


Effects of multiple aspects of anthropogenic landscape change on mesopredator relative abundance

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ABSTRACT

Context. Anthropogenic landscape changes have substantial effects on biodiversity and animal populations worldwide. However, anthropogenic landscape change can take a variety of forms, and its effects on wildlife species can vary by landscape context and scale. It is therefore critical that studies of the effects of anthropogenic landscape change on wildlife consider landscape context and model effects of landscape change at multiple scales. Mesopredators serve as an excellent case study of scale-dependent and even contradictory effects of anthropogenic landscape change, because mesopredator populations can respond both positively and negatively to landscape change depending on its form (e.g. agricultural production, urbanisation) and scale. **Aims.** The aim of this study was to model relationships between multiple aspects of anthropogenic landscape change, including agricultural production and the proliferation of non-native shrubs, and relative abundance of three mesopredator species: Virginia opossum (*Didelphis virginiana*), striped skunk (*Mephitis mephitis*), and raccoon (*Procyon lotor*). **Methods.** We summarised landscape variables at two scales and built both single-scale and multi-scale models linking relative abundance of mesopredators to landscape variables. **Key results.** We found that relative abundance of all three species was most related to either the transition from natural areas to agricultural areas (brown-to-green gradient) or the likelihood of presence of non-native shrubs. We also found that responses to anthropogenic landscape change varied by spatial scale; for instance, skunks and raccoons had higher relative abundance in parts of Illinois with more forest cover and agriculture, respectively, but avoided more highly forested and agricultural areas, respectively, at smaller scales. **Conclusions.** Mesopredator responses to landscape change were highly variable and scale-dependent, but were generally related to transitions from forest to agriculture or the presence of non-native shrubs. **Implications.** Our study demonstrates the need to model effects of anthropogenic landscape change at multiple scales, given the differing results that can be achieved when landscape variables are measured at multiple scales.

Keywords: anthropogenic landscape change, invasive plants, landscape context, mesopredators, northern raccoon, spotlight surveys, striped skunk, Virginia opossum.

Introduction

Human modification of landscapes, including agricultural production, construction of roads and buildings, and proliferation of non-native species, poses a major threat to biodiversity (Matson *et al.* 1997; Seto *et al.* 2012; Venter *et al.* 2016). Agricultural production and intensification have been leading causes of landscape change over the past century both globally (Lambin and Meyfroidt 2011; Venter *et al.* 2016) and in the Midwestern USA (Walk *et al.* 2010; Berry *et al.* 2017). Agricultural production can negatively affect wildlife and ecosystems by increasing habitat fragmentation and decreasing habitat connectivity (Cosentino *et al.* 2011), while also reducing the functional diversity of wildlife communities (Flynn *et al.* 2009). Agricultural production also provides anthropogenic food subsidies (Demeny *et al.* 2019), which can have positive effects on synanthropic species but detrimental effects on others (Oro *et al.* 2013). Other aspects of landscape change such as urbanisation can have complex effects on wildlife

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species, with some effects that are positive (e.g. refuge from predators, anthropogenic resources) and some that are negative (e.g. habitat loss and fragmentation) (Moll *et al.* 2020; Padilla and Sutherland 2021). It is therefore critical to understand how species respond to anthropogenic change and what aspects of change are most influential.

The effects of anthropogenic landscape changes on wildlife can be indirect and depend on landscape context and scale (Berry *et al.* 2017; Moll *et al.* 2019). Conceptually, anthropogenic landscape change can be characterised along a hard-to-soft gradient based on the amount of impervious ground cover and along a brown-to-green gradient based on the presence of human-modified but open (i.e. not impervious surface) landscapes, such as agriculture, vs natural areas (i.e. forests or wetlands; Padilla and Sutherland 2021). These gradients can have different effects on wildlife species and are often context-dependent. For instance, American robin (*Turdus migratorius*) occupancy is consistently related to 'greenness' of US urban areas but responses to 'hardness' are city-specific (Padilla and Sutherland 2021). Furthermore, the scale at which a species responds to major drivers of anthropogenic landscape change, including agricultural production and urban development, also varies (Gehring and Swihart 2003; Moll *et al.* 2020), as does the magnitude and direction of response (Lesmeister *et al.* 2015). Given the complexity of landscape changes and species' responses to them, it is imperative that studies ideally include sufficient data to investigate multiple dynamic, temporally variable, and scale-dependent aspects of landscape change (Moll *et al.* 2019).

Mesopredators are an ecologically important group which can have large effects on humans and other wildlife (Prugh *et al.* 2009; Ritchie and Johnson 2009). Several North American mesopredators, including striped skunk (*Mephitis mephitis*, hereafter skunk), Virginia opossum (*Didelphis virginiana*, hereafter opossum), and northern raccoon (*Procyon lotor*, hereafter raccoon), are synanthropic and may respond positively to multiple anthropogenic landscape changes, although scale can affect responses to landscape features (Gehring and Swihart 2003; Moll *et al.* 2020). For instance, skunks are commonly associated with human structures and sometimes with agricultural fields at landscape scales (Gehring and Swihart 2003; Lesmeister *et al.* 2015; Allen *et al.* 2022a). In both urban and rural areas, opossums are associated with forests and water sources at local scales (Gehring and Swihart 2003; Fidino *et al.* 2016; Wait *et al.* 2020). Raccoons prefer forest cover in rural landscapes (Dijak and Thompson 2000; Gehring and Swihart 2003) and often use anthropogenic food sources (Demeny *et al.* 2019). Relative abundance metrics for all three species have changed alongside landscape changes in Illinois and the Midwestern USA, with raccoon relative abundance strongly increasing according to multiple metrics, opossum relative abundance slightly increasing, and skunk relative abundance changing non-linearly but remaining relatively stable (Gehrt *et al.* 2002, 2006; Bauder *et al.* 2021). Causes of these changes

are uncertain but may include changing patterns in harvest, winter temperatures, and disease, among other factors (Gehrt *et al.* 2002, 2006; Bauder *et al.* 2021). Given the importance of mesopredators in human-modified landscapes, it is crucial to understand which aspects of landscape change may have affected mesopredator abundance and trends in the heavily modified landscapes of Illinois.

