

Butterfly diversity is lower in historically redlined neighborhoods: evidence from 151 US cities

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Abstract

Historical redlining — the racially discriminatory neighborhood grading system implemented by the Home Owners' Loan Corporation (HOLC) in the 1930s, has left enduring legacies on the physical environment of American cities. Ecologically relevant impacts include reduced green space, elevated temperatures, and greater impervious surface cover in formerly redlined areas. Whether these environmental disparities have produced lasting differences in urban biodiversity remains incompletely understood, particularly for insects. Here we test the hypothesis that historically redlined neighborhoods support lower butterfly diversity than higher-graded neighborhoods across the contiguous United States. We overlaid 58,669 research-grade iNaturalist butterfly observations (2016–2025) with digitized HOLC neighborhood maps for 151 cities, treating 1,143 individual labelled HOLC zones as the spatial unit of analysis and quantifying butterfly diversity using Hill numbers ($q = 0, 1, 2$). Linear mixed-effects models with city as a random intercept revealed that grade A (“Best”) zones had significantly higher Shannon diversity ($q = 1$) than grade D (“Hazardous”) redlined zones ($\beta = 0.055$, 95% CI: 0.009–0.101), after controlling for zone area, year, and sampling effort. This pattern was substantially mediated by land cover: grade D zones had more than five times less developed open space than grade A zones (3.9% vs 20.4%) and were dominated by high-intensity development (30.3% vs 3.1%), and inclusion of land cover covariates largely eliminated the grade diversity gradient. Forest cover was the only individually significant land cover predictor, positively associated with species richness, Shannon diversity, and Simpson diversity. Grade effects were of comparable magnitude at $q = 2$ (Simpson diversity), which downweights rare species, indicating that differences among grades extend to the relative abundances of common species rather than being confined to rare taxa. Results were robust to exclusion of the pandemic year 2020, exclusion of Monarch butterfly records, restriction to cities with all four HOLC grades represented, and variation of the minimum observation threshold. Our findings extend recent evidence of redlining-associated biodiversity disparities from four Californian cities to a national scale, identify developed open space as the primary land cover mechanism linking historical redlining to present-day butterfly diversity, and highlight urban greening in formerly redlined neighborhoods as a tractable intervention for simultaneously addressing biodiversity loss and environmental injustice.

Introduction

Urban areas cover approximately 3% of the Earth's land surface but are home to more than half of the global human population, a proportion projected to reach two thirds by 2050 (United Nations 2019). Despite their small footprint, cities are disproportionately important for biodiversity conservation, as they frequently overlap with biodiversity hotspots (Ives et al. 2016), support substantial numbers of native species including many of conservation concern (Aronson et al. 2014), and provide critical habitat for wildlife in increasingly fragmented landscapes (Grimm et al. 2008). At the same time, urbanization is one of the leading drivers of biodiversity loss globally, operating through habitat destruction, impervious surface expansion, urban heat island effects, light and noise pollution, and the introduction of non-native species (McKinney 2008; Seto et al. 2012). Understanding the ecological consequences of urban development decisions is therefore a pressing conservation challenge.

Within cities, biodiversity is not uniformly distributed. A substantial body of research has documented the “luxury effect”, the positive relationship between neighborhood socioeconomic status and local biodiversity (Hope et al. 2003; Kinzig et al. 2005). Wealthier neighborhoods consistently support higher species richness and abundance of birds (Boone et al. 2009; Schell et al. 2020) and trees (Nesbitt et al. 2019). This pattern has profound implications for environmental justice. If biodiversity is concentrated in wealthy neighborhoods, then lower-income communities, which are disproportionately communities of color in the United States, are denied the ecosystem services that diverse biological communities provide, including mental health benefits, pollination, air filtration, temperature regulation, and stormwater management (Kondo et al. 2018; Schell et al. 2020).

The contemporary socioeconomic geography of American cities has deep historical roots, and nowhere is this more apparent than in the lasting legacy of the Home Owners’ Loan Corporation (HOLC). Established in 1933 as part of the New Deal, HOLC tasked appraisers with grading residential neighborhoods across more than 200 cities into four categories: A (“Best”), B (“Still Desirable”), C (“Declining”), and D (“Hazardous”). Grading was ostensibly to guide mortgage lending decisions (Jackson 1985) but, in practice, grading criteria were explicitly racial. The presence of Black, immigrant, or working-class residents was treated as a marker of neighborhood decline, and areas with significant minority populations were systematically assigned the lowest grade and colored red on appraisers’ maps – hence “redlining” (Rothstein 2017; Michney and Winling 2020). Banks used these maps to deny mortgages and restrict investment in redlined areas, concentrating poverty and disinvestment in minority communities for generations. Although redlining was outlawed by the Fair Housing Act of 1968, its consequences for neighborhood wealth, health, and physical environment persist to the present day (Crossney and Bartelt 2005; Nardone et al. 2020).

The environmental consequences of historical redlining have received growing attention in recent years. Redlined neighborhoods experience higher summer temperatures than higher-graded areas in the same city, a consequence of reduced tree canopy and greater impervious surface cover that directly reflects the built environment legacy of disinvestment (Hoffman et al. 2020; Wilson 2020). They also have lower access to parks and green space (Nesbitt et al. 2019), higher exposure to air pollution (Mikati et al. 2018), and elevated rates of cardiovascular disease, asthma, and other conditions linked to environmental quality (Nardone et al. 2021; Bailey et al. 2021). More recently, researchers have begun to document the ecological consequences of these environmental disparities, finding that historically redlined areas support lower bird species richness (Schell et al. 2020), reduced genetic diversity in urban wildlife populations (Schell et al. 2020), less access to pollinating insects for residents (Lynch and Miller 2022), and lower overall wildlife biodiversity across multiple taxa in four Californian cities (Estien et al. 2024). However, the relationship between historical redlining and urban insect diversity has received comparatively little systematic investigation at a national scale.

Butterflies are well suited to address this gap. They are among the most thoroughly studied insect groups, with a well-characterized North American fauna of approximately 750 species and extensive citizen science infrastructure that generates large volumes of occurrence data (Cohn 2008; Prudic et al.

2017). As adults, butterflies are conspicuous, diurnal, and relatively easy to identify from photographs, making them ideal targets for citizen science monitoring via platforms such as iNaturalist (Ueda 2023). As larvae, butterflies are specialized herbivores with often intimate associations with specific host plant species, such that butterfly diversity is closely linked to plant community diversity and composition (Dennis et al. 2006; Ghazanfar et al. 2016). Butterflies are widely used as ecological indicators of habitat quality and ecosystem health (Fleishman and Mac Nally 2003; Forister et al. 2016), and their sensitivity to vegetation structure and microclimate makes them particularly likely to reflect the land cover differences documented between HOLC grades. Furthermore, declining butterfly populations across North America — driven by habitat loss, pesticide use, and climate change — make understanding the distribution of butterfly diversity within cities an increasingly urgent conservation priority (Forister et al. 2016; Sánchez-Bayo and Wyckhuys 2019).

