. In our system, melanic abundance was more sensitive to landscape change via
408 deforestation, fragmentation, and distance to high speed roads than gray abundance (Fig. 4).
409 While many studies have demonstrated phenotypic changes across the urban-rural gradient
410 (Campbell-Staton et al., 2020; Santangelo et al., 2018, 2020; Winchell et al., 2016), our study

411 provides a clear example of anthropogenic impacts operating differently on two phenotypes.
412 These differences reveal a suite of mechanisms and processes underlying observed trait variation
413 across the landscape. For example, our results show divergent sensitivity to predation between
414 phenotypes. Indeed, greater predator activity drove lower melanic abundance, but not gray
415 abundance. Thus, modeling the abundances of each phenotype separately revealed important
416 differences in mechanisms at play affecting both phenotypes and shows both habitat change and
417 predator activity play key roles in determining the observed urban-rural clines, albeit by
418 operating differently on each phenotype.

419 The difference in effects of predator activity on each morph's abundance—with predator
420 activity negatively affecting melanic morphs, but positively affecting gray morphs—is consistent
421 with the hypothesis that melanic squirrels are more visible to predators and thus exposed to
422 greater predation risk (Bryan, 2020; Gibbs et al., 2019). The melanic morph is generally less
423 cryptic than the gray morph in urban and rural habitats (Bryan, 2020), so crypsis is likely a key
424 factor driving patterns in melanism across urban-rural gradients. However, in addition to
425 differences in crypsis, it is possible the two morphs differ in behavior or activity patterns in ways
426 that alter their predation risk (Engel et al., 2020; Sarno et al., 2015). For example, the melanic
427 and gray morph may exhibit different diel activity patterns, or activity patterns across vertical
428 space (from ground and canopy) resulting in differing susceptibility to predation or thermal
429 conditions (Bryan, 2020; Ciurej et al., 2020; Ducharme et al., 1989). One hypothesis for such
430 differences in spatial or temporal activity patterns is that each morph's thermal constraints differ
431 (Ciurej et al., 2020). Indeed, evidence suggests melanism can provide a thermal benefit in
432 squirrels, particularly in colder winter months, allowing them to be more active during cold times
433 (Ciurej et al., 2020; Ducharme et al., 1989). As thermal microclimates vary both throughout the

434 day and across vertical strata of arboreal habitats (Gámez & Harris, 2022; Nakamura et al.,
435 2017), differences in thermal constraints between morphs could result in differential activity
436 patterns. Thus, future research should investigate how thermal conditions and squirrel activity
437 patterns may contribute to patterns in melanism across the landscape.

438 While our models showed forest loss and fragmentation did not directly alter predator
439 activity patterns (Fig. 3), it is likely the effects of such habitat alteration and predator activity are
440 still connected. Many studies have shown fragmentation can increase exposure to predation risk
441 (Fischer & Lindenmayer, 2007; Robinson et al., 1995; Schneider et al., 2012). Thus, given
442 melanic squirrels were found to be more susceptible to predation pressure (Bryan, 2020), it may
443 explain one reason they are also more susceptible to landscape change, as it could expose them
444 to more predation and reduce their ability to camouflage. Indeed melanic squirrels are more
445 easily detected visually in urban landscapes (Gibbs et al., 2019) and thus, landscape change and
446 predator activity could synergistically drive lower melanic abundance. Our models do not
447 explicitly test for synergistic effects and future studies should explicitly test for synergies arising
448 in such systems.

449 The sensitivity of melanic abundance to multiple common axes of environmental change
450 in cities, such as habitat loss and fragmentation, raises an important question about what
451 maintains urban-rural clines in melanism. Indeed, the environmental variables in our
452 urbanization submodel showed that melanic abundance had an indirect positive relationship with
453 distance to city center, which should result in greater melanic abundance further from the city
454 center (Tab. S2). However, these indirect effects were counteracted by a strong, negative direct
455 effect of distance to city center on melanic abundance, ultimately resulting in a total negative
456 effect, with melanic abundance declining further from the city center (Tab. S2). The direct

negative effect of distance to city center on melanic abundance indicates our urbanization submodel is missing some variables or processes that could cause melanic abundance to be high in cities (Dee et al., 2023).