A major consequence of human modification of landscapes is the spread of invasive species (Mosher *et al.* 2009), but invasive species are only occasionally addressed in models of wildlife distribution and abundance. Invasive species are more common in highly disturbed (i.e. low forest cover) landscapes and near roads (Fan *et al.* 2013; Moser *et al.* 2016), and invasive shrubs, in particular, can have wide-ranging effects on wildlife and ecosystems (Pimentel *et al.* 2000). These effects range from altering nest predation rates on birds (Schmidt and Whelan 1999; Schlossberg and King 2010) to attracting rodents and mesopredators (Dutra *et al.* 2011; Vernon *et al.* 2014). Additionally, proliferation of invasive shrub species can influence detection of mesopredators, because invasive species are often found in low-density forests, open areas (i.e. edges), and near roads (Fan *et al.* 2013; Moser *et al.* 2016), where mesopredators are most common.

Many different methods have been used to study the responses of wildlife distribution and abundance to landscape change. Long-term monitoring programs using different survey methods (e.g. pellet counts or spotlight surveys) provide opportunities to study the effects of landscape change over much longer time scales than those of recently developed methods (e.g. camera traps). For instance, spotlight and roadkill surveys have been conducted in Illinois for over four decades and are generally concordant with each other and other indices of abundance of mesopredators in Illinois (Gehrt *et al.* 2002; Bauder *et al.* 2021). However, these long-term monitoring programs may suffer from sampling biases that necessitate the inclusion of covariates or random effects to account for observation error, changes in effort, and other possible causes of changes in detectability of species (Bauder *et al.* 2021).

We used data from long-term spotlight and vegetation surveys in Illinois to characterise the effects of multiple anthropogenic landscape changes at two scales on the relative abundance of three mesopredator species: striped skunk, Virginia opossum, and northern raccoon. We built a model set of single landscape variables to describe which variables best predicted mesopredator relative abundance at two scales: the local scale (i.e. how individual segments of a spotlight survey route differed from the route); and the landscape scale (i.e. how spotlight survey routes differed from other spotlight survey routes in Illinois). We also built cross-scale models using the top local-scale and landscape-scale predictors and their interactions to investigate whether landscape context mediated local-scale responses to landscape change. We expected that skunk relative abundance would be greater in areas with higher proportion of agricultural land

cover or density of human structures (i.e. housing) at the landscape scale (Gehring and Swihart 2003; Lesmeister *et al.* 2015; Crimmins *et al.* 2016; Allen *et al.* 2022a). Although opossums and raccoons are often associated with urban areas (Fidino *et al.* 2016, 2020; Wait *et al.* 2020), given that the landscape of Illinois is primarily agricultural or forested, we expected that opossum relative abundance would be greater in areas with high proportions of forest cover or water (Gehring and Swihart 2003; Fidino *et al.* 2016; Wait *et al.* 2020) at local scales, and that raccoon relative abundance would be greater in areas with high proportion of forest cover at local scales due to raccoon preferences for forest edges (Dijak and Thompson 2000; Gehring and Swihart 2003). We expected that all three mesopredator species would exhibit a negative response to presence of invasive shrub species, because these species' thick vegetation can leaf out early and obscure detection of animals during spotlight surveys.

Methods

Study area

The study area spanned the US state of Illinois (Fig. 1). Bauder *et al.* (2020) provide a detailed description of Illinois' land cover and communities, which we summarise here. Row-crop agriculture is the predominant land cover, particularly in northwestern and central Illinois, accounting for approximately 75% of all land cover throughout the state (US Department of Agriculture 2017). Agriculture has also been a predominant driver of landscape change in Illinois and

the Midwestern USA over the past century (Walk *et al.* 2010; Berry *et al.* 2017). Forest cover, although rare, is increasingly dominant in southern Illinois (Walk *et al.* 2010). The Chicago metropolitan area is in the northeastern portion of the state and constitutes the majority of urban development (Walk *et al.* 2010). In addition to the three focal species of this study, the study area includes several other carnivore species, including red fox (*Vulpes vulpes*), grey fox (*Urocyon cinereoargenteus*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*) (Lesmeister *et al.* 2015).

Spotlight survey data

Spotlight surveys were conducted from 1981 to 2017 prior to leaf-out (21 March–4 April in southern Illinois and 11–25 April in northern Illinois) (Fig. 1). However, due to the limited temporal extent of our landscape change covariates, we used only the years 2001–2017 in our analysis. Illinois Department of Natural Resources (IDNR) staff drove along roads and generally surveyed 40-km routes starting an hour after sunset and travelling between 16 and 24 km per hour. Each route was divided into 25 segments of approximately 1.6 km each. In total, 51 routes were surveyed; not every route was surveyed every year (45 on average were surveyed each year), but consistent methods and effort were used when routes were surveyed. Survey-specific covariates included date and starting and ending average temperature and humidity. For each route segment, the number of opossum, skunk, and raccoon individuals were counted. Further details can be found in Bauder *et al.* (2021).