Here we test the hypothesis that historically redlined neighborhoods support lower butterfly diversity than higher-graded neighborhoods across the contiguous United States and ask whether any such differences are mediated by contemporary land cover composition. We overlay a decade of research-grade iNaturalist butterfly observations (2016–2025) with digitized HOLC neighborhood maps for 151 cities, treating individual labelled HOLC zones as the spatial unit of analysis and using city as a random effect in mixed-effects models. We quantify butterfly diversity using Hill numbers, which provide a unified framework encompassing species richness, Shannon diversity, and Simpson diversity, and characterize land cover at the zone level using the National Land Cover Database, with developed land cover split into four ecologically distinct intensity classes. Building on recent work demonstrating lower multi-taxon biodiversity in redlined neighborhoods across four Californian cities (Estien et al. 2024), we extend this analysis to a national scale across 151 cities, focus specifically on butterflies as sensitive ecological indicators, and use individual HOLC neighborhood zones rather than city-level grade aggregations as the primary spatial unit of analysis. To our knowledge, this represents the most geographically extensive examination of redlining and urban insect diversity to date, and the first to test whether land cover acts as a mechanistic mediator of the grade-diversity relationship.

Methods

Study system and redlining data

HOLC neighborhood boundary maps were obtained from the Mapping Inequality project at the University of Richmond (Nelson et al. 2023), which has digitized HOLC maps for 314 cities across the contiguous United States. Each digitized map consists of individual labelled polygons corresponding to the original HOLC neighborhood assessments (e.g. A1, B3, D12). We treated each labelled polygon as a distinct spatial unit (a “zone”) rather than aggregating to the four grade categories within each city, as this preserves the spatial resolution of the original HOLC assessment and avoids averaging over within-grade heterogeneity. Raw polygon geometries contained minor topological errors which were repaired prior to analysis using a small positive-then-negative buffer operation (0.0001 decimal degrees) in conjunction

with `st_make_valid()` in the R package `sf` (Pebesma 2018). Ungraded polygons were excluded. This process yielded a total of 9,029 labelled zones across 223 cities.

Butterfly occurrence data

Butterfly occurrence records were obtained from the Global Biodiversity Information Facility (GBIF; gbif.org) via the `rgbif` package in R (Chamberlain et al. 2023). We downloaded all research-grade iNaturalist observations (Ueda 2023) of Lepidoptera from the contiguous United States for the period 2016–2025 (GBIF download DOI: [10.15468/dl.h9h6uq](https://doi.org/10.15468/dl.h9h6uq); $n = 6,039,387$ raw records). Research-grade iNaturalist observations have been validated by at least two independent users and have been shown to produce diversity estimates comparable to those obtained from standardized monitoring protocols (Dennis et al. 2017).

We restricted the dataset to the six North American butterfly families: Papilionidae, Pieridae, Lycaenidae, Riodinidae, Nymphalidae, and Hesperidae, excluding all moths and other Lepidoptera. Records were further filtered to retain only those with species-level identifications, removing genus-only records, slash taxa (uncertain identifications between two species), and records containing the terms “complex” or “hybrid”. Records with coordinate uncertainty exceeding 100 m were removed to minimize spatial misassignment of observations to HOLC zones. After filtering, 1,399,046 records of 660 butterfly species were retained.

Each butterfly observation was spatially joined to the HOLC zone within which it fell using the `st_intersects()` function in `sf` (Pebesma 2018), with planar geometry used in place of spherical geometry (`sf_use_s2(FALSE)`) to accommodate minor topological imperfections in the HOLC polygons. Observations falling outside any HOLC zone, or duplicated records resulting from observations at zone boundaries, were removed. These criteria yielded 58,669 observations assigned to HOLC zones across 177 cities. Of these, 151 cities contained at least one zone $\times$ year combination meeting the criteria for diversity estimation described below, and these 151 cities form the basis of all models reported here. Cities were retained in the analysis if at least one zone within the city had a minimum of five butterfly observations across the study period; this threshold was chosen to ensure meaningful diversity estimates at the zone level while maximizing geographic coverage. The 1,934 zones retained on this criterion varied in area from 5.5 to 7,680.5 ha (median 156.6 ha, interquartile range 82.3–286.7 ha). Sensitivity of results to this threshold was examined at values of 3, 5, 10, and 15 observations per zone.

Diversity metrics

Butterfly diversity was quantified using Hill numbers (Hill 1973), which provide a unified framework for measuring species diversity as the “effective number of species” — the number of equally abundant species that would produce the observed diversity value. Hill numbers are parameterized by an order q that determines sensitivity to species relative abundances: $q = 0$ corresponds to species richness, $q = 1$

to the exponential of Shannon entropy (equally weighting all species by their relative abundance), and $q = 2$ to the inverse Simpson index (downweighting rare species). We calculated all three Hill numbers for each zone $\times$ year combination using the *vegan* package in R (Oksanen et al. 2022). Zone $\times$ year combinations with fewer than two species or fewer than five observations were excluded. Annual observation counts per zone were retained as a proxy for sampling effort (Kéry and Royle 2016).

Because iNaturalist data are collected opportunistically, observation effort varies substantially among zones and years. Rather than standardizing diversity estimates via rarefaction prior to modelling, which would require discarding a large proportion of the data given the sparsity of observations in many zones, sampling effort was included as a covariate in all models (Isaac et al. 2020). We defined sample effort as the total number of iNaturalist observations across all species in that year and zone.

Land cover data

Land cover composition within each HOLC zone was characterized using the 2021 Annual National Land Cover Database (NLCD; Dewitz 2023), obtained from the Multi-Resolution Land Characteristics Consortium (mrlc.gov). We retained the four developed intensity classes separately: developed open space (class 21, including parks and large-lot residential areas), developed low intensity (class 22, suburban residential), developed medium intensity (class 23, denser residential and commercial), and developed high intensity (class 24, downtown core and industrial). These classes are ecologically distinct for butterflies — developed open space can support substantial butterfly diversity through provision of nectar plants and larval host plants, while high-intensity development is largely unsuitable (Lizée et al. 2012; Sánchez-Bayo and Wyckhuys 2019). We additionally extracted forest (classes 41, 42, 43, 52), pasture and agricultural (classes 71, 81, 82), and water and wetland (classes 11, 90, 95) cover. Fractional cover of each class within each HOLC zone was extracted using the *exactextractr* package in R (Baston 2023), with HOLC polygons reprojected to the NLCD native coordinate reference system (Albers Equal Area) prior to extraction.

Statistical analysis

We used linear mixed-effects models (LMMs) to test whether butterfly diversity differed among HOLC grades, while accounting for the non-independence of zones within the same city and the influence of sampling effort on observed diversity. Models were fitted using the *lme4* package in R (Bates et al. 2015), with city included as a random intercept. The zone $\times$ year was the unit of observation. Response variables were log-transformed Hill number estimates of biodiversity $q = 0$, $q = 1$, and $q = 2$. Grade D (redlined) was specified as the reference level, such that coefficients for grades A, B, and C represent differences in diversity relative to previously redlined zones.