The intriguing and seemingly contradictory pattern, in which melanic abundance is more sensitive to urban environmental changes but found in greater abundance closer to the city center, may be due to the interaction of historic and contemporary forces, including ecological, evolutionary, and social forces (Des Roches et al., 2021). For example, melanic squirrels, once common across the landscape, were largely extirpated with the rise of European colonial settlement, the accompanied deforestation and logging in surrounding old growth forests, and extensive hunting (Benson, 2013; Cronon, 1991; Robertson, 1973). Evidence suggests urban areas functioned as refugia for gray squirrels in general, including the melanic morph (Benson, 2013; Gibbs et al., 2019). Additionally in the 1930s some naturalists promoted feeding gray squirrels, introducing them to urban areas, and celebrated them as “our most loved” species in cities, establishing a social attitude of tolerance and even celebration (Benson, 2013). Thus, urban-rural clines in abundance in gray squirrels likely arose from both ecological and social processes, which together can drive patterns in present day urban biodiversity (Cosentino et al., 2023; Cosentino & Gibbs, 2022; Des Roches et al., 2021). But, with nearly two centuries of forest recovery (Thompson et al., 2013) and a decline in hunting across the United States (Price Tack et al., 2018), it is striking that a cline with distance to city center persists for melanic abundance, but not the gray morph (Fig. 4a & 4b). Thus, urban-rural clines in melanism are likely maintained by novel contemporary forces, perhaps by a combination of predation pressure (including human hunting), social forces (such as humans providing food via bird feeders), and dispersal constraints, more strongly impacting melanics than gray morphs, despite much

surrounding forest recovery (Cosentino et al., 2023). These findings point to the importance of considering historical social and ecological context when seeking to understand present day patterns associated with urbanization and highlights historic and contemporary forces often operate together determine current biodiversity patterns (Des Roches et al., 2021).

One surprising finding from our work is that predator activity had a positive effect on gray morph abundance but a negative effect on melanic abundance. There are at least two possible explanations for the positive effect of predators in gray morphs. First, there may be unobserved confounders driving this association, for example a particular unmeasured habitat characteristic or resource that benefits both the gray morph and predators. Alternatively, it is possible this positive association is evidence of unmodeled indirect paths by which predator activity drives greater gray morph abundance (Abrams, 2009; Holt & Bonsall, 2017). For example, predator activity could reduce competition pressure if it disproportionately negatively impacted competing species, thus indirectly allowing greater gray morph abundance (Abrams & Matsuda, 1996). However, it should be noted that our methods only allowed us to account for mammalian predators and future research should incorporate raptor activity, as they are also important squirrel predators. Incorporating raptor predation risk may further elucidate complex predator-prey dynamics in urban systems.

Another mechanism hypothesized to contribute to urban-rural clines in melanism of eastern gray squirrels is road mortality (Gibbs et al., 2019). Prior research shows melanic squirrels are underrepresented among road kill, relative to the gray morph—a finding attributed to humans more easily detecting and avoiding melanic squirrels against gray asphalt when driving (Gibbs et al., 2019). Our findings provide important insights into this hypothesis showing melanic abundance is lower closer to roads (Fig. 4b). This finding suggests underrepresentation

of melanic squirrels among roadkill may be due in part to behavioral avoidance of roads by melanic squirrels, rather than simply a reduced risk of mortality through human detections while driving. However, these mechanisms are not mutually exclusive, as reduced road mortality risk for melanic morphs may be driven by both behavioral avoidance of roads and vehicle drivers being more likely to see and avoid hitting melanic individuals.

An important consideration for future research is camera trap placement, as our camera traps were placed near ground level, limiting our ability to account for arboreal activity (Moore et al., 2020). However, considering a species' vertical niche is critical when studying arboreal species, as vertical niche lability has been linked to mitigating changes in climate, avoiding predation, reducing competition between species, and can even change with urbanization (Basham & Scheffers, 2020; Borden et al., 2021; Gámez & Harris, 2022; Rankin et al., 2018). How urbanization affects the vertical stratification and movement of species through arboreal space is poorly understood (Borden et al., 2021; Lakatos et al., 2022). Incorporating point count surveys in which an observer visually counted squirrels across the available vertical habitat likely mitigated the ground-level-bias in our study by accounting for squirrels in trees. Nevertheless, some of the observed patterns in morph abundances could be influenced by shifts in vertical niche, particularly if vertical niche use differs between morphs. For example, if one morph shifts to a more arboreal niche in the presence of certain predators or under certain habitat conditions (Borden et al., 2021; Neilly et al., 2017), it would alter the detection probability between morphs in ways we cannot presently account for. Thus, future camera trap studies in cities targeting arboreal species should consider including canopy camera traps to distinguish between changes in abundance or activity, and the possibility that species are instead shifting

vertically across their vertical niche along the urban-rural gradient (Borden et al., 2021; Culbertson & Herrmann, 2019).