For each segment, we calculated the approximate midpoint (the midpoint between the start of the segment and the start of

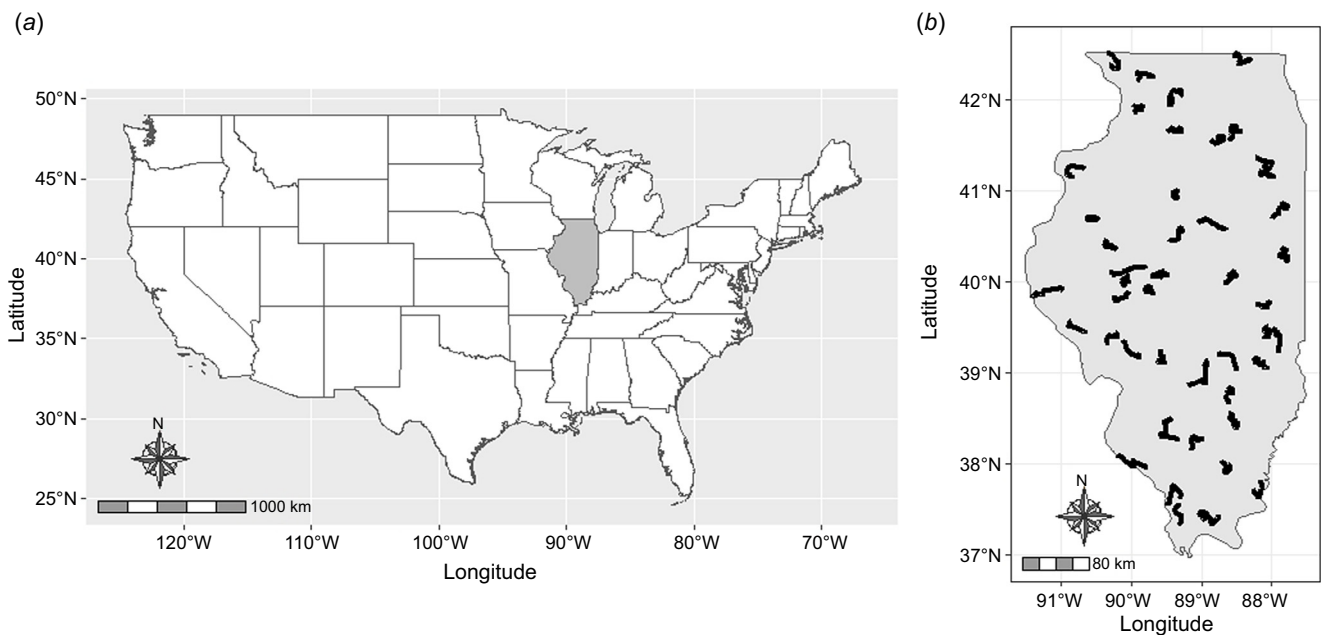


Fig. 1. (a) Map of the continental United States with the state of Illinois highlighted in grey. (b) Study area map with locations of spotlight survey routes in Illinois, USA.

the next segment). Where a segment was broken up into multiple sub-segments, we calculated the midpoints of each sub-segment separately and averaged covariate values extracted at those midpoints prior to analysis. We discarded six segments for which endpoints were not clear. For the purposes of extracting and calculating covariate values, we used a 1-km buffer around each segment midpoint. This buffer size was chosen to be consistent with previous studies (Wait *et al.* 2018; Fidino *et al.* 2020) and to capture variation in land cover across each segment and surrounding areas.

Spatial covariates

We used primarily R packages tidyverse (Wickham *et al.* 2019), sf (Pebesma 2018), raster (Hijmans 2022), velox (Hunziker 2021), and sp (Pebesma and Bivand 2005) in R ver. 4.1.1 (R Core Team 2021) for processing of covariates. For each year 2001–2017, we extracted land cover data from the National Land Cover Database (NLCD) (Homer *et al.* 2020) within a 1-km buffer around each segment midpoint. We extracted land cover data from the latest NLCD data set prior to each year; for instance, we used the 2008 NLCD for the years 2008–2010 and the 2011 NLCD for the years 2011–2012. We calculated the proportion of each land cover type within each buffer and summarised these proportions down to four covariates: the proportion of agricultural land cover (NLCD land cover categories 81 and 82); the proportion of urban (>20% impervious surface) land cover (NLCD land cover categories 22, 23, and 24); the proportion of forest cover (NLCD land cover categories 41, 42, and 43); and the proportion of water (NLCD land cover categories 11, 90, and 95). For each year 2001–2017, we also extracted the latest available housing density (units/km²) from the SILVIS Lab housing density data layer (Helmerts 2021) within the 1-km buffer around each segment midpoint. We extracted density of primary and secondary roads (linear km of road/km²) from the US Census Bureau's TIGER dataset (US Census Bureau 2019). We calculated landscape-scale averages of housing density and road density in the same manner as for land cover proportions (Supplementary Figs S1–S6).

