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RESEARCH

Trophic downgrading in the city: urban structural simplification erodes the snake component of reptile assemblages

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Abstract

Urbanization is widely recognized as a major driver of biodiversity loss, yet its effects on the trophic structure of reptile communities remain poorly understood. This study re-analysed reptile presence–absence data from urban green-space fragments in Rome, Italy, to examine how urban habitat simplification affects the snake component and the trophic and functional structure of reptile assemblages. Fifteen reptile species were classified into functional and trophic groups, and several assemblage metrics were evaluated, including snake richness, lizard and gecko richness, trophic complexity, community trophic index, and dominance of urban-tolerant species. These metrics were related to fragment size, woodland cover, wetland presence, connectivity, and distance from the city centre. Results revealed a sharp, data-supported transition in snake occurrence across the woodland-cover gradient. Small fragments with limited woodland cover were dominated by urban-tolerant lizards and geckos, while snakes were largely absent. In contrast, larger and more structurally complex fragments retained diverse snake assemblages, particularly where wetlands were present. Woodland cover and wetlands were the strongest predictors of snake richness, whereas snake occurrence was best explained by total fragment size and wetland presence. Additional sensitivity analyses showed that the main pattern was robust to the exclusion of empty fragments and to alternative trophic-scoring schemes, although the strength of the trophic-complexity signal was reduced under the most conservative classification. Overall, our results suggest that urbanization-related habitat simplification is associated with taxon-linked trophic and functional simplification: small fragments retain some urban-tolerant lizards and geckos, but largely lose the snake component of the assemblage. These findings indicate that reptile assemblages can provide useful information on functional erosion in urban landscapes, while also emphasizing that trophic position, taxonomic affiliation and habitat-use traits may be difficult to disentangle in small vertebrate assemblages.

Keywords Habitat fragmentation · Woodland cover · Functional homogenization · Green-space fragments · Reptile community · Rome

Introduction

Urbanization is one of the most pervasive forms of land-use change and acts through multiple, interacting mechanisms, including habitat loss, fragmentation, reduced permeability of the urban matrix and disruption of dispersal routes, altered disturbance regimes, changes in microclimate, and the replacement of semi-natural habitats by built structures. These processes rarely affect all species equally. Instead, urbanization usually acts as an ecological filter, favouring species that tolerate disturbance, exploit anthropogenic resources or persist in small habitat fragments, while reducing the occurrence of habitat specialists, disturbance-sensitive species and taxa requiring large or structurally complex habitats. As a result, urban communities are often

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characterized not only by reduced species richness, but also by functional homogenization and increased dominance of a limited set of urban-tolerant species (McKinney 2006; Croci et al. 2008; Aronson et al. 2016; Ducatez et al. 2018; Lokatis and Jeschke 2022).

Most research on urban biodiversity has focused on birds and mammals, whereas reptiles have historically received less attention despite being potentially sensitive indicators of habitat structure, fragmentation and microhabitat availability. Recent reviews have shown that reptile responses to urbanization are highly variable among species, populations and urban features, but that negative effects on abundance, occurrence or richness are common, especially where urbanization reduces habitat quality and connectivity (French et al. 2018; Brum et al. 2023). At broad spatial scales, recent work on amphibian and reptile communities across North American cities has also shown that urban assemblages tend to be poorer than surrounding non-urban assemblages, although the magnitude and direction of compositional change can vary among regions and taxa (Marsh et al. 2023).

However, the consequences of urbanization for reptiles are still most often described in terms of species richness, occurrence or abundance. Much less attention has been given to whether urbanization changes the vertical structure of reptile assemblages, that is, the relative persistence of different trophic levels and functional groups. This is a critical gap because a community may lose ecological complexity even when some species persist. For example, a small urban fragment may still support lizards and geckos but may no longer maintain snakes or other higher-level predators. In such cases, urbanization would not merely reduce diversity; it would compress the assemblage into a simplified, low-trophic, generalist-dominated system (Shochat et al. 2006; Garden et al. 2007; French et al. 2018; Doherty et al. 2020).

Urban food-web studies increasingly suggest that urbanization can alter ecological interactions and trophic structure in ways that are not captured by species counts alone. Urban environments may modify predator–prey dynamics, reduce top-down control, increase the role of anthropogenic resources, and favour generalist or mesopredatory species over specialist predators (Fischer et al. 2012; Start et al. 2020). In urban food webs, specialist predators may be particularly vulnerable to fragmentation, and the loss or reduction of higher trophic levels can modify interaction structure throughout the community (Start et al. 2020). Recent empirical work in urban dry grasslands similarly showed that urbanization can disproportionately affect top predators and weaken biotic interactions, including systems where reptiles are part of the upper trophic structure (Straka et al. 2025).

Snakes are especially relevant in this context. Compared with many lizards and geckos, snakes often have lower detectability, larger spatial requirements, lower population densities, and stronger dependence on prey availability, shelter, habitat continuity and structural complexity. They also occupy higher trophic positions within reptile assemblages, frequently feeding on vertebrates, including amphibians, lizards, small mammals or other reptiles (Shine et al. 1998; Webb and Shine 1998; Willson and Dorcas 2004; Luiselli 2006; Reading et al. 2010; Steen 2010). Trait-based analyses have shown that snake species feeding primarily on vertebrates, species associated with aquatic habitats, and species with smaller geographic ranges tend to occur more frequently in natural landscapes and less frequently in human-dominated landscapes (Todd et al. 2017). This suggests that snakes, particularly vertebrate predators and species requiring complex or wet habitats, may be disproportionately sensitive to urban structural simplification.