Three models were compared for each response variable using the Akaike Information Criterion (AIC; Burnham and Anderson 2002): a base model including HOLC grade, log-transformed zone area (hectares), and year as a fixed factor; the base model with log-transformed annual observation count

added as a sampling effort covariate; and the effort model with land cover covariates added (developed open space, low intensity, medium intensity, high intensity, and forest cover, expressed as proportions of zone area). Log zone area was included because larger areas are expected to support more species through the species–area relationship (Preston 1962; MacArthur and Wilson 1967). Year was included as a fixed factor rather than a continuous covariate to absorb non-linear temporal trends in iNaturalist observation effort, which grew substantially over the study period and showed an anomalous pattern in 2020 associated with the COVID-19 pandemic (Callaghan et al. 2021). Confidence intervals for fixed effects were computed using the Wald method. All analyses were conducted in R version 4.5.2 (R Core Team 2025).

We conducted four sensitivity analyses to assess the robustness of results. First, we excluded observations from 2020 to test whether the pandemic-year anomaly in citizen science effort influenced grade coefficients. Second, we excluded records of the Monarch butterfly (*Danaus plexippus*), which comprised 18.8% of observations and whose distribution reflects continental migratory routes rather than local habitat quality (Oberhauser and Solensky 2004), potentially obscuring neighborhood-level diversity signals. Third, we compared results between the full 151-city dataset and a subset of cities constrained to have all four HOLC grades present, to assess whether inclusion of cities with incomplete grade representation affected conclusions. Fourth, we refitted the primary model at minimum observation thresholds of 3, 5, 10, and 15 records per zone, to assess whether conclusions depended on the threshold used to define analysable zones.

Results

Study extent and data summary

HOLC redlining maps were available for 223 cities across the contiguous United States (Fig. 1). After spatial joining of butterfly observations to HOLC zones and application of the minimum observation threshold (≥ 5 observations per zone), 177 cities met this threshold; of these, 151 cities containing 1,143 individual HOLC zones contributed at least one zone $\times$ year diversity estimate and form the basis of all analyses reported here (Fig. 1). A further 26 cities met the observation threshold but contained no zone $\times$ year combination with at least two species. Excluded cities were distributed across all regions but were disproportionately represented in the rural midwest and southeast, reflecting lower iNaturalist observer density in those areas. The final dataset comprised 58,669 butterfly observations of 660 species recorded between 2016 and 2025. Observation counts increased substantially over the study period across all HOLC grades (Fig. S1). This was driven almost entirely by a concentrated four-day recording event at a single site, a community garden on the Indiana State University campus in Terre Haute, Indiana, which contributed 655 records from 269 distinct observers between 10 and 13 September 2019. Excluding either the event or the city altogether changed HOLC grade coefficients by less than 0.005 on the log scale, well within confidence intervals. Grade B and C zones accumulated the greatest total observations over the study period, reflecting their greater number and area of zones rather than higher per-zone sampling effort. Grade B and C zones accumulated the greatest total observations over the

study period, reflecting their greater number and area of zones rather than higher per-zone sampling effort.

Land cover composition differed substantially among HOLC grades (Table 1). Grade A zones had the highest proportion of developed open space (mean 20.4% of zone area), which declined monotonically through grades B (11.1%), C (6.0%), and D (3.9%). Conversely, high-intensity developed land cover increased from 3.1% in grade A zones to 30.3% in grade D zones. Forest cover was low across all grades but was highest in grade A zones (1.8%) and similar among grades B, C, and D (approximately 1.0%). These patterns are clearly visible in the Philadelphia example (Fig. 2), where grade D zones in the city center are dominated by high-intensity developed land cover, while grade A zones in the northwest of the city contain substantially more developed open space and forest patches.

Table 1

Mean percentage land cover by HOLC grade across 151 cities. Developed land cover is split into four NLCD intensity classes: open space (class 21, including parks and large-lot residential), low intensity (class 22, suburban residential), medium intensity (class 23, denser residential and commercial), and high intensity (class 24, downtown core and industrial). Values represent mean percentage of zone area.

HOLC Grade	Dev: Open	Dev: Low	Dev: Med	Dev: High	Forest	Pasture	Water
A – Best	20.4	47.7	26.4	3.1	1.8	0.1	0.6
B – Still Desirable	11.1	35.9	43.9	7.5	1.0	0.0	0.5
C – Declining	6.0	22.5	53.1	17.1	0.6	0.1	0.6
D – Hazardous	3.9	15.7	47.2	30.3	1.0	0.3	1.4

Butterfly diversity by HOLC grade

Mean butterfly diversity was highest in grade A and B zones and lowest in grade D (redlined) zones across all three Hill number orders (Table 2; Fig. 3). At the zone × year level, mean Shannon diversity ($q = 1$) was 6.25 effective species in grade A zones, 6.29 in grade B zones, 5.58 in grade C zones, and 5.51 in grade D zones. Species richness ($q = 0$) followed a similar pattern, with means of 7.37, 7.56, 6.52, and 6.61 for grades A, B, C, and D respectively. Simpson diversity ($q = 2$) followed the same ordering, with means of 5.46, 5.48, 4.94, and 4.82 effective species for grades A, B, C, and D respectively.

Table 2

Summary of butterfly diversity metrics by HOLC grade at the zone × year level. Hill numbers are reported as effective number of species (mean ± SD). $q = 0$: species richness; $q = 1$: Shannon diversity; $q = 2$: Simpson diversity. Grade D (Hazardous) was the reference category in all mixed-effects models.

HOLC Grade	Zones (n)	Zone-years	Richness (mean ± SD)	Shannon (mean ± SD)	Simpson (mean ± SD)
A – Best	171	429	7.37 ± 4.78	6.25 ± 3.58	5.46 ± 2.91
B – Still Desirable	324	858	7.56 ± 5.98	6.29 ± 4.28	5.48 ± 3.44
C – Declining	425	1064	6.52 ± 4.29	5.58 ± 3.18	4.94 ± 2.63
D – Hazardous	223	605	6.61 ± 4.85	5.51 ± 3.33	4.82 ± 2.62

Mixed-effects model results

The model including HOLC grade, log zone area, year, and log annual observations consistently had the lowest AIC across all three Hill number orders and is reported as the primary result. Sampling effort (log annual observations) was the strongest predictor of diversity in all models ($\beta = 0.48$, 95% CI: 0.46–0.50 for Shannon diversity), confirming that controlling for effort was essential. Zone area was positively associated with species richness ($\beta = 0.03$, 95% CI: 0.02–0.05) but not significantly associated with Shannon or Simpson diversity after controlling for effort.