To quantify invasive shrub species' potential presence along spotlight survey routes, we built a presence–absence model for 11 shrub species using long-term monitoring data from the Illinois Critical Trends Assessment Program (CTAP). The CTAP, administered by the Illinois Natural History Survey since 1997, includes data on occurrence and density of invasive shrub species at 574 sites throughout Illinois (Fig. S7). Monitoring protocols are described in detail in Molano-Flores (2002) but we summarise them briefly here. Each site selected for CTAP was surveyed once every 5 years. Sites were selected using area-weighted sampling of townships across Illinois. Within each township, grassland, wetland, and forest sites were selected using habitat-specific criteria (Molano-Flores 2002). At forest sites, shrub and tree plots were surveyed

along three 50-m transects. At wetland and grassland sites, shrub and tree plots were surveyed along one 41-m transect.

We used shrub stem density data from shrub plots for the following 11 invasive shrub species or species groups: honeysuckles (*Lonicera × bella*, *Lonicera japonica*, *Lonicera maackii*, *Lonicera prolifera*, *Lonicera tatarica*, *Lonicera* species that were identified only to genus); Russian and autumn olive (*Elaeagnus angustifolia* and *Elaeagnus umbellata*, respectively); because 106 out of 110 observations of olives were autumn olive, we refer to this group as autumn olive); buckthorns (*Rhamnus cathartica*, *Rhamnus frangula*); and multiflora rose (*Rosa multiflora*). We recorded a species as present at a site if its shrub stem density was greater than 0, and absent otherwise. We built a presence–absence model for each species group (honeysuckle, autumn olive, buckthorn, or multiflora rose) and an overall presence–absence model for all 11 invasive shrubs combined using binomial logistic regression and including year, longitude, latitude, a longitude–latitude interaction, and a custom categorical land cover variable we compiled because CTAP habitat classifications do not readily translate to the land cover types we used in our models of skunk, opossum, and raccoon relative abundance. Specifically, we summarised underlying NLCD land cover categories at CTAP sites as 'Forest' (NLCD land cover categories 41, 42, 43, and 90), 'Grassland' (NLCD land cover categories 21, 81, and 82), or 'Other' (all other NLCD land cover categories), using the land cover category extracted at the latitude and longitude of each CTAP site. We then predicted the probability of each invasive species group's presence or overall invasive shrub presence at each spotlight survey route segment midpoint for each custom categorical land cover type. We calculated overall probability of invasive species' presence within each 1-km buffer, for each invasive species group and for all invasive species combined, by taking a weighted average of land-cover-type-specific predictions for the segment midpoint weighted by the proportion of each custom categorical land cover type within the buffer. This resulted in local-scale and landscape-scale covariates describing probability of invasive species' presence for honeysuckles, autumn olive, buckthorns, and multiflora rose, and all 11 invasive shrub species combined (Figs S8–S12).

We calculated spatial covariates at two scales, a local scale and a landscape scale. At the local scale, spatial covariates were rescaled so that each covariate measured how different the covariate value in a given segment was to the average for that route and year (e.g. how different the proportion of agriculture at one segment in Adams County in 2001 was from the average proportion of agriculture on the Adams County route in 2001). At the landscape scale, we took the mean of each covariate described above for each route and year, then rescaled the means so that the landscape-scale covariate measured how different each route was for the average value for that year (e.g. how different the proportion of agriculture along the Adams County route in 2001 was from the mean proportion of agriculture of all spotlight survey

routes in 2001). This resulted in summaries, for each segment for which we had counts, of how that segment differed from the average for the route and how the route in which the segment was located differed from the average from all spotlight survey routes in the same year. These local- and landscape-scale covariates were used in the same models of spotlight counts, with segment-level counts as the response, to compare the effects of local- and landscape-level statewide variation in habitat. We describe the scaling process further below in *Statistical analysis*, and summaries of unscaled covariate values are given in Table S1.

Statistical analysis

We used a total of 17 646 observations in our analysis. We fit generalised linear mixed models for each mesopredator species with a Poisson likelihood using package lme4 (Bates et al. 2015) in R ver. 4.1.1 (R Core Team 2021). All candidate models, including a model without landscape covariates ('null model'), contained linear and quadratic fixed effects of year, segment of the route surveyed, average humidity, average temperature, and day of year, and a random effect of route. These effects were included to account for survey, ecological, and meteorological processes that might affect detection probability. For instance, average humidity and temperature reflected general meteorological conditions that might affect animal behaviour and visibility, day of year represented possible effects of time-varying survey conditions such as the timing of leaf-out, which could obscure animals, and the random effect of route captured other possible, unmodelled route-specific variables that might affect both relative abundance and detection. As observers likely varied in their experience level, this variation in experience level might be accounted for partially by a random effect of observer. However, observer was often confounded with route, because many observers only surveyed one to two routes and most routes had relatively few observers over the study period. Therefore, we included only a random effect of route. We fitted a total of 26 candidate models for each mesopredator species. The models fell into seven categories of landscape composition and potential change drivers of mesopredator abundance (Table S2): urban land cover; agriculture; forest; water; human structures (the effects of housing density and road density); invasive species (the effects of the probability of each invasive species group's presence or overall invasive species presence); or other (the base model and a model of latitude, longitude, and their interaction). We first fitted models of each covariate at the local and landscape scales separately. We then combined the top local- and landscape-scale covariates (as measured by AIC) into a single model and compared models with and without their interaction to the local-scale-only and landscape-scale-only models using AIC. The goal of this analysis was not to describe all factors affecting mesopredator relative abundance, but to identify the factors with the greatest

explanatory ability at each scale and to understand whether there was any interaction between the top drivers of mesopredator relative abundance between scales. We reported all models with $\Delta\text{AIC} < 2$ as top models and $\Delta\text{AIC} < 8$ as competitive models that are potentially ecologically relevant (Symonds and Moussalli 2011). We calculated AIC weight (w) as $w_m = \frac{e^{-0.5 \times \Delta\text{AIC}_m}}{\sum_{m \in M} e^{-0.5 \times \Delta\text{AIC}_m}}$ for each model m .