Mediterranean cities provide particularly useful systems for testing these ideas because they often contain a heterogeneous mosaic of ancient villas, remnant woodlands, agricultural patches, wetlands, archaeological areas, gardens and densely built urban matrix. Rome is an especially informative case. Previous work on the herpetofauna of Rome showed that green-space fragments can still host a rich assemblage of amphibians and reptiles, but that fragment size, woodland area and water bodies strongly influence species richness and occurrence (Vignoli et al. 2009). In that study, reptile richness was strongly associated with fragment size and woodland cover, a threshold effect was observed around 50 ha of wooded surface, and distance from the city centre did not explain fragment species richness. The same study already suggested that snakes and lizards of the family Lacertidae, hereafter referred to as lacertids, may respond differently to fragment structure, with snakes being more constrained by woodland size, shape and position along the gradient than secondary consumers such as lacertids.

A parallel study on breeding birds in Rome further showed that urbanization affects not only species richness but also community structure and functional groups (Vignoli et al. 2013a). Along the rural–urban gradient, bird species richness and evenness declined, dominant species increased, generalist species became more frequent, and predators showed a negative relationship with urbanization, whereas omnivores showed the opposite pattern. The presence of old villas and large remnant green areas also disrupted simple radial patterns, allowing relatively rich assemblages to persist even in inner urban sectors. This suggests that, in old Mediterranean cities, the ecological gradient experienced by animal communities may not be adequately represented by distance from the city centre alone, but rather by a structural gradient of habitat loss, woodland reduction, wetland availability and fragment complexity.

Here, we conduct a hypothesis-guided re-analysis of the reptile assemblage dataset from Rome originally analysed by Vignoli et al. (2009). Previous analyses of the same system had already indicated that snakes and lacertid lizards responded differently to green-space structure, with snakes being more strongly constrained by woodland size and fragment configuration. The aim of the present study was therefore not to test a completely independent prediction, but to evaluate whether this previously observed taxonomic pattern corresponds to a measurable change in trophic and functional assemblage structure. Specifically, we ask whether small and structurally simplified fragments are characterized by: (i) pronounced loss of the terrestrial-snake component; (iii) lower trophic complexity and a lower community trophic index; and (iv) increased dominance of urban-tolerant lizards and geckos. Because trophic position, taxonomic affiliation and habitat-use traits are partly confounded in this assemblage, we interpret trophic metrics as a functional lens for describing assemblage change rather than as evidence that trophic position alone drives snake loss. Guided by ecological theory on urbanization and trophic simplification, we expected habitat simplification to be associated with the progressive loss of the snake component and with increasing dominance of tolerant, predominantly low-trophic species in small woodland fragments, particularly where wetlands are absent.

Materials and methods

Re-analysis dataset

We re-analysed the reptile presence–absence dataset originally compiled for green-space fragments within the municipality of Rome (Vignoli et al. 2009). The reconstructed dataset consisted of a site × species matrix including 63 green-space fragments and 15 reptile species. For each fragment, species occurrence was coded as presence/absence. The environmental variables associated with each fragment included total fragment size, woodland patch size within the fragment, a connectivity index describing the proximity of neighbouring green fragments, presence/absence of wetlands, and linear distance of the fragment centroid from the city centre.

Total reptile richness was calculated as the sum of all reptile species recorded in each fragment. Because the aim of the present re-analysis was to examine whether urbanization-related habitat simplification affects the trophic and functional structure of reptile assemblages, species were further assigned to functional groups based on broad ecological and trophic traits.

Functional and trophic classification of species

Species were classified into functional groups representing major components of reptile assemblage structure. Lizards and geckos included *Anguis fragilis*, *Chalcides chalcides*, *Hemidactylus turcicus*, *Lacerta bilineata*, *Podarcis muralis*, *Podarcis siculus* and *Tarentola mauritanica*. Snakes included *Natrix natrix*, *Natrix tessellata*, *Hierophis viridiflavus*, *Zamenis longissimus*, *Elaphe quatuorlineata* and *Vipera aspis*. Terrestrial snakes were analysed separately by excluding the two semi-aquatic *Natrix* species, thus including only *H. viridiflavus*, *Z. longissimus*, *E. quatuorlineata* and *V. aspis*. *Testudo hermanni* and *Emys orbicularis* were not assigned to the lizard/gecko or snake groups and contributed only to trophic metrics and, for *E. orbicularis*, to aquatic/semi-aquatic richness.

We defined urban-tolerant species a priori as taxa known to persist and reproduce in highly modified urban and peri-urban environments, including gardens, walls, villas, small green fragments and other anthropogenic microhabitats. This classification was based on published ecological information and long-term (>35 years of research by each of the coauthors) natural history knowledge of reptile ecology in the Rome metropolitan area, rather than on species occurrence patterns in the present dataset, thereby avoiding circularity between species classification and subsequent analyses. Under this definition, *Hemidactylus turcicus*, *Tarentola mauritanica*, *Podarcis siculus* and *Podarcis muralis* were considered urban-tolerant.

For each species, we assigned an ordinal trophic score representing its relative functional position within the reptile assemblage food web, based on its predominant feeding strategy and principal prey type as reported in the ecological literature. The scores distinguish broad functional guilds, ranging from predominantly arthropod-feeding lizards and geckos, through omnivorous or mixed-diet taxa and generalist predators, to obligate vertebrate predators occupying the highest functional position within the assemblage. These scores were used solely to derive site-level indices of trophic structure. Species classifications and trophic scores are reported in Table S2. The assigned values should therefore be interpreted as ordinal descriptors of functional trophic position rather than quantitative estimates of trophic level or trophic distance among species.