Overall, our research demonstrates how urban effects on abundance and phenotypic trait variation are complex, involving a system of direct and indirect mechanisms. We illustrate how scientific models represented with DAGs and statistical analysis with structural equation models can be used to disentangle the effects of environmental variables commonly used to broadly represent urbanization. By applying a structural causal model framework, this study allowed us to characterize the structure of relationships between drivers in our system and mechanistically understand how this system drives ecological and evolutionary patterns in a ubiquitous mammal (Arif & MacNeil, 2023). There is great opportunity for research in urban ecology and evolution to incorporate structural causal modeling frameworks to disentangle the mechanisms at play in urban systems and understand the causal drivers of intra and inter-city variation. By elucidating these complex systems, we will gain valuable insight into the role distinct urban drivers play in determining ecological and evolutionary patterns both within and between cities.

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Data Availability: Data and code are available in the following repository:

https://github.com/bcosentino/urbanCausalInference

Conflict of Interest Statement: We, the authors, declare no conflict of interest in conducting and writing this work.

554 **Figures**
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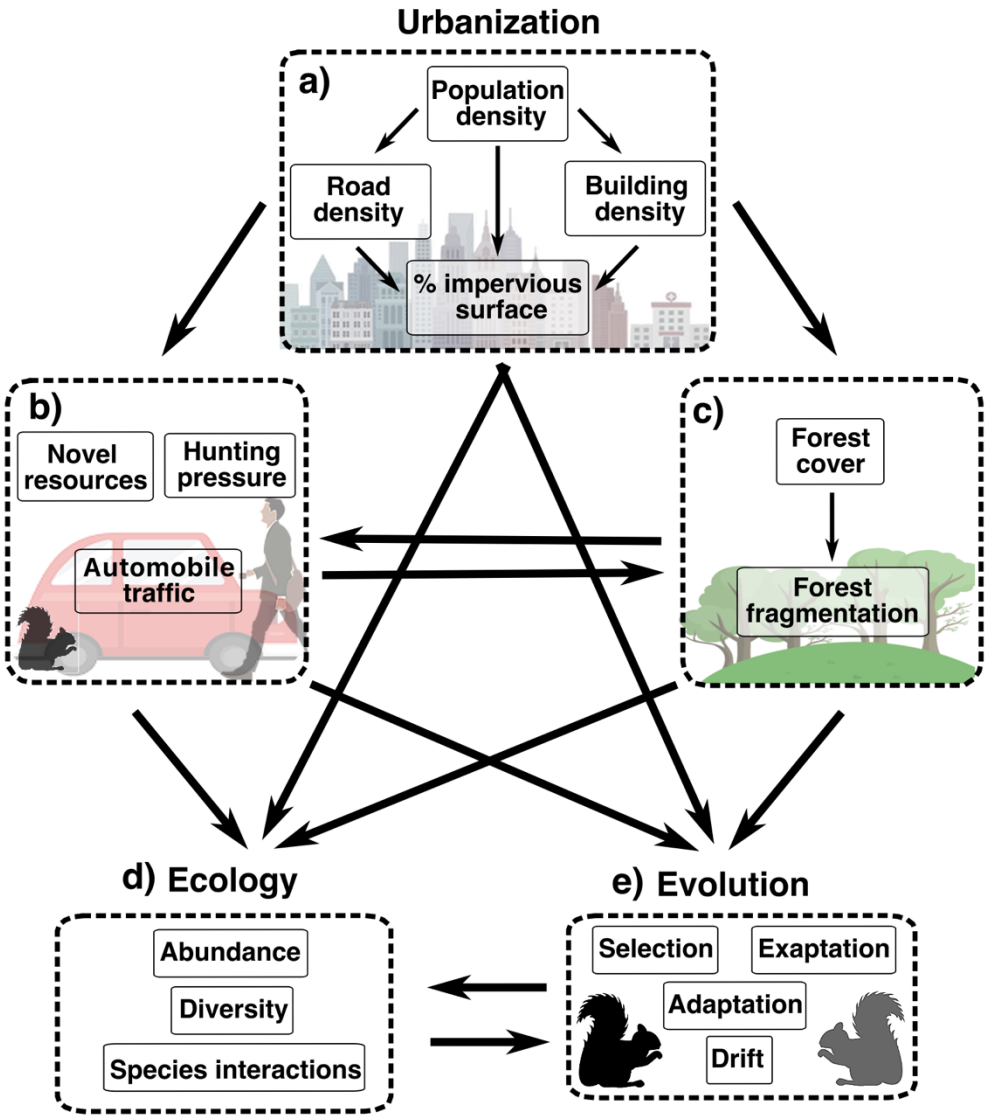