Relative to grade D (redlined) zones, grade A zones had significantly higher Shannon diversity ($\beta = 0.055$, 95% CI: 0.009–0.101; Fig. 4) and species richness ($\beta = 0.043$, 95% CI: 0.004–0.082). Grade B zones showed a similar but non-significant positive trend for Shannon diversity ($\beta = 0.015$, 95% CI: –0.026–0.056). Grade C zones showed no consistent difference from grade D zones for any diversity metric. Simpson diversity showed the same directional patterns as did Shannon diversity, with a grade A effect of comparable magnitude. Because $q = 2$ downweights rare species, the persistence of the grade contrast at this order indicates that differences among grades are not confined to rare taxa but extend to the relative abundances of common species.

Land cover as a mediator of grade effects

Adding land cover covariates to the base model substantially improved model fit for Shannon diversity ($\Delta\text{AIC} = 31.5$ relative to the effort-only model) and produced a similar improvement for Simpson diversity ($\Delta\text{AIC} = 30.2$). Forest cover was positively associated with Shannon diversity ($\beta = 0.63$, 95% CI: 0.10–1.17) and positively associated with Simpson diversity ($\beta = 0.68$, 95% CI: 0.09–1.28), indicating that forested patches within HOLC zones support both additional species and a more even distribution of individuals among them. None of the four developed land cover classes was individually significant after controlling for grade and effort, though their collective inclusion substantially improved model fit, suggesting collinearity among the developed classes. Land cover coefficients for both diversity orders are shown in Fig. 6.

When land cover covariates were included in the model, the grade A and B coefficients for Shannon diversity became negative relative to grade D (grade A: $\beta = -0.055$, 95% CI: -0.113 to 0.003 ; grade B: $\beta = -0.041$, 95% CI: -0.087 to 0.004), indicating that once land cover composition is accounted for, zones in higher-graded neighborhoods are not inherently more diverse than redlined zones of equivalent land cover. This pattern suggests that the diversity advantage of grade A and B zones is substantially mediated by their greater proportion of developed open space and forest cover, rather than by grade per se.

Sensitivity analyses

Results were consistent in direction across all four sensitivity analyses (Figs. S2–S4, S6). Excluding the pandemic year 2020 produced grade coefficients that were directionally consistent with and overlapping those from the full model, with slightly larger point estimates for grade A (Shannon: $\beta = 0.057$ without 2020 vs $\beta = 0.055$ with 2020), indicating that the anomalous observer effort in 2020 did not meaningfully influence conclusions. Excluding Monarch butterfly records, which comprised 18.8% of all observations, slightly strengthened the grade A and B effects (Fig. S3), consistent with Monarch distribution being driven by migratory routes rather than local habitat quality; this exclusion sharpened the local habitat signal. Restricting the analysis to cities with all four HOLC grades present produced coefficients that overlapped those from the full 151-city analysis (Fig. S4), confirming that inclusion of cities with incomplete grade representation did not bias results. Refitting the primary model across minimum observation thresholds produced positive grade A coefficients at every threshold (Fig. S6): $\beta = 0.025$ (95% CI: -0.009 – 0.058) at ≥ 3 observations per zone, 0.055 (0.009 – 0.101) at ≥ 5 , 0.067 (-0.007 – 0.140) at ≥ 10 , and 0.061 (-0.040 – 0.162) at ≥ 15 . Confidence intervals widened at higher thresholds as fewer cities contributed, and the grade A effect was statistically significant at the primary threshold of five observations per zone.

Discussion

Overview

Historical redlining is associated with lower urban butterfly diversity across 151 American cities, and this pattern is substantially explained by differences in land cover composition between HOLC grades. Redlined (grade D) neighborhoods had the lowest Shannon diversity and species richness of the four grade categories, consistent with the hypothesis that the legacy of racially discriminatory housing policy has left an enduring imprint on urban biodiversity. However, the grade effect was largely mediated by land cover: once the proportion of developed open space, forest, and high-intensity development was accounted for, intrinsic differences among grades diminished substantially. This finding identifies a concrete and actionable mechanism — the type rather than simply the amount of development — linking historical redlining to present-day ecological impoverishment.

Redlining and the luxury effect

Our finding that butterfly diversity is lower in redlined neighborhoods is consistent with the broader “luxury effect” — the positive relationship between neighborhood wealth and urban biodiversity documented across multiple taxa including birds (Boone et al. 2009), lizards (Ackley et al. 2015), and carnivores (Magle et al. 2016). However, our results reveal important nuances in the luxury effect of butterflies specifically. Grade B (“Still Desirable”) zones showed diversity levels comparable to or exceeding those of grade A (“Best”) zones for species richness and Shannon diversity, a pattern inconsistent with a simple linear wealth-diversity gradient. This mirrors findings from Lynch and Miller (2022), who found that butterfly and moth density was lower in wealthier urban neighborhoods, and suggests that the luxury effect may operate differently for butterflies than for vertebrates. The NLCD land cover classification used here cannot distinguish intensively managed green space from naturalistic vegetation within the same land cover class, and fine-resolution vegetation quality data would be needed to fully explain the non-linear relationship between HOLC grade and butterfly diversity. Resolving this question represents an important direction for future research.

Land cover as the mediating mechanism

The most striking finding of this study is that the diversity difference between redlined and higher-graded neighborhoods is largely explained by land cover composition, and specifically by the proportion of developed open space. Grade A zones had more than five times the proportion of developed open space compared to grade D zones (20.4% vs 3.9%), while grade D zones were dominated by high-intensity development (30.3% vs 3.1% in grade A). This gradient in development intensity directly reflects the original HOLC grading criteria, which favored neighborhoods with lower building density, greater setbacks, and more green space, and penalized areas of dense industrial and commercial development (Greer 1948). The persistent difference in land cover between grades nearly nine decades after the original assessments speaks to the extraordinary durability of built environment decisions — once high-intensity development is established, it is rarely reversed (Grimm et al. 2008).

Forest cover was the only individually significant land cover predictor in our models, with a positive effect on species richness, Shannon diversity, and Simpson diversity alike. Forested zones therefore supported more species distributed more evenly, suggesting that urban forest patches add butterfly species that are absent from more developed zones without any single taxon coming to dominate. Urban forests are known to support specialist butterfly taxa associated with woodland edge habitats and specific larval host plants (Dennis et al. 2006), and we found higher forest cover in Grade A than the lower grades. That the forest effect persisted at $q = 2$, which downweights rare species, indicates that forest cover was associated with higher abundance of common species as well as the addition of uncommon ones.

Notably, none of the four developed land cover intensity classes was individually significant in our models after controlling for grade and effort, despite their collective inclusion substantially improving model fit. This likely reflects high collinearity among the developed classes — zones with high proportions of developed open space necessarily have lower proportions of high-intensity development — rather than a true absence of independent effects. The strong AIC improvement with all four classes

included suggests that the full gradient from open to high-intensity development matters for butterfly diversity and that future analyses with larger datasets may be able to resolve the independent contributions of each class.