Derived community metrics

For each green-space fragment, we calculated the following community-level metrics:

1. Lizard/gecko richness: number of lizard and gecko species recorded in the fragment.

2. Total snake richness: number of snake species recorded in the fragment.
3. Terrestrial snake richness: number of terrestrial snake species recorded in the fragment, excluding *Natrix* species.
4. Aquatic/semi-aquatic reptile richness: number of semi-aquatic reptile species, including *Emys orbicularis*, *Natrix natrix* and *Natrix tessellata*.
5. Urban-tolerant species richness: number of urban-tolerant species recorded in the fragment.
6. Proportion of snakes: total snake richness divided by total reptile richness.
7. Proportion of urban-tolerant species: urban-tolerant richness divided by total reptile richness.
8. Snake occurrence: binary variable indicating whether at least one snake species occurred in the fragment.
9. Trophic height: maximum trophic score among species recorded in each fragment; this metric was retained for descriptive comparison among woodland-cover classes but was not subjected to separate inferential modelling.
10. Trophic complexity: number of trophic/functional guilds represented in each fragment.
11. Community trophic index: mean trophic score of all species recorded in each fragment.
12. Snake retention index: proportion of the regional snake species pool retained in a fragment divided by the proportion of the lizard/gecko species pool retained in the same fragment.
13. Terrestrial snake retention index: proportion of the terrestrial snake species pool retained in a fragment divided by the proportion of the lizard/gecko species pool retained.

Relative richness values were also calculated by dividing observed richness in each group by the number of species available in the corresponding regional pool: seven species for lizards/geckos, six species for all snakes and four species for terrestrial snakes.

Environmental predictors and woodland-cover classes

Fragment size and woodland patch size were log-transformed as $\log10(x+1)$, where x is area in hectares. This transformation reduced the influence of very large fragments while allowing fragments with very small woodland areas to be retained. Distance from the city centre was retained as a descriptor of the radial rural–urban gradient. We also derived an urbanity index by rescaling distance from the city centre so that values close to 1 represented more central/urban fragments and values close to 0 represented peripheral fragments.

To provide an interpretable description of functional changes across the woodland-cover gradient, fragments were assigned to three woodland-cover classes: <12 ha, 12–49 ha and >49 ha of woodland cover. These classes were used only for descriptive summaries and visualization, not as the basis for the main statistical inference. All formal analyses testing relationships between fragment structure and reptile occurrence, richness or functional structure used fragment size or woodland patch size as continuous predictors. The two intermediate classes initially explored, 12–24 ha and 24–49 ha, were merged because they contained few sites and showed similar functional profiles.

To address the possibility that the descriptive woodland classes were influenced by the observed reptile patterns, we also conducted an additional data-driven breakpoint analysis for snake occurrence. For each candidate breakpoint in log-transformed woodland patch size and total fragment size, we fitted a binomial GLM with snake occurrence as the response and a binary term indicating whether the fragment was above or below the candidate breakpoint. Candidate breakpoints were evaluated only when at least eight fragments occurred on each side of the split, and models were ranked using AICc. This analysis was treated as the primary assessment of a threshold-like transition in snake occurrence, whereas woodland-cover classes and associated contingency tests were used only for descriptive presentation.

Statistical analyses

All analyses were conducted in R using generalized linear models and generalized estimating equations. We first explored relationships among environmental predictors using Pearson correlation coefficients. Because total fragment size and woodland patch size were strongly correlated, they were not included together in the same candidate models. Distance from the city centre and the derived urbanity index were also not included in the same models because they are exact inverse representations of the same radial gradient.

To test whether snake occurrence increased along the structural gradient, we modelled the binary snake-occurrence response using binomial generalized linear models with a logit link. Candidate predictors included log-transformed fragment size, log-transformed woodland patch size, connectivity, wetland presence, distance from the city centre and urbanity index. Candidate models were compared using Akaike's Information Criterion corrected for small sample size (AICc). Because fragment size and woodland patch size were strongly correlated, model selection was used to identify which of these two structural predictors best explained snake occurrence.

To analyse richness responses, we fitted Poisson generalized linear models for lizard/gecko richness, total snake richness, terrestrial snake richness and trophic complexity. Overdispersion was assessed using the ratio between the sum of squared Pearson residuals and residual degrees of freedom. Since dispersion values were close to or below 1, Poisson models were retained. For snake richness and terrestrial snake richness, candidate models included log-transformed woodland patch size, wetland presence, connectivity and urbanity index. Models were compared using AICc.

The proportion of urban-tolerant species was analysed using a binomial GLM with a logit link, in which the response was specified as a two-column matrix containing the number of urban-tolerant species and the number of non-urban-tolerant species recorded in each assemblage. This model tested whether the relative dominance of urban-tolerant species declined with increasing woodland patch size. The predictor variable (woodland patch size) was independent of the species counts defining the binomial response, and therefore no mathematical coupling between predictors and response variables occurred.

To compare the responses of lizards/geckos and snakes directly while accounting for repeated species records within fragments, we converted the dataset to species-level presence–absence observations and fitted a binomial generalized estimating equation using the geeglm function in the geepack package. Species identity was included as a fixed effect to account for differences in baseline occurrence among taxa, while separate woodland-cover slopes were estimated for lizards/geckos and snakes. Fragment was treated as the clustering unit, with an exchangeable within-fragment correlation structure. The contrast between the two group-specific slopes provided the formal test of whether responses to woodland cover differed between functional groups.