556
557 **Figure 1.** The conceptual metamodel of the complex network of effects from urbanization and
558 the many potential direct and indirect paths of impact to ecological and evolutionary processes.
559 a) Urbanization consists of a suite of interacting anthropogenic impacts, which can represent
560 distinct mechanisms of impact to biotic systems. This suite of changes directly alters b) human
561 wildlife interactions, c) habitat quality and configuration, d) ecological processes, and e)
562 evolutionary processes. However, there are also many indirect pathways by which urbanization
563 can impact ecological and evolutionary processes.
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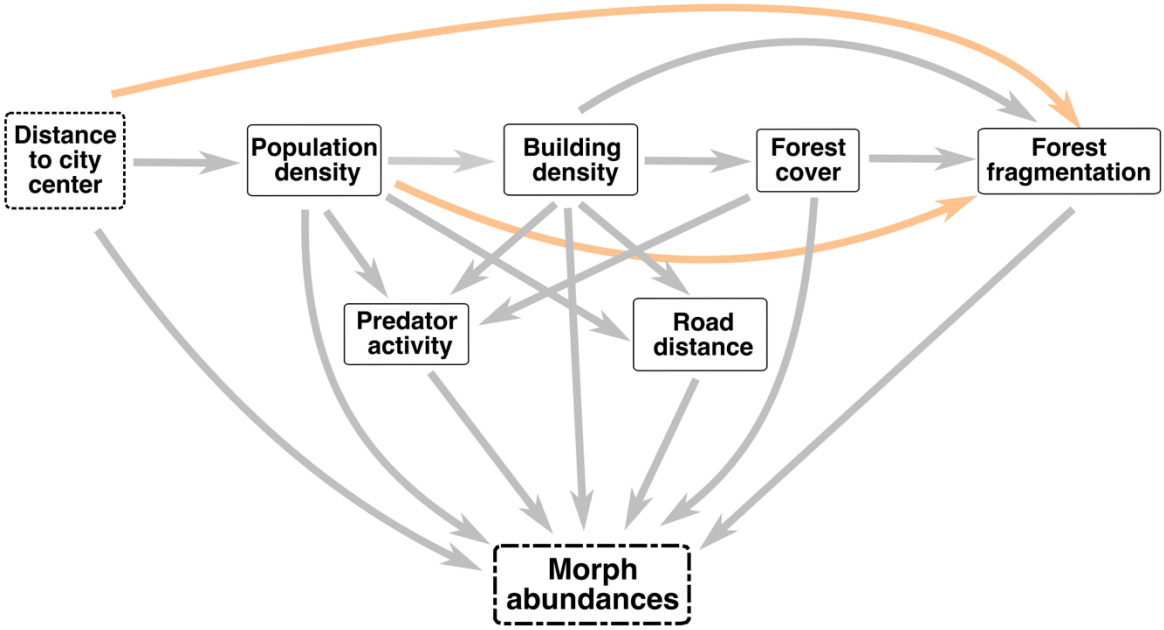

Figure 2. Diagram of our full scientific model, showing the hypothesized causal relationships between drivers and morph abundances. Gray arrows show the initial paths we hypothesized, and orange arrows indicate paths added after D-separation test revealed missing important causal paths.