Citizen science data: strengths and limitations

The use of iNaturalist observations via GBIF represents both a major strength and a key limitation of this study. The scale and temporal depth of citizen science data — 58,669 butterfly observations across 151 cities over a decade — would be impossible to achieve with systematic survey methods, and the research-grade filter applied by iNaturalist provides a meaningful quality control that has been validated against professional survey data (Dennis et al. 2017; Prudic et al. 2017). However, iNaturalist observations are inherently biased towards areas and times where observers are active, and this observer distribution is not random with respect to HOLC grade. Redlined neighborhoods have historically had lower incomes, and lower-income communities may have lower rates of smartphone ownership, internet access, and participation in citizen science platforms (Callaghan et al. 2019). This means that the lower observed diversity in grade D zones could reflect lower observer effort rather than, or in addition to, genuinely lower butterfly diversity. Opportunistic records can also concentrate in space and time in ways that annual observation counts do not fully capture. The four-day, 269-observer event described above contributed effort at a single site that is not equivalent in detection breadth to the same number of records accumulated across a season, even though the log observation count treats the two alike.

We addressed this potential bias by including log annual observation count as a covariate in all models, which absorbs much of the variation in observer effort across zones and years. The positive association between observation effort and diversity in all models confirms that effort is a strong predictor of observed diversity, and the consistency of grade effects before and after controlling for effort suggests that observer bias alone cannot account for the grade diversity gradient. Nevertheless, we cannot fully exclude the possibility of residual confounding between observer effort and grade, and future studies using systematic transect-based butterfly surveys in HOLC-graded neighborhoods would provide stronger causal inference.

The Monarch butterfly (*Danaus plexippus*) comprised 18.8% of all observations in our dataset, reflecting both its conspicuousness and the active citizen science interest in its population decline (Oberhauser and Solensky 2004). Because Monarch abundance at any given location is determined by migratory routing rather than local habitat quality, including Monarch records risks obscuring neighborhood-level habitat effects. Our sensitivity analysis showed that excluding Monarch records slightly strengthened the grade A and B diversity advantage, consistent with the interpretation that Monarchs dampen the local habitat signal by appearing in all neighborhood types along migratory corridors regardless of habitat quality. We report the full-dataset analysis as our primary result and note that conclusions are unchanged by Monarch exclusion.

Conservation and environmental justice implications

Our findings have direct implications for urban conservation planning and environmental justice. The persistence of lower butterfly diversity in historically redlined neighborhoods nearly a century after the original HOLC assessments represents a form of environmental inequity that has received comparatively little attention in the biodiversity literature relative to documented disparities in greenspace access, air quality, and heat exposure (Hoffman et al. 2020; Nardone et al. 2021; Schell et al. 2020). Butterflies are widely recognized as sensitive ecological indicators (Fleishman and Mac Nally 2003; Forister et al. 2016) and as important providers of pollination ecosystem services (Potts et al. 2010), and their reduced diversity in redlined neighborhoods implies broader ecological impoverishment at multiple trophic levels.

The identification of developed open space as the primary land cover mediator of the grade-diversity relationship points to a concrete intervention pathway. Increasing the proportion of naturalistic green space, particularly plantings that support larval host plants and adult nectar resources, within former redlined neighborhoods has the potential to substantially increase butterfly diversity while simultaneously delivering co-benefits for human wellbeing, including reduced urban heat island effects (Bowler et al. 2010), improved mental health outcomes (Bratman et al. 2019), and increased opportunities for nature contact in communities that have historically been denied them (Schell et al. 2020). The growing body of evidence on the effectiveness of urban greening interventions for pollinators (Baldock et al. 2019; Tew et al. 2021) suggests that targeted planting programs in formerly redlined areas could produce measurable biodiversity gains within short periods.

Residents of formerly redlined neighborhoods also have less access to the nature experiences associated with reduced stress, improved mental health, and increased wellbeing (Bratman et al. 2019; Kondo et al. 2018), compounding the direct ecological impoverishment documented here. This “nature deficit” in communities already bearing disproportionate environmental burdens underscores the importance of addressing biodiversity inequity as a component of broader environmental justice efforts.

Conclusions

We provide evidence that historical redlining is associated with lower urban butterfly diversity across the contiguous United States, operating primarily through the legacy effect of redlining on land cover composition — specifically the reduced proportion of developed open space and the elevated proportion of high-intensity development in formerly redlined neighborhoods. These differences in land cover, established through discriminatory housing policy nearly a century ago, persist in the built environment today and continue to shape the ecological communities that residents of those neighborhoods can access and experience. Addressing this biodiversity inequity will require targeted urban greening in formerly redlined areas, with particular emphasis on naturalistic plantings that support butterfly larval host plants and adult nectar resources. More broadly, our findings underscore the value of integrating historical land use policy into contemporary urban biodiversity research and demonstrate the potential of large-scale citizen science datasets to reveal ecological legacies of social injustice at continental scales.

Declarations

Author Contribution

Meghan Clark (MC), Natasha Gownaris (NG), and Andrew M. Wilson (AW) conceived the study. MC and AW prepared and analyzed the data. AW, NG, and MC wrote the manuscript. All authors read and approved the final manuscript.

Data Availability

This study analyzed publicly available data from three sources. Butterfly occurrence records were obtained from the Global Biodiversity Information Facility (GBIF) as a mediated download of research-grade iNaturalist observations (GBIF.org, <https://doi.org/10.15468/dl.h9h6uq>). Home Owners' Loan Corporation neighborhood boundaries were obtained from the Mapping Inequality project, University of Richmond (<https://dsl.richmond.edu/panorama/redlining>). Land cover data were obtained from the Annual National Land Cover Database 2021, US Geological Survey (<https://www.mrlc.gov/data>). The derived zone-level datasets and the complete analysis code required to reproduce all results, tables, and figures are provided as supplementary material.