Finally, Fisher's exact tests were used to evaluate differences in snake occurrence among woodland-cover classes. A three-class test compared fragments with <12 ha, 12–49 ha and >49 ha of woodland cover. A second test contrasted small fragments with <12 ha of woodland cover against all fragments with at least 12 ha of woodland cover. These tests were retained solely as descriptive checks of the class-based summaries and were not used as the main basis for statistical inference, which relied on continuous-predictor GLMs and the data-driven breakpoint analysis.

Model coefficients from binomial models were converted to odds ratios by exponentiation. Coefficients from Poisson models were converted to rate ratios. Because the main continuous area predictors were log10-transformed, effect ratios can be interpreted as the expected multiplicative change associated with a tenfold increase in fragment size or woodland patch size.

Trophic height was summarized descriptively but was not analysed using a separate inferential model because, in this assemblage, the maximum trophic score was largely determined by snake occurrence and would therefore provide little information independent of the snake-occurrence analysis.

Additional sensitivity analyses were conducted to evaluate the robustness of results to potentially subjective classification decisions. First, we repeated the analysis of urban-tolerant dominance using a stricter classification that excluded *Podarcis muralis*. Second, as a post hoc diagnostic rather than as a basis for classification, we examined whether a simple ubiquity criterion identified the same urban-tolerant species as the a priori classification. Third, we recalculated trophic complexity and community trophic index under alternative trophic-scoring schemes, including scenarios in which turtles were excluded, snakes were scored more conservatively as trophic levels 3 and 4 rather than 4 and 5, all snakes were collapsed into a single vertebrate-predator category, and *Vipera aspis* was assigned a lower score. Fourth, because fragments with no reptile species may represent unsuitable sites rather than simplified assemblages, we repeated trophic-complexity analyses using only fragments with at least one reptile species recorded. Finally, we evaluated whether the main snake models were sensitive to the inclusion of the smallest fragments by repeating models after excluding fragments below increasing minimum-size thresholds.

See Data Availability Statement and Supplementary Dataset S1 for the raw site × species matrix and derived variables.

Results

Woodland-cover classes and functional structure of reptile assemblages

Reptile assemblages showed a marked functional shift across woodland-cover classes (Table 1; Fig. 1). Fragments with less than 12 ha of woodland cover hosted highly simplified assemblages, with low lizard/gecko richness, near absence of snakes, low trophic complexity, and a strong dominance of urban-tolerant species. In these small woodland fragments, mean snake richness was only 0.11 species and snakes occurred in 8.9% of fragments. Mean trophic height increased from 1.33 in fragments with <12 ha of woodland cover to 3.75 and 4.70 in the intermediate and largest classes, respectively; these values are reported descriptively in Table 1.

By contrast, fragments with 12–49 ha of woodland cover showed a clear functional transition. In this intermediate class, mean lizard/gecko richness increased from 1.38 species

Table 1 Reptile community structure across woodland-cover classes. Mean reptile community metrics across three woodland-cover classes in green-space fragments of Rome: small fragments (< 12 ha woodland cover), intermediate fragments (12–49 ha), and large fragments (> 49 ha). Reported metrics include lizard/gecko richness (S_LIZ), total snake richness (S_SNK), terrestrial snake richness (S_TSNK), trophic height (TH), trophic complexity (TCOMP), snake occurrence (SNK_O), proportion of urban-tolerant species (UT_RATIO), community trophic index (COMM_TI), snake retention index (SNK_RI), and terrestrial snake retention index (TSNK_RI). TH is reported as a descriptive metric and was not analysed separately because it is largely determined by snake occurrence in this assemblage. Values show a shift from simplified assemblages dominated by urban-tolerant lizards/geckos in small fragments to more trophically structured assemblages with higher snake richness and trophic complexity in larger fragments

Wood Class	*N*	S_LIZ	S_SNK	S_TSNK	TH	TCOMP	UT_RATIO	COMM_TI	SNK_RI	TSNK_RI	SNK_O
< 12 ha	45	1.378	0.111	0.089	1.333	0.689	0.942	2.081	0.067	0.079	0.089
12–49 ha	8	3.250	1.250	1.000	3.750	2.125	0.479	2.535	0.486	0.642	0.875
> 49 ha	10	6.200	3.600	2.800	4.700	3.300	0.392	2.717	0.678	0.796	1.000

in fragments with < 12 ha of woodland cover to 3.25 species in intermediate fragments and 6.20 species in fragments with > 49 ha of woodland cover. Snake richness showed an even sharper transition, increasing from 0.11 to 1.25 and 3.60 species across the same classes. (Table 1; Fig. 1A).

The proportion of urban-tolerant species declined sharply across the same gradient. In fragments with less than 12 ha of woodland cover, urban-tolerant species represented, on average, 94.2% of the reptile assemblage. This proportion declined to 47.9% in intermediate fragments and to 39.2% in fragments with more than 49 ha of woodland cover. The decline in the proportion of urban-tolerant species with increasing woodland cover was robust to the exclusion of *P. muralis* from the urban-tolerant group. Under the stricter classification, the mean percentage of urban-tolerant species was 66.9% in fragments with < 12 ha of woodland cover, but only 27.8% and 29.2% in the 12–49 ha and > 49 ha classes, respectively. A binomial GLM confirmed a strong negative relationship between woodland cover and the proportion of strictly urban-tolerant species (odds ratio = 0.405, 95% CI = 0.272–0.591, $p < 0.001$; Table S3). Similarly, trophic complexity increased from 0.69 in the smallest woodland fragments to 2.13 in intermediate fragments and 3.30 in the largest fragments (Table 1; Fig. 1B).