We scaled year, average temperature, average humidity, and mile surveyed by subtracting the mean and dividing by the standard deviation for the whole data set included in our analysis. We scaled day of year by subtracting the mean date and dividing by the standard deviation for all dates of surveys on a given route (e.g. day of year for Adams County surveys was scaled by the mean and standard deviation of all survey dates for Adams County across all years). We scaled landscape-scale covariates by subtracting the mean and dividing by the standard deviation of the covariate at all routes in a given year (e.g. we scaled landscape-scale proportion of urban land cover in 2001 using the mean and standard deviation of average proportion of urban land cover along routes in 2001). We scaled local-scale covariates by subtracting the mean and dividing by the standard deviation for the same route and year (e.g. we scaled local-scale proportion of urban land cover for Adams County in 2001 using the mean and standard deviation for Adams County in 2001). We scaled local-scale covariates in this way to test whether there was a local-scale effect of a covariate regardless of landscape context that could be compared across survey routes and years.

Results

Striped skunk models

The top model for skunk included local-scale proportion of forest cover and landscape-scale probability of autumn olive presence ($w = 0.72$; Table 1). Skunk relative abundance decreased as local-scale proportion of forest cover increased ($\beta = -0.21$, s.e. = 0.04) and increased as landscape-scale probability of autumn olive presence increased ($\beta = 0.40$, s.e. = 0.12) (Table S3, Fig. 2). After accounting for landscape-scale covariates, skunk relative abundance also changed non-linearly over time, and had non-linear relationships with average temperature humidity and mile surveyed (Table S3).

Table 1. Top ($\Delta\text{AIC} < 2$) and competitive ($\Delta\text{AIC} < 8$) models for relative abundance of striped skunks in Illinois, ranked by AIC weight (w).

	K	AIC	ΔAIC	w
Proportion of forest (local) + probability of autumn olive (landscape)	14	6158.50	0.00	0.72
Proportion of forest (local) \times probability of autumn olive (landscape)	15	6160.50	2.00	0.26
Proportion of forest (local)	13	6166.20	7.70	0.02

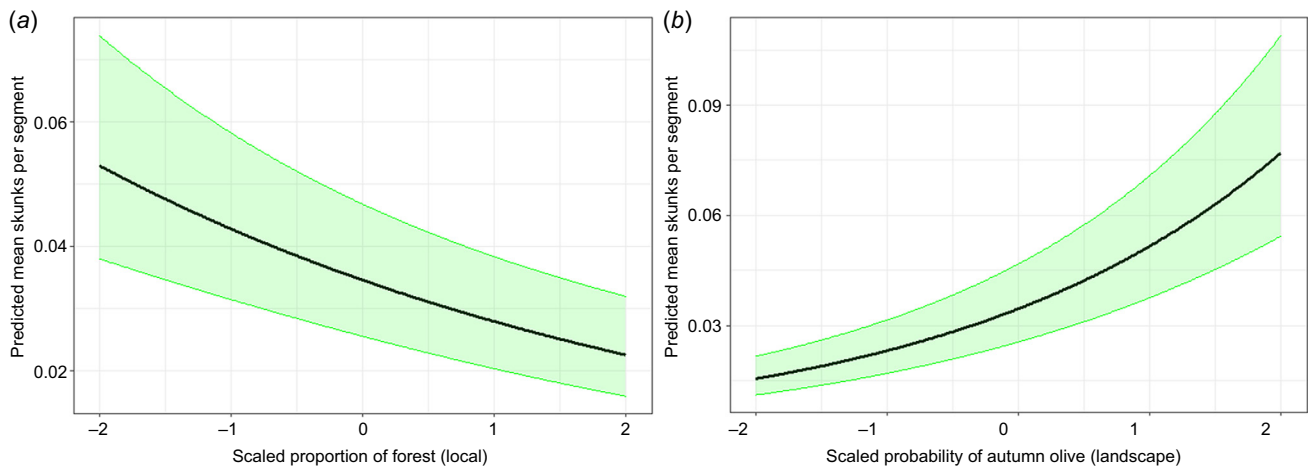


Fig. 2. Predicted relationship of mean striped skunk count per spotlight survey route segment (~1.6 km per segment) to (a) local-scale proportion of forest and (b) landscape-scale probability of autumn olive in the year 2017. All other variables in each plot are held at values of 0 (average temperature and humidity, average survey date for the route, etc.). Ribbons are the 95% confidence intervals for the predictions accounting for error from fixed effects only.

Virginia opossum models

The top model for opossum included local-scale probability of multiflora rose presence and landscape-scale probability of autumn olive presence ($w = 0.63$; Table 2). Opossum relative abundance increased as local-scale probability of multiflora rose increased ($\beta = 0.07$, s.e. = 0.02) and increased as landscape-scale probability of autumn olive presence increased ($\beta = 0.60$, s.e. = 0.09) (Table S4, Fig. 3). After accounting for landscape covariates, opossum relative abundance also increased non-linearly over time, increased as average humidity increased, and had a non-linear relationship with average temperature and mile surveyed (Table S4).