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Figures

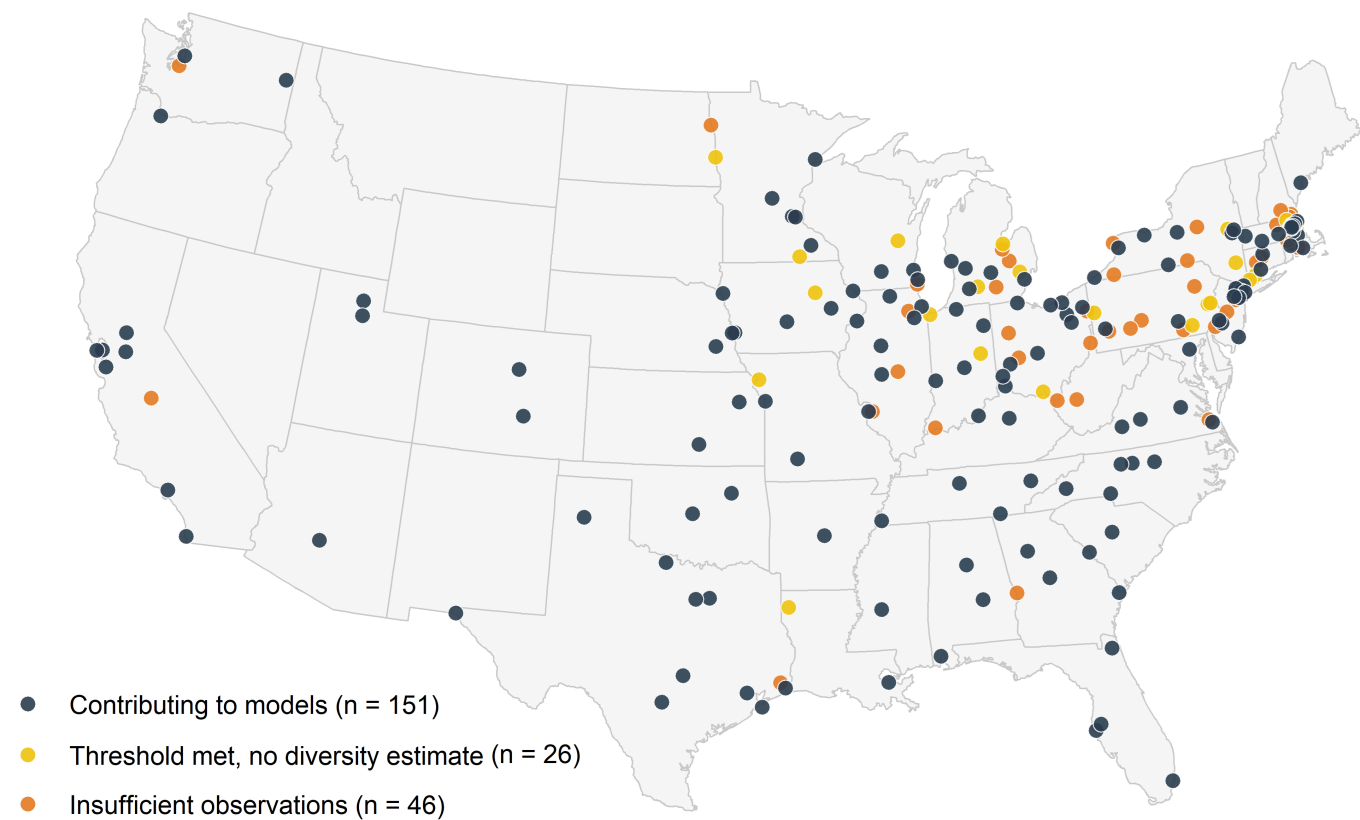
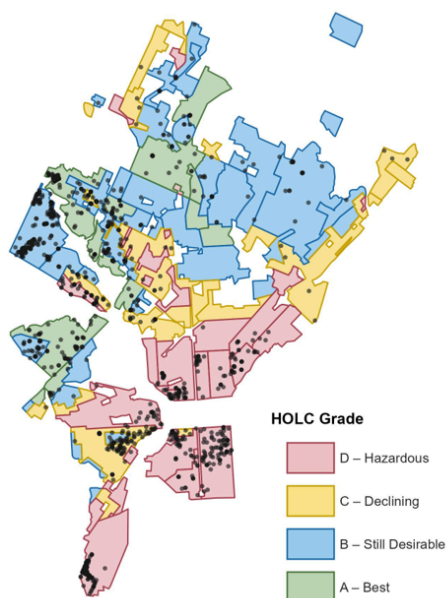


Figure 1

Distribution of HOLC-mapped cities across the contiguous United States. Circles indicate cities contributing at least one zone × year diversity estimate (n = 151), cities in which at least one zone met the ≥ 5 observation threshold but no zone × year combination contained at least two species (n = 26). All 223 cities retaining at least one graded HOLC polygon are shown

A. HOLC zones and butterfly observations
Philadelphia, PA | n = 1616 iNaturalist records (2016–2025)



B. HOLC zones and land cover
National Land Cover Database 2021

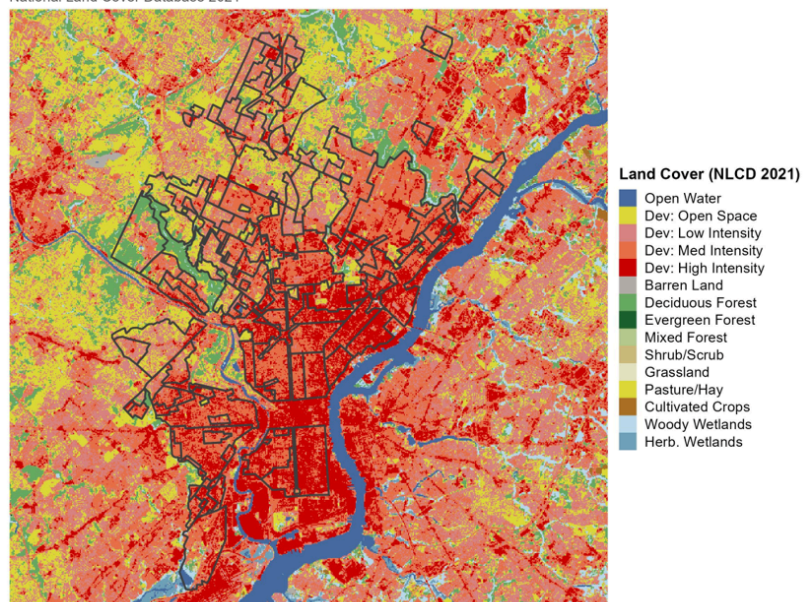


Figure 2

Philadelphia, Pennsylvania as an illustrative example of the study system. (A) Individual HOLC zones coloured by grade (A–D), with research-grade iNaturalist butterfly observations (black points; n = 1,616) overlaid. (B) The same HOLC zone boundaries (dark grey lines) overlaid on 2021 National Land Cover Database (NLCD) land cover, illustrating the gradient from developed open space and forest (yellows and greens) in grade A zones to high-intensity development (red) in grade D zones.