Model selection: structural predictors of snake occurrence and richness

Model selection showed that snake occurrence was best explained by total fragment size and wetland presence (Table 2). This model received the strongest support among candidate models (AICc weight = 0.703), although a model including woodland cover and wetland presence also received some support. In the best-supported model, snake occurrence increased with fragment size and was positively associated with wetland presence (Table 3; Fig. 2A). A tenfold increase in fragment size increased the odds of snake occurrence by approximately 34 times, while wetland presence increased the odds of occurrence by approximately 17 times. This large effect ratio should be interpreted in light of the near-absence of snakes from the smallest fragments.

Total snake richness was best explained by woodland patch size and wetland presence (Table 2). This model had the lowest AICc and accounted for most of the model weight (AICc weight = 0.857), whereas the corresponding model including total fragment size and wetland presence received weaker support. In the best-supported model, a tenfold increase in woodland cover nearly tripled expected snake richness, while wetland presence had an additional positive effect (Table 3; Fig. 2B).

A similar, although less exclusive, pattern was observed for terrestrial snakes. The best-supported model included

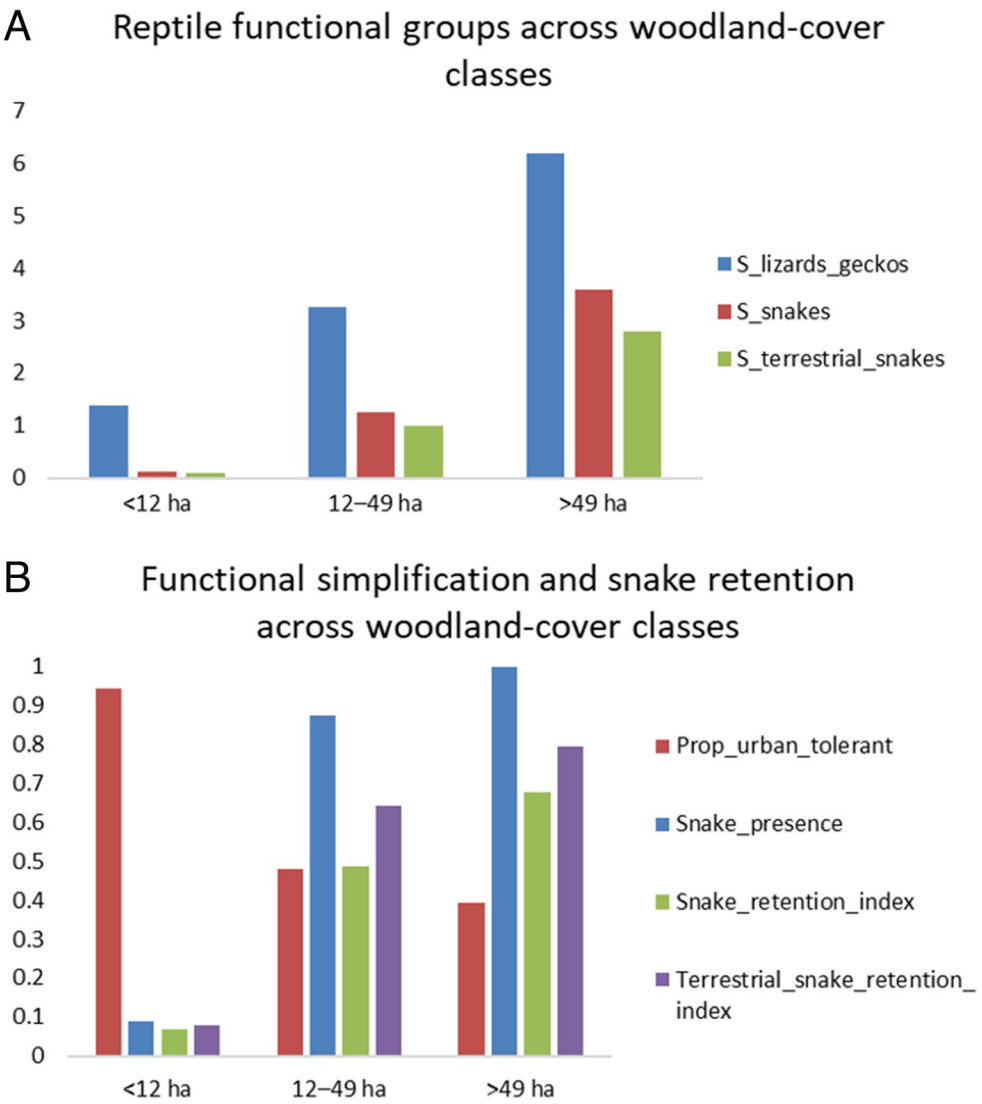

Fig. 1 Functional structure of reptile assemblages across woodland-cover classes in urban green fragments of Rome

woodland patch size and wetland presence (AICc weight = 0.643), but the model including fragment size and wetland presence also received some support (AICc weight = 0.229). Thus, terrestrial snake richness was most strongly associated with woodland cover and wetland presence, while total fragment size also captured part of the structural gradient relevant to terrestrial snakes. In the best-supported model, a tenfold increase in woodland patch size increased expected terrestrial snake richness by approximately 2.9 times, and wetland presence also had a positive effect (Table 3; Fig. 2C).