Northern raccoon models

The top models for raccoon were a model that included both local- and landscape-scale proportion of agricultural land cover ($w = 0.62$; Table 3), and the model with the interaction ($w = 0.38$; Table 3). Raccoon relative abundance decreased as local-scale proportion of agricultural land cover increased ($\beta = -0.06$, s.e. = 0.007) and increased as landscape-scale

Table 2. Top ($\Delta AIC < 2$) and competitive ($\Delta AIC < 8$) models for relative abundance of Virginia opossums in Illinois, ranked by AIC weight (w).

	K	AIC	ΔAIC	w
Probability of multiflora rose (local) + probability of autumn olive (landscape)	14	13 828.96	0.00	0.63
Probability of multiflora rose (local) \times probability of autumn olive (landscape)	15	13 830.27	1.31	0.33
Longitude \times latitude	15	13 834.72	5.76	0.04
Probability of autumn olive (landscape)	13	13 836.95	7.98	0.01

proportion of agricultural land cover increased ($\beta = 0.19$, s.e. = 0.06) (Table S5, Fig. 4). After accounting for landscape covariates, raccoon relative abundance also increased non-linearly over time, and had non-linear relationships with average temperature, mile surveyed, and survey date (Table S5).

Discussion

We found that the factors best explaining skunk, opossum, and raccoon relative abundance were highly variable and scale-dependent (Figs S13–S15). Skunk relative abundance decreased on mile segments with a higher proportion of forest cover than the average mile on the route. Given the negative correlation of local-scale proportion of forest cover and agriculture along spotlight survey routes, this suggests that skunks may have higher relative abundance in areas with high relative proportions of agriculture. Contrary to previous results, however, we found that skunks may be responding more to higher proportions of agriculture relative to the surrounding landscape (i.e. local-scale variation in agriculture), rather than responding to the actual proportion of agriculture on the landscape (landscape-scale variation in agriculture) as expected (Gehring and Swihart 2003; Lesmeister et al. 2015). Opossum relative abundance was highly correlated with invasive species' probabilities of presence at multiple scales; although proportion of forest cover had lower explanatory ability than many invasive species' probabilities of presence, many of these invasive species' probabilities were highly correlated with forest cover. Raccoons displayed an opposite response to agricultural land cover to that of skunks at the local scale, occurring at higher relative abundances in areas with higher proportion of forest cover than the

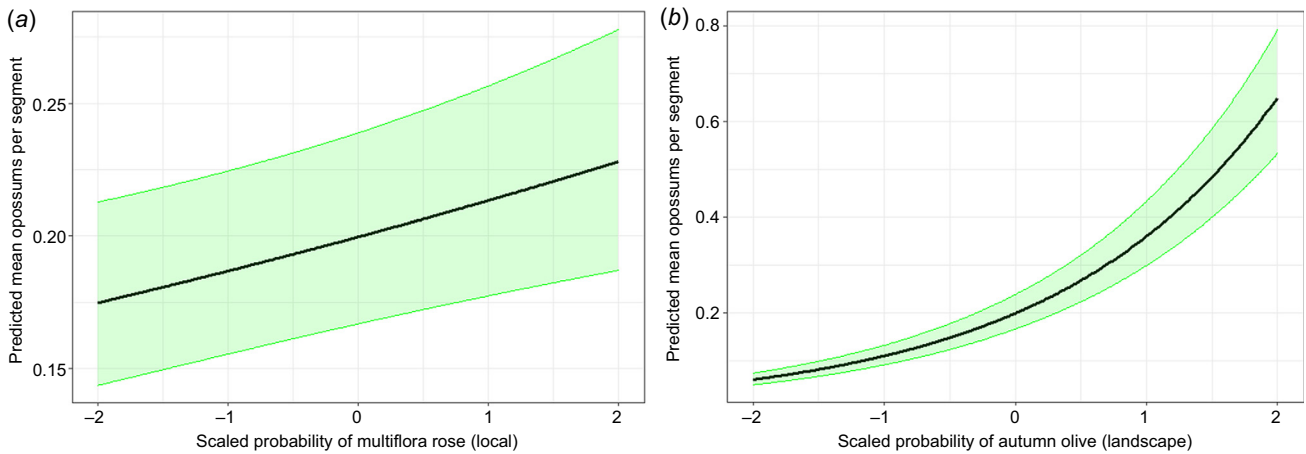


Fig. 3. Predicted relationship of mean Virginia opossum count per spotlight survey route segment (~1.6 km per segment) to (a) local-scale probability of multiflora rose and (b) landscape-scale probability of autumn olive in the year 2017. All other variables in each plot are held at values of 0 (average temperature and humidity, average survey date for the route, etc.). Ribbons are the 95% confidence intervals for the predictions accounting for error from fixed effects only.

Table 3. Top ($\Delta AIC < 2$) and competitive ($\Delta AIC < 8$) models for relative abundance of northern raccoons in Illinois, ranked by AIC weight (w).

	<i>K</i>	AIC	ΔAIC	<i>w</i>
Proportion of agriculture (local) + proportion of agriculture (landscape)	14	52 767.86	0.00	0.62
Proportion of agriculture (local) \times proportion of agriculture (landscape)	15	52 768.84	0.98	0.38

surrounding landscape. Surprisingly, raccoons responded positively to proportion of agriculture at the landscape scale, contrary to several previous results (Dijak and Thompson 2000; Gehring and Swihart 2003).