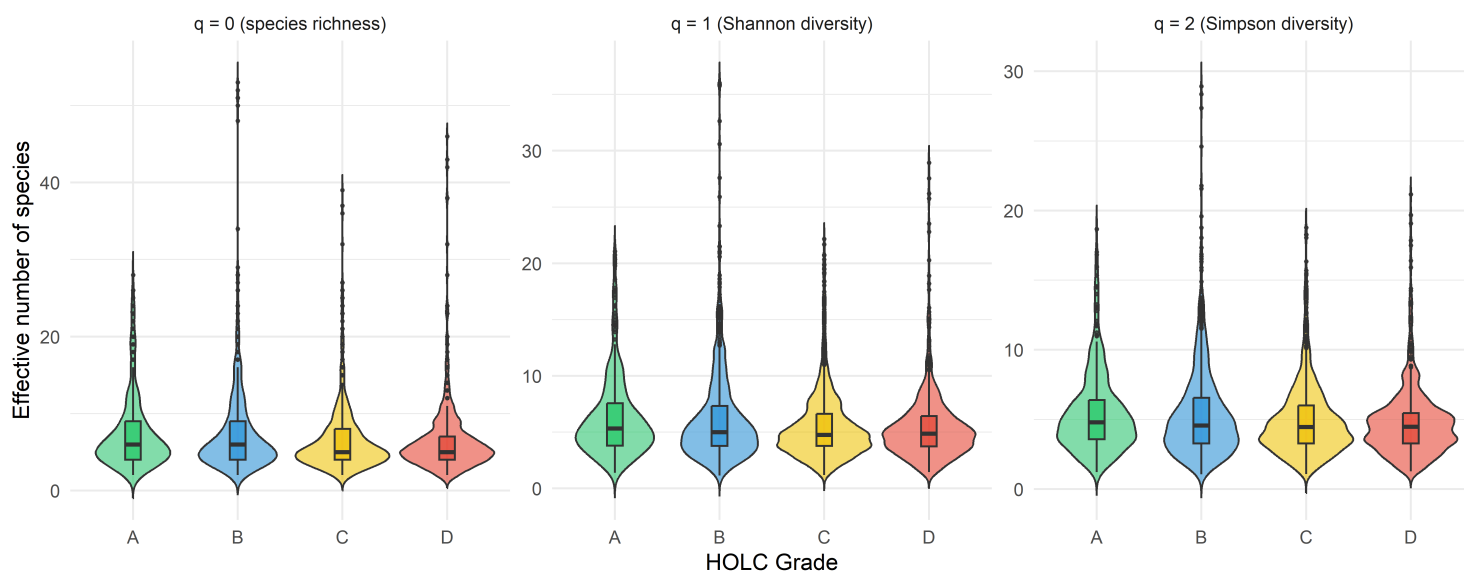


Figure 3

Butterfly diversity by HOLC grade. Violin plots show the distribution of Hill number diversity estimates at the zone $\times$ year level; embedded box plots show the median and interquartile range. Hill numbers are

shown for $q = 0$ (species richness), $q = 1$ (Shannon diversity), and $q = 2$ (Simpson diversity). Grade D (“Hazardous,” historically redlined) is the reference category in the mixed-effects models. Diversity was generally higher in grades A and B than in grade D, particularly for Shannon and Simpson diversity, although the distributions overlap substantially among grades. Colors correspond to the conventional HOLC grade colors used in the original maps.

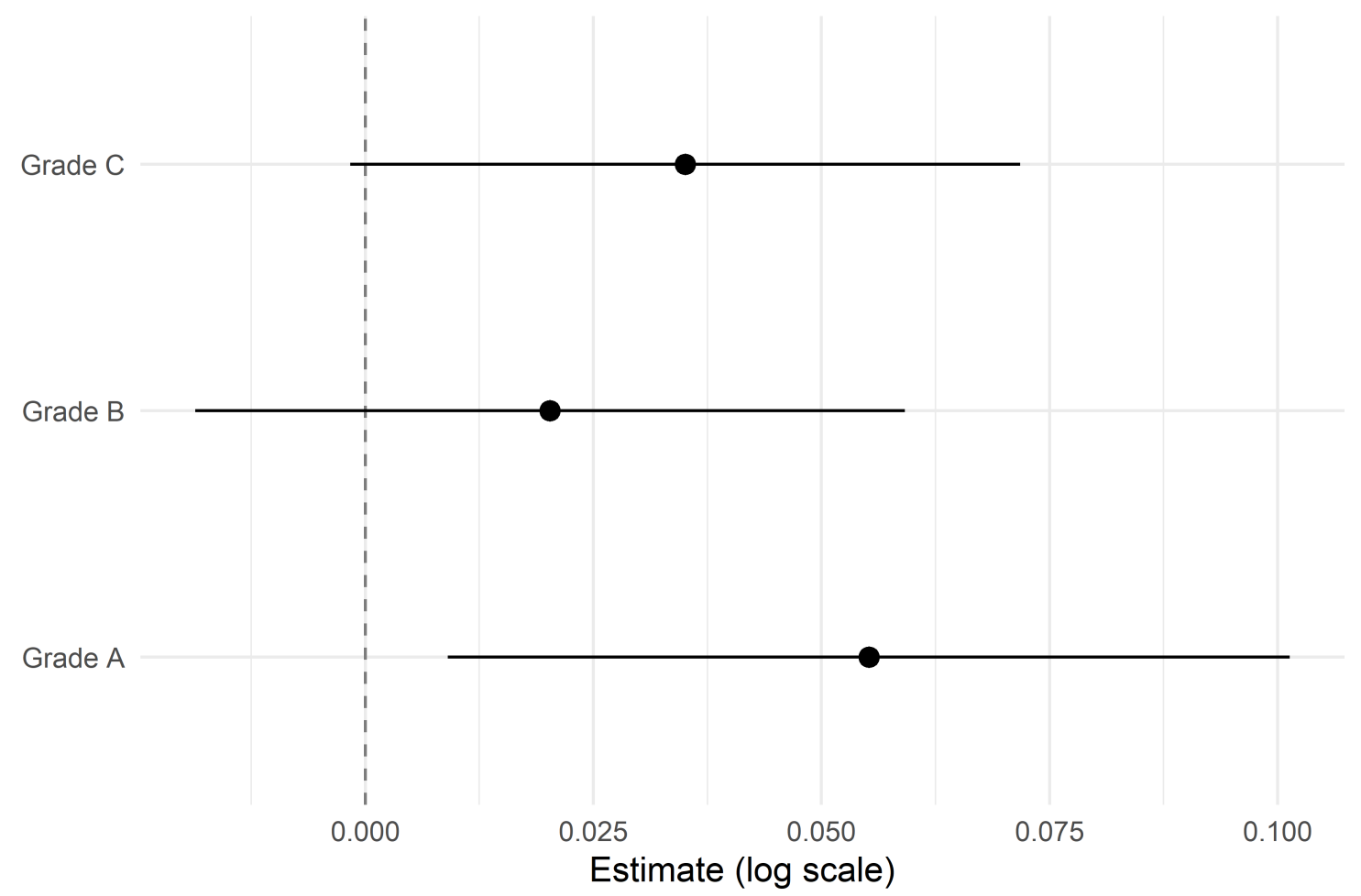


Figure 4

Estimated effects of HOLC grade on Shannon butterfly diversity ($q = 1$) relative to the reference category (Grade D, redlined zones). Points show model coefficients and horizontal lines show 95% Wald confidence intervals from the best-fitting mixed-effects model (grade + log area + year + log effort, city as random intercept; $n = 151$ cities). Positive values indicate higher Shannon diversity than grade D. Grade A zones had significantly higher Shannon diversity than redlined zones ($\beta = 0.055$, 95% CI: 0.009–0.101).