Contrasting responses of snakes and lizards/geckos to woodland cover

Woodland patch size had a positive effect on both lizard/gecko and snake richness, although the estimated magnitude of the response was greater for snakes. In separate Poisson models, a tenfold increase in woodland cover was associated with a 2.3-fold increase in lizard/gecko richness, a 4.9-fold increase in total snake richness and a 4.8-fold increase in terrestrial snake richness (Table S1). However, the direct functional-group comparison provided only marginal evidence that the response to woodland cover differed between lizards/geckos and snakes (species-level GEE, group × woodland-cover interaction: $\beta = 1.10$, SE = 0.59, $z = 1.85$, $p = 0.064$; Table S8). The larger estimated response of snakes should therefore be interpreted as a consistent difference in magnitude rather than as a statistically conclusive divergence between functional groups.

Data-driven breakpoint in snake occurrence

The data-driven breakpoint analysis identified the strongest transition in snake occurrence at 10.17 ha of woodland cover, reported as 10.2 ha after rounding (Table S4). Importantly,

Table 2 Model selection for snake occurrence and snake richness along the urban structural gradient. Candidate generalized linear models explaining snake occurrence, total snake richness and terrestrial snake richness in green-space fragments of Rome. Snake occurrence was analysed using binomial GLMs, whereas snake richness and terrestrial snake richness were analysed using Poisson GLMs. Models were compared using Akaike's Information Criterion corrected for small sample size (AICc). For each response variable, models are ranked by increasing AICc. ΔAICc indicates the difference from the best-supported model, and AICc weights indicate relative model support. Fragment size and woodland patch size were not included in the same candidate models because of strong collinearity

Response	Model	df	AIC	AICc	Delta_AICc	AICc_weight
Snake occurrence	fragment size + wetland	3	28.408	28.815	0	0.703
Snake occurrence	woodland cover + wetland	3	32.069	32.476	3.661	0.113
Snake occurrence	fragment size only	2	32.693	32.893	4.079	0.091
Snake occurrence	fragment size + connectivity	3	33.765	34.171	5.357	0.048
Snake occurrence	fragment size + urbanity	3	34.585	34.992	6.178	0.032
Snake occurrence	woodland cover only	2	37.983	38.183	9.368	0.006
Snake occurrence	woodland cover + connectivity	3	39.553	39.960	11.145	0.003
Snake occurrence	woodland cover + urbanity	3	39.970	40.377	11.562	0.002
Snake occurrence	wetland only	2	41.285	41.485	12.671	0.001
Snake occurrence	connectivity only	2	81.639	81.839	53.024	0
Snake occurrence	urbanity only	2	82.271	82.471	53.657	0
Total snake richness	woodland cover + wetland	3	85.350	85.757	0	0.857
Total snake richness	fragment size + wetland	3	89.260	89.667	3.910	0.121
Total snake richness	fragment size + urbanity	3	93.402	93.809	8.052	0.015
Total snake richness	woodland cover + connectivity	3	97.220	97.627	11.870	0.002
Total snake richness	woodland cover + urbanity	3	97.450	97.857	12.100	0.002
Total snake richness	woodland cover only	2	97.736	97.936	12.179	0.002
Total snake richness	fragment size only	2	104.549	104.749	18.993	0
Total snake richness	fragment size + connectivity	3	106.533	106.940	21.183	0
Total snake richness	wetland only	2	111.107	111.307	25.551	0
Total snake richness	urbanity only	2	177.211	177.411	91.654	0
Total snake richness	connectivity only	2	181.321	181.521	95.764	0
Terrestrial snake richness	woodland cover + wetland	3	76.412	76.819	0	0.643
Terrestrial snake richness	fragment size + wetland	3	78.475	78.881	2.063	0.229
Terrestrial snake richness	fragment size + urbanity	3	80.135	80.541	3.723	0.100
Terrestrial snake richness	woodland cover only	2	84.974	85.174	8.355	0.010
Terrestrial snake richness	woodland cover + connectivity	3	85.116	85.523	8.704	0.008
Terrestrial snake richness	woodland cover + urbanity	3	85.278	85.685	8.866	0.008
Terrestrial snake richness	fragment size only	2	88.758	88.958	12.140	0.001
Terrestrial snake richness	fragment size + connectivity	3	90.737	91.144	14.325	0
Terrestrial snake richness	wetland only	2	95.771	95.971	19.152	0
Terrestrial snake richness	urbanity only	2	146.056	146.256	69.438	0
Terrestrial snake richness	connectivity only	2	149.264	149.464	72.645	0

Table 3 Generalized linear models explaining snake occurrence and snake richness. Parameter estimates from the best-supported models for snake occurrence, total snake richness and terrestrial snake richness in urban green-space fragments of Rome. Snake occurrence was modelled using a binomial GLM with logit link, whereas total snake richness and terrestrial snake richness were modelled using Poisson GLMs with log link. Effect ratios correspond to odds ratios for the binomial model and rate ratios for the Poisson models. Because fragment size and woodland patch size were log10-transformed, effect ratios for these predictors represent the expected multiplicative change associated with a tenfold increase in fragment or woodland area. Confidence intervals are 95% profile-likelihood intervals