Overall, the results suggest that a brown-to-green gradient (e.g. agriculture to natural areas; Padilla and Sutherland (2021)) is a major factor in variation in mesopredator relative abundance in Illinois. The brown-to-green gradient operated at both scales, though there was little evidence of interaction between scales (e.g. mediation of local-scale responses by landscape context or actual composition). Considering scale in responses to anthropogenic landscape change gradients such as the brown-to-green gradient is crucial because responses to the brown-to-green gradient could be opposite at different scales. For instance, predicted raccoon relative abundance was lower in agricultural areas at local scales but higher in agricultural areas at landscape scales. The hard-to-soft gradient was likely not a major factor along spotlight routes – spotlight

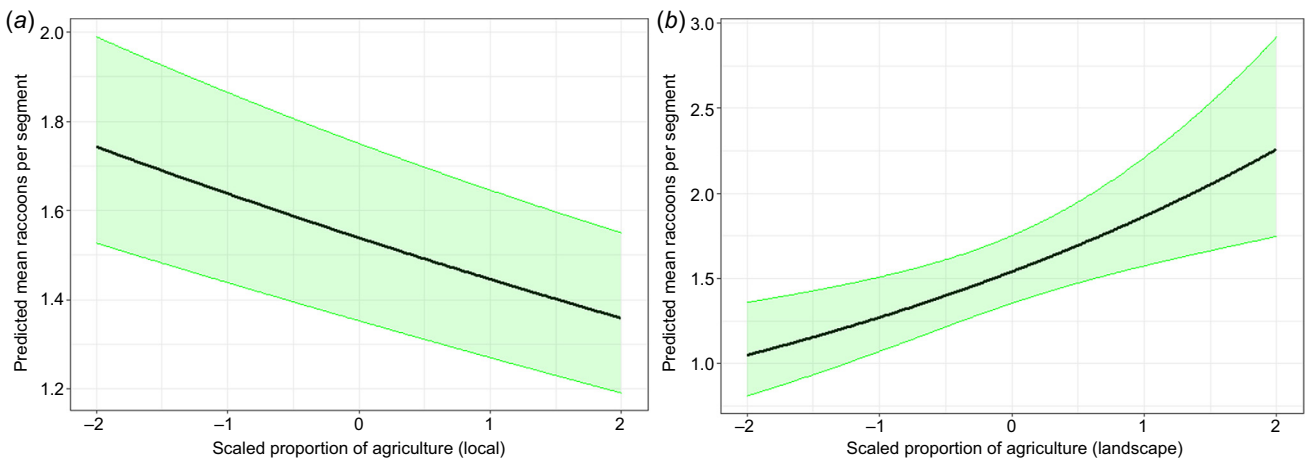


Fig. 4. Predicted relationship of mean northern raccoon count per spotlight survey route segment (~1.6 km per segment) to (a) local-scale proportion of agriculture and (b) landscape-scale proportion of agriculture in the year 2017. All other variables in each plot are held at values of 0 (average temperature and humidity, average survey date for the route, etc.). Ribbons are the confidence intervals for the predictions accounting for error from fixed effects only.

routes were generally located in rural areas where levels of urbanisation and housing density were relatively low (Figs S1 and S5).

Surprisingly, invasive species' probability of presence often had similar or higher explanatory power relative to local-scale proportion of forest or agricultural land cover, particularly for opossums, and had generally positive effects on relative abundance of our study species, contrary to our predictions (Tables S6–S8). Skunk and opossum relative abundance were strongly correlated with autumn olive presence at the landscape scale. Landscape-scale probability of autumn olive presence is negatively correlated with latitude and positively correlated with proportion of forest cover; their combination may be the best explanation for opossum relative abundance (Kanda *et al.* 2006; Wait *et al.* 2020). Thus, landscape-scale probability of autumn olive presence is likely in the top model for opossum because it is more information-rich as a covariate than either latitude or proportion of agriculture or forest. There is not as strong evidence for positive effects of latitude and forest cover on skunks in the literature, but the landscape-scale probability of autumn olive presence by itself has relatively little explanatory power for skunk relative abundance (Table S6). Thus, the effect of landscape-scale probability of autumn olive presence is likely describing the increased relative abundance of skunks and especially opossums in southern Illinois, a relatively warm and forested part of the state. However, the presence of the local-scale probability of multiflora rose presence among the top models for opossum suggests that there may be some small-scale structural aspect of invasive species' presence to which opossums are responding. There is some evidence that opossums increase activity in areas with invasive shrubs, including buckthorn and honeysuckle species (Dutra *et al.* 2011; Vernon *et al.* 2014). It is possible that in parts of southern Illinois with lower population density and higher forest cover, shrubby natural areas that are increasingly affected by invasive species offer food or refuge opportunities that outweigh the advantages of more human-modified areas. Moreover, either the positive effects of presence of invasive shrub species on opossums and skunks, or their correlation with habitats suitable for opossums and skunks in Illinois, apparently outweigh any of the potential negative effects of early leaf-out and thick vegetation on detection of mesopredators along spotlight survey routes with a high probability of invasive species' presence.