571 **Table 1.** List of initial hypothesized causal paths by which drivers interact and impact squirrel
572 ecology in our system. Arrows in the first column indicate the hypothesized direction of effect
573 and bolded rows show hypothesized direct causal effects on abundance and morph prevalence in
574 eastern gray squirrels.
575

Effect	Expected direction	Rationale	References
Human population density → building density	**(+)**	Greater human population drives land conversion, including expansion of urban areas and greater building cover	(Ehrlich et al., 2018; Güneralp et al., 2020; Xu et al., 2018)
Human population density → road distance	**(-)**	Greater human population is linked to greater infrastructure including higher road density, reducing the distance to roads	(Xu et al., 2018)
Human population density → mammalian predator activity	**(-)**	Greater human activity alters mammalian predator activity through altered human-wildlife interactions, niche shifts, habitat and resource alteration	(Cervantes et al., 2023; Gilbert et al., 2022; Tucker et al., 2021)
Building cover → forest cover	**(-)**	Greater building density, by definition, reduces forest cover, and is a major driver of deforestation in urban settings.	(Güneralp et al., 2020)
Building cover → road distance	**(-)**	Greater building cover requires greater infrastructure resulting in smaller distance to roads as building cover increases	(Bi et al., 2010)
Building cover → mammalian predator activity	**(+/-)**	Urbanization and building cover can alter landscape connectivity for mammalian predators, reduce habitat availability, and alter prey availability	(Bateman et al., 2012; Cervantes et al., 2023; Li et al., 2022; Tucker et al., 2021)
Building cover → forest fragmentation	**(+)**	Building cover replaces natural habitats and therefore drives forest loss and fragmentation	(Güneralp et al., 2020)
Forest cover → fragmentation	**(-)**	Forest loss and fragmentation, while different, are closely correlated and greater forest cover reduces fragmentation	(Fahrig, 2017; Fletcher et al., 2018)
Forest cover → mammalian predator activity	**(+/-)**	Forest cover alters mammalian predator activity and can be either negative or positive depending on the species and context.	(Dijak & Thompson, 2000; Regolin et al., 2017)

Human population density → squirrel/morph abundances	**(+/-)**	**Human population density can drive greater squirrel abundance through provisions of novel resources (bird feeders, buildings for nesting), and through indirect paths altering predator activity and habitat availability. Effects may differ by morph.**	**(Benson, 2013; Mccleery et al., 2007; Reed & Bonter, 2018)**
Building cover → squirrel/morph abundances	**(+/-)**	**Alters habitat availability by reducing tree cover but also providing novel nesting sites in buildings**	**(Benson, 2013; Parker & Nilon, 2008)**
Road distance → squirrel/morph abundances	**(+/-)**	**Roadkill is a major driver of squirrel mortality in urban contexts and road mortality rates differ between morphs**	**(Gibbs et al., 2019)**
Forest cover → squirrel/morph abundances	**(+/-)**	**Reduces fragmentation and increases connectivity. Increases available natural resources (including food and nesting resources), increases predator activity**	**(Koprowski et al., 2016; Merrick et al., 2016; Parker & Nilon, 2008)**
Forest fragmentation → squirrel/morph abundances	**(+/-)**	**Reduces habitat connectivity and available natural resources, and constrains movement. May affect the morphs differently.**	**(Koprowski et al., 2016; Parker & Nilon, 2008)**
Mammalian predator activity → squirrel/morph abundances	**(+/-)**	**Mammalian predator activity alters predation risk as well as the landscape of fear, likely altering squirrel abundance patterns. Differences in crypsis or behavior may cause morphs to be affected differently by predator activity.**	**(Cosentino & Gibbs, 2022; Gibbs et al., 2019)**

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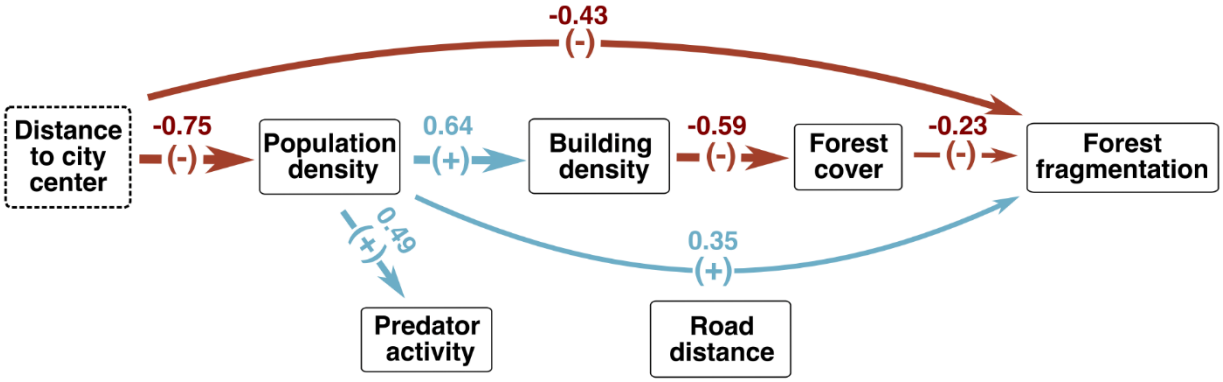