Response	Model_type	Predictor	Estimate	SE	Z	*P*	Eff. ratio	CI_low	CI_high
Snake occurrence	Binomial logistic	(Intercept)	−7.114	1.887	−3.770	0	0.001	0.000	0.016
Snake occurrence	Binomial logistic	log_fragment_size	3.521	1.325	2.657	0.008	33.818	4.158	965.923
Snake occurrence	Binomial logistic	PRESENCE_WATER	2.831	1.250	2.264	0.024	16.961	1.820	384.092
Snake richness	Poisson	(Intercept)	−4.108	1.006	−4.084	0	0.016	0.001	0.074
Snake richness	Poisson	log_wood_patch_size	1.081	0.216	5.011	0.000	2.946	1.950	4.551
Snake richness	Poisson	PRESENCE_WATER	2.889	1.059	2.728	0.006	17.973	3.356	333.310
Terrestrial snake richness	Poisson	(Intercept)	−4.104	1.008	−4.073	0	0.017	0.001	0.074
Terrestrial snake richness	Poisson	log_wood_patch_size	1.072	0.244	4.399	0	2.921	1.834	4.782
Terrestrial snake richness	Poisson	PRESENCE_WATER	2.653	1.075	2.469	0.014	14.201	2.520	267.257

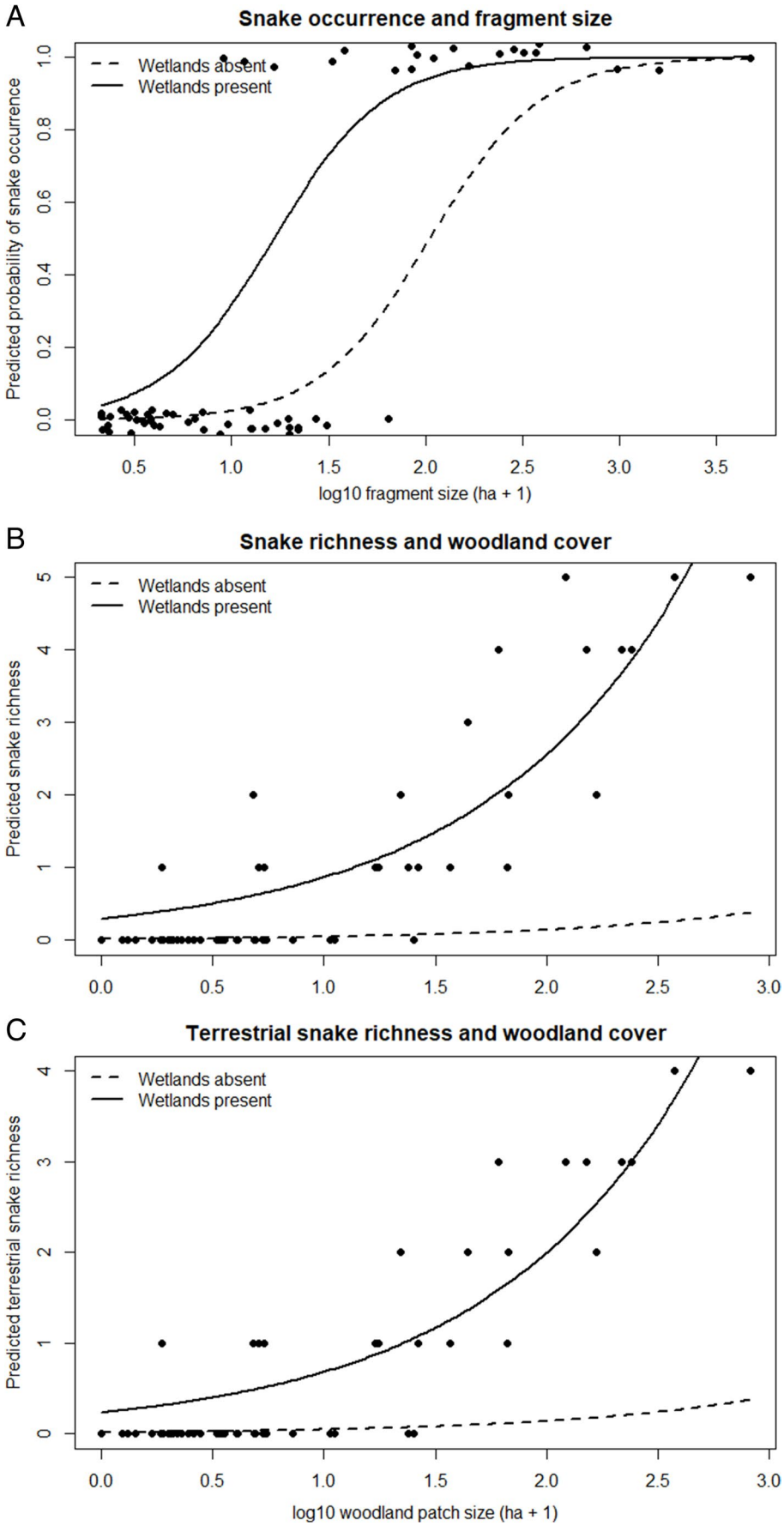

Fig. 2 Model-predicted responses of snakes to structural features of urban green fragments

although estimated without reference to the descriptive woodland classes, this breakpoint produced exactly the same binary partition as the rounded 12-ha boundary: the same 45 fragments fell below the transition and the same 18 fragments occurred above it. Fragments above this breakpoint were substantially more likely to retain snakes than fragments below it. A complementary analysis based on total fragment size identified the best-supported breakpoint at 29.8 ha, consistent with the model-selection result indicating that total fragment size was the strongest predictor of snake occurrence.