Our results for skunk, opossum, and raccoon relative abundance models and models of invasive species' presence are likely influenced by the landscape context of both the spotlight and vegetation surveys. Many of the spotlight surveys were conducted in rural areas where the proportion of urban land cover was low (2.7% of land cover within 1-km segment midpoint buffers on average). Thus, it may be difficult to compare predictors of relative abundance from spotlight surveys to predictors of occupancy from camera traps in more urbanised areas (Wang *et al.* 2015; Wait *et al.* 2018;

Fidino *et al.* 2020), and urban land cover and housing density may be so low along many spotlight survey routes that their effects, if any, would be difficult to detect. Given the relatively low urban land cover along many spotlight survey routes, resource selection trade-offs for mesopredators along these routes would likely involve balancing anthropogenic food sources from primarily agricultural areas with foraging opportunities in or near forests with higher prey abundance, rather than attraction to or avoidance of heavily urbanised areas. It is also possible that invasive shrubs' presence at CTAP sites may not reflect their presence within the broader landscape. CTAP surveys include forest, grassland, and wetland sites for every sampled location, but forest locations are much more likely to be relatively small forest fragments in northern Illinois than in southern Illinois, and wetland and grassland sites may also be located in different kinds of habitats throughout the state based on what sorts of grasslands are available (e.g. natural grasslands vs hayfields vs cemeteries). Invasion routes for invasive shrubs may vary throughout the state. Thus, invasive shrubs may be present along spotlight survey routes even in areas where the predicted probability of presence is low. This could be verified along some spotlight survey routes to improve predicted probability of presence, or a presence–absence model could be built using more sources of data (e.g. iNaturalist.com records).

In addition to landscape context, it is possible that intraguild species interactions affected the relative abundance of skunks, opossums, and raccoons along spotlight survey routes in Illinois. Skunks are known to co-occur with grey foxes across the latter's range in the contiguous USA (Allen *et al.* 2022b), and raccoons tended to be detected along with coyotes and bobcats in southern Illinois (Lesmeister *et al.* 2015). Coyotes, red foxes, grey foxes, and bobcats all occur in Illinois, and could be influencing the distributions of the smaller carnivores we studied. However, intraguild interactions are highly complex, and the spotlight data used in this study face limitations in terms of study design that make ecological inference about species interactions difficult.

Although the spotlight data used in this study provide a valuable long-term (2001–2017) dataset to study factors affecting relative abundance, multiple limitations in both the data and modelling require that the results be interpreted with caution. The primary limitation in the data set is that the survey design did not allow us to account for imperfect detection, which informed the choice of generalised linear models for modelling relative abundance rather than abundance. In general, relative abundance may not scale linearly with abundance, particularly when detection probability is not accounted for, so our results should not be interpreted as inference on abundance. Survey routes were only run once per year, at most, and no auxiliary data on time-to-detection or distance to detected individuals were collected, thus eliminating N-mixture (Royle 2004), distance sampling (Ruelle *et al.* 2003), or time-to-detection (Strebel *et al.* 2021)

models. The lack of detection probability in our models also means that it is impossible to fully differentiate between effects of landscape covariates on abundance and detection. For instance, the result that skunk relative abundance increased as forest cover decreased may be due both to skunks' attraction to agricultural and other human-dominated landscapes and to a decreased ability to detect skunks in forested areas. However, given that the results of our models for opossum and skunk largely followed predictions from studies that accounted for detection probability (Lesmeister *et al.* 2015; Wait *et al.* 2020; Allen *et al.* 2022b), we believe that our results are still valid. However, we recommend altering spotlight survey designs to account for distance to individuals, incorporate repeat surveys, or integrate time-to-detection (Strebel *et al.* 2021), allowing for true abundance to be estimated instead of relative abundance.

Among factors included in the models to explicitly to account for variation in detection, we found that aspects of spotlight survey timing and weather conditions may affect observed relative abundance of mesopredators. Predicted skunk relative abundance was highest when average temperature was moderate and as average humidity increased (though this effect was non-linear). Predicted opossum relative abundance was highest when surveys were conducted earlier than the average survey date for a given route, when average humidity was higher and average temperature was moderate. Predicted raccoon relative abundance was highest around average survey dates for a given route, when average temperature was moderate and when average humidity was higher. Relative abundance had a non-linear relationship with mile segment surveyed for all three species, with negative coefficients implying that detection peaked near the middle of surveys. Illinois spotlight survey protocols are based on humidity and temperature recommendations from Rybarczyk (1978), who only calculated correlations between temperature and humidity and counts from spotlight surveys and thus did not account for possible non-linear effects of humidity and temperature. Therefore, temperature and average humidity recommendations for spotlight surveys may need to be adjusted to maximise the probability of detecting mesopredators, especially because these effects may be non-linear and thus better represented by ranges of temperatures than minimum temperatures.

In summary, we modelled relationships between skunk, opossum, and raccoon relative abundance and various aspects of anthropogenic landscape change using spotlight surveys in Illinois. The results suggest that all three mesopredator species may be responding to the brown-to-green gradient in Illinois at multiple scales, or responding to invasive species' probabilities of presence that are themselves highly correlated with brown-to-green gradients. Our results support the idea that local landscape effects should be put in the context of broader surrounding landscapes, and that potential interactions between local and landscape scales should be investigated (Fidino *et al.* 2020). Our results also suggest

that invasive shrubs' presence or probability of presence may be an aspect of landscape change that can affect mesopredator presence and abundance at multiple spatial scales. More broadly, our results demonstrate the complexity of landscape change and how effects of landscape change on mesopredators can depend on the landscape context, such as the degree of human footprint from urbanisation and agriculture in the surrounding landscape.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data used to generate results in this paper will be made available on the Illinois Data Bank.

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