Figure 3. Results from the urbanization covariate sub model. This model reveals the complex and interactive structure and causal relationships between the urbanization variables in our system. Arrows represent effects for which the confidence intervals did not overlap zero and no arrows are included for effects for which the confidence interval did overlap zero. Arrow thickness represents the strength of the effect, and colors and symbols shows the direction of the effect (blue = positive, red = negative). Distance to city center represents a non-mechanistic spatial variable which accounts for unmeasured variance in our system, likely due to unmeasured covariates.

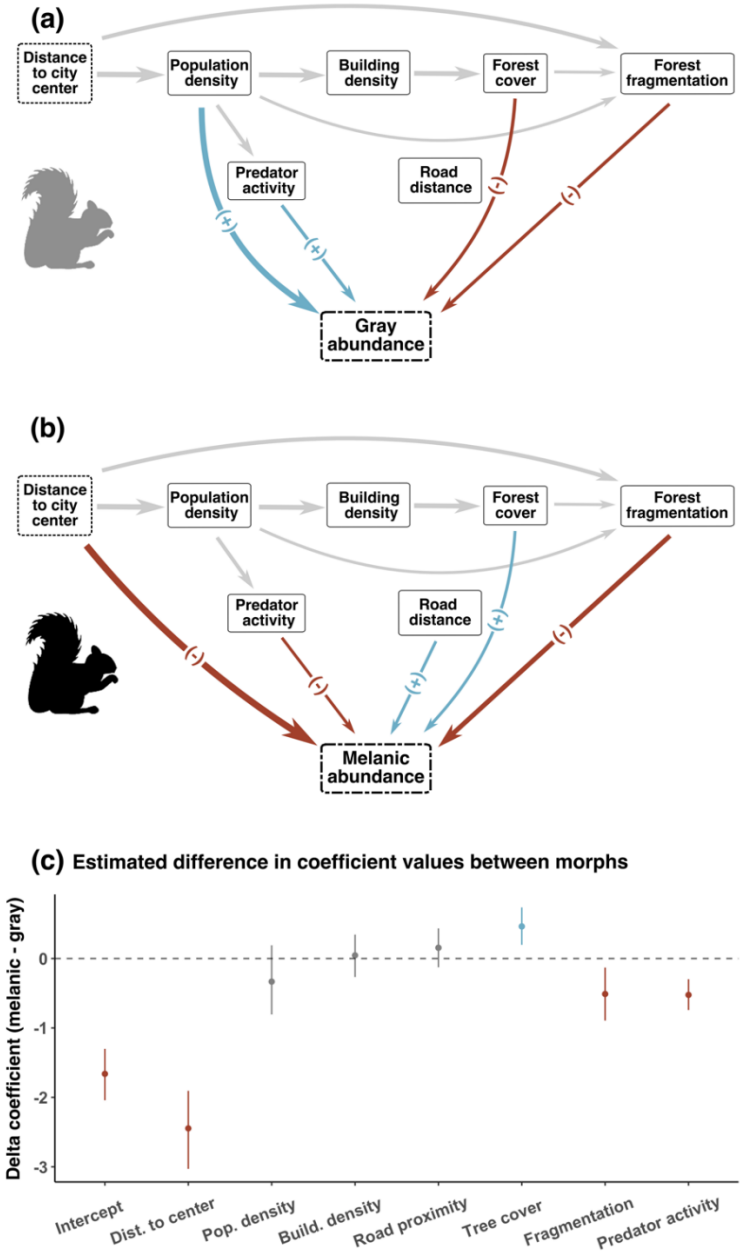

Figure 4. Models revealed markedly different direct and indirect pathways driving abundance patterns in (a) gray morph, and (b) melanic morph, eastern gray squirrels. Specifically, abundance of (a) the gray morph was positively affected by human population density and predator activity, and negatively affected by forest cover and forest fragmentation. Abundance of (b) the melanic morph was positively affected by road distance and greater forest cover, but negatively affected by distance to city center, predator activity, and forest fragmentation. Differences in model coefficients between morphs (c) revealed effects of distance to city center, tree cover, fragmentation and predator activity all varied significantly between morphs. For all panels, red and blue represent negative and positive values, respectively. Gray points (c) represent values for which the credible interval overlaps zero.