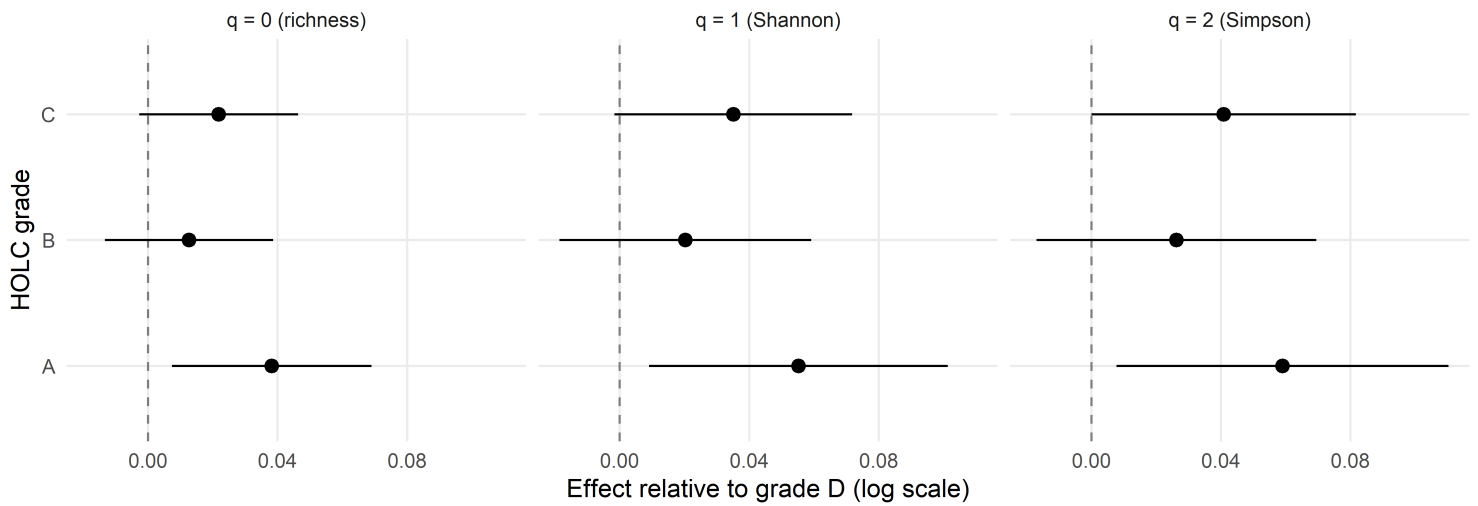


Figure 5

Estimated effects of HOLC grade on butterfly diversity relative to the reference category (grade D, redlined zones) across Hill numbers of order $q = 0$ (species richness), $q = 1$ (Shannon diversity), and $q = 2$ (Simpson diversity). Points show model coefficients and horizontal lines show 95% Wald confidence intervals from the best-fitting mixed-effects model. Because higher orders of q progressively downweight rare species, the persistence of the grade A contrast from $q = 0$ to $q = 2$ indicates that diversity differences among grades extend to the relative abundances of common species rather than being driven by rare taxa alone.

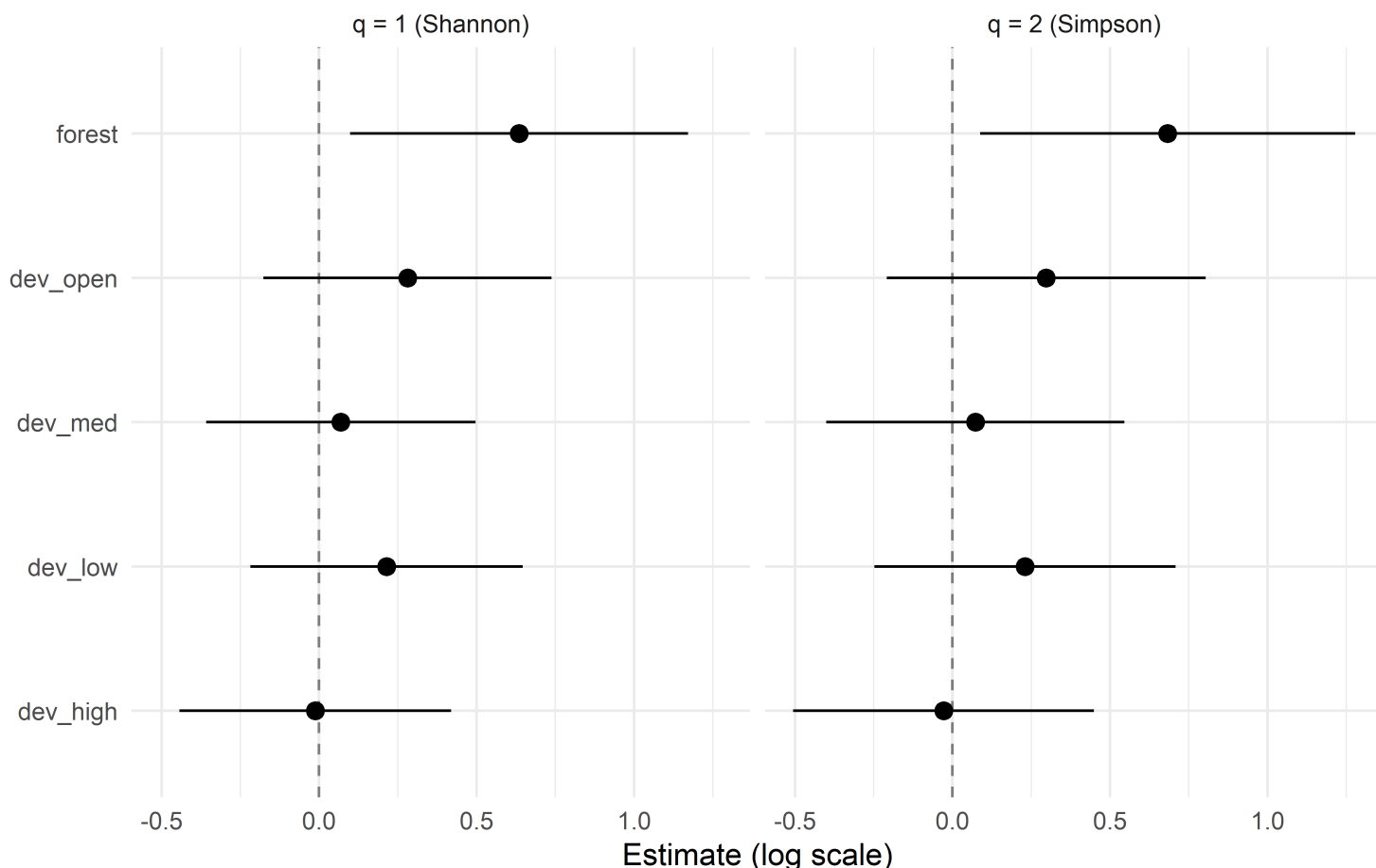


Figure 6

Estimated effects of land cover composition on Shannon ($q = 1$, left) and Simpson ($q = 2$, right) butterfly diversity. Points show model coefficients and horizontal lines show 95% Wald confidence intervals from the full land cover models, which additionally include HOLC grade, log zone area, year, and log sampling effort, with city as a random intercept. Developed land cover is split into four NLCD intensity classes. Forest cover was the only individually significant land cover predictor, with a positive effect on both diversity orders.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterial.docx](#)