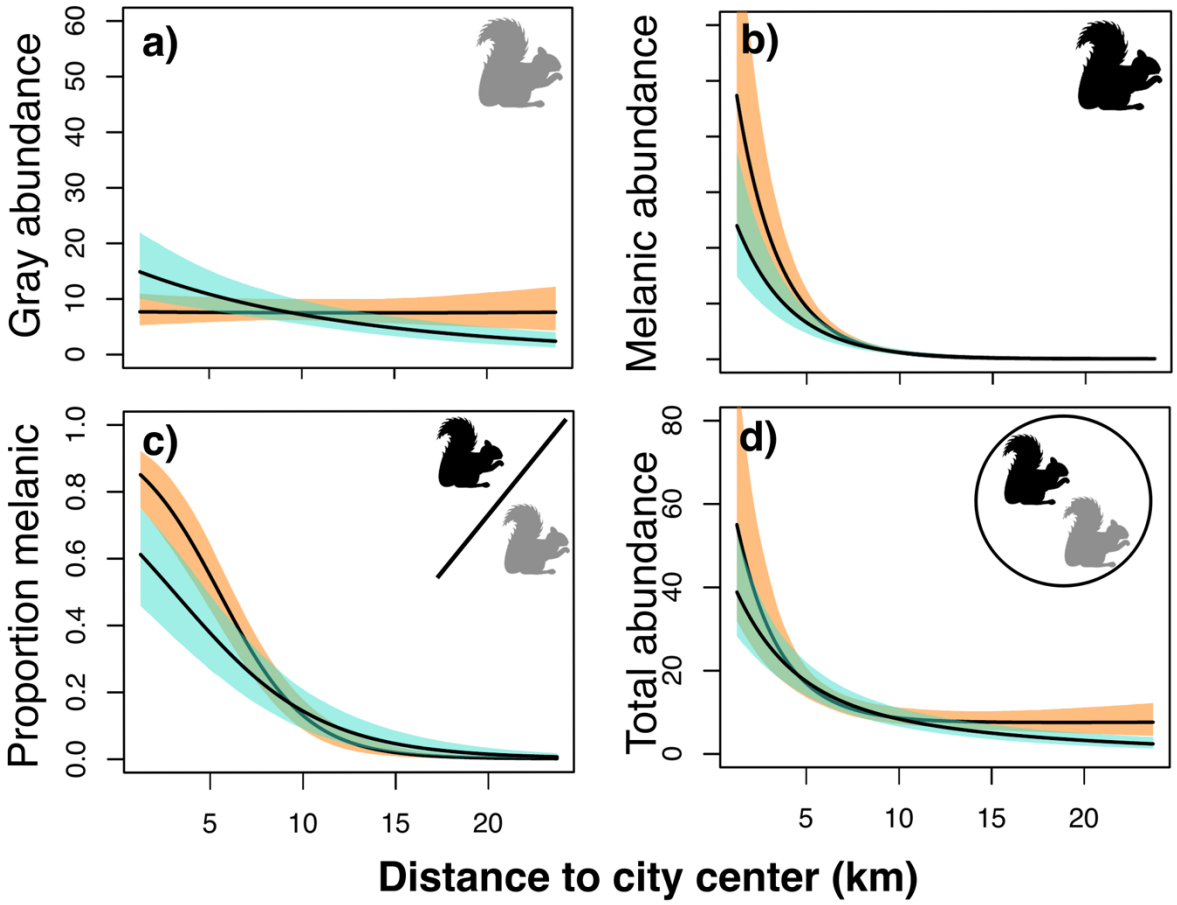

Figure 5. Predicted (a) melanic and (b) gray morph abundances, (c) proportion melanic, and (d) total squirrel abundance in relationship to distance to city center for eastern gray squirrels (*Sciurus carolinensis*) in Syracuse, NY, USA. Differences between direct (orange shading) and total (blue shading) effects in each panel provides a visual representation of the degree to which the environmental covariates in our study accounted for observed variation in abundance and color morph proportions.

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