For descriptive purposes, the woodland transition was summarized using the rounded classes < 12 ha and ≥ 12 ha. Snakes occurred in only 4 of 45 fragments with < 12 ha of woodland cover, compared with 17 of 18 fragments containing at least 12 ha. Fisher's exact test confirmed the strong difference between these descriptive classes, but this test was used only as a descriptive check; inferential support for the transition was based on the continuous-predictor GLMs and the data-driven breakpoint analysis.

Thus, small woodland fragments were not simply species-poor but almost entirely lacking the snake component of the reptile assemblage. More broadly, the rural–urban gradient in Rome was not captured by distance from the city centre alone, but by a structural gradient involving fragment size, woodland cover and wetland presence.

Sensitivity analyses

The main trophic-complexity pattern was robust to the exclusion of fragments without reptiles. In the full dataset, a tenfold increase in woodland cover was associated with a 2.34-fold increase in trophic complexity. When only occupied communities were analysed, the effect remained positive and significant, although reduced in magnitude, with a 1.74-fold increase in trophic complexity per tenfold increase in woodland cover (Table S5). Alternative trophic-scoring schemes produced the same qualitative pattern in most cases. The association between woodland cover and trophic complexity remained significant when turtles were excluded and snakes were scored more conservatively as trophic levels 3 and 4, and also when Vipera aspis was assigned a lower score. Under the most conservative scenario, in which turtles were excluded and all snakes were collapsed into a single trophic category, the effect remained significant in the full dataset but became marginal when only occupied communities were analysed. In contrast, the community trophic index remained positively and significantly associated with woodland cover under all alternative scoring schemes (Table S6).

The classification of urban-tolerant species was also supported by a simple post hoc ubiquity check. The four species classified a priori as urban-tolerant were the only species occurring in at least 30% of fragments, whereas all snake species and the remaining non-urban-tolerant reptiles occurred below this threshold (Table S9). This check was not used to define urban tolerance, but it indicates that the a priori classification was consistent with an independent pattern of broad occurrence across the urban fragment network.

The large effect ratio obtained for snake occurrence partly reflected the near-absence of snakes from the smallest fragments. However, the positive effect of fragment size remained significant after excluding fragments smaller than 2 ha (odds ratio = 32.4, $p = 0.009$) and 5 ha (odds ratio = 18.8, $p = 0.033$). After excluding fragments smaller than 10 ha, the estimate remained positive but became non-significant, reflecting the smaller sample size and reduced environmental contrast. The positive effect of woodland cover on total snake richness remained significant under all minimum woodland-size thresholds examined (Table S7).

Discussion

This study provides evidence that urbanization in Mediterranean landscapes does not only reduce reptile species richness, but also fundamentally restructures the trophic organization of reptile assemblages. By re-analysing a long-term dataset from green-space fragments in Rome, we show that urban habitat fragmentation is associated with a pronounced functional filtering effect, strongly affecting the snake component, which represents the higher trophic component of the reptile assemblage, while allowing a subset of low-trophic, urban-tolerant lizards and geckos to persist. These findings support the interpretation that urbanization-related habitat simplification may act as a trophic and functional filter, simplifying reptile communities beyond what is apparent from taxonomic metrics alone.

A key result is the strong threshold-like response in snake occurrence and richness across the woodland-cover gradient. The data-driven breakpoint analysis located the strongest transition in snake occurrence at 10.2 ha of woodland cover, close to the rounded 12-ha boundary used for descriptive summaries. Below this portion of the woodland-cover gradient, snakes were almost entirely absent, whereas they became widespread in intermediate and large fragments. A complementary breakpoint at 29.8 ha of total fragment size further supports the conclusion that the occurrence of the snake component depends on the overall spatial extent of green-space fragments, whereas snake richness is more closely associated with the amount of woodland habitat retained within them. This non-linear response suggests that snakes are particularly sensitive to habitat loss and structural simplification, consistent with their ecological

requirements for continuous cover, suitable refuges, and sufficient prey availability (Shine et al. 1998; Webb and Shine 1998; Luiselli 2006). The near-complete absence of snakes in small fragments indicates that urbanization can be associated with local trophic simplification even when other reptile groups remain present. It is also noteworthy that, in central Italy, reptiles in general (Dendi et al. 2026) and snakes in particular (Luiselli and Capizzi 1997) have been shown to be strictly dependent on the relative availability of woodlands and wooded corridors, even in natural and seminatural landscapes outside cities.

Importantly, our results highlight that different structural components of urban green spaces play distinct roles in shaping reptile assemblages. While total fragment size best predicted snake occurrence, woodland patch size was the strongest predictor of snake richness and terrestrial snake richness. Wetland presence also consistently enhanced snake occurrence and richness, suggesting that aquatic and semi-aquatic habitat features contribute disproportionately to maintaining higher trophic-level reptiles. These findings reinforce the idea that habitat quality and internal structural heterogeneity may be more important than simple area effects in determining the persistence of sensitive taxa in urban landscapes.

The estimated response to woodland cover was stronger for snakes than for lizards and geckos. However, the formal group-by-woodland interaction was marginal, and the difference between group-specific effect estimates should therefore be interpreted cautiously. The robust result is that small woodland fragments retained some lizard and gecko species but largely lacked the snake component of the assemblage (Fig. 3). This pattern is consistent with previous trait-based studies showing that reptiles feeding on vertebrates, species with larger spatial requirements, and species dependent on specific habitat structures are more vulnerable to anthropogenic disturbance (Todd et al. 2017; French et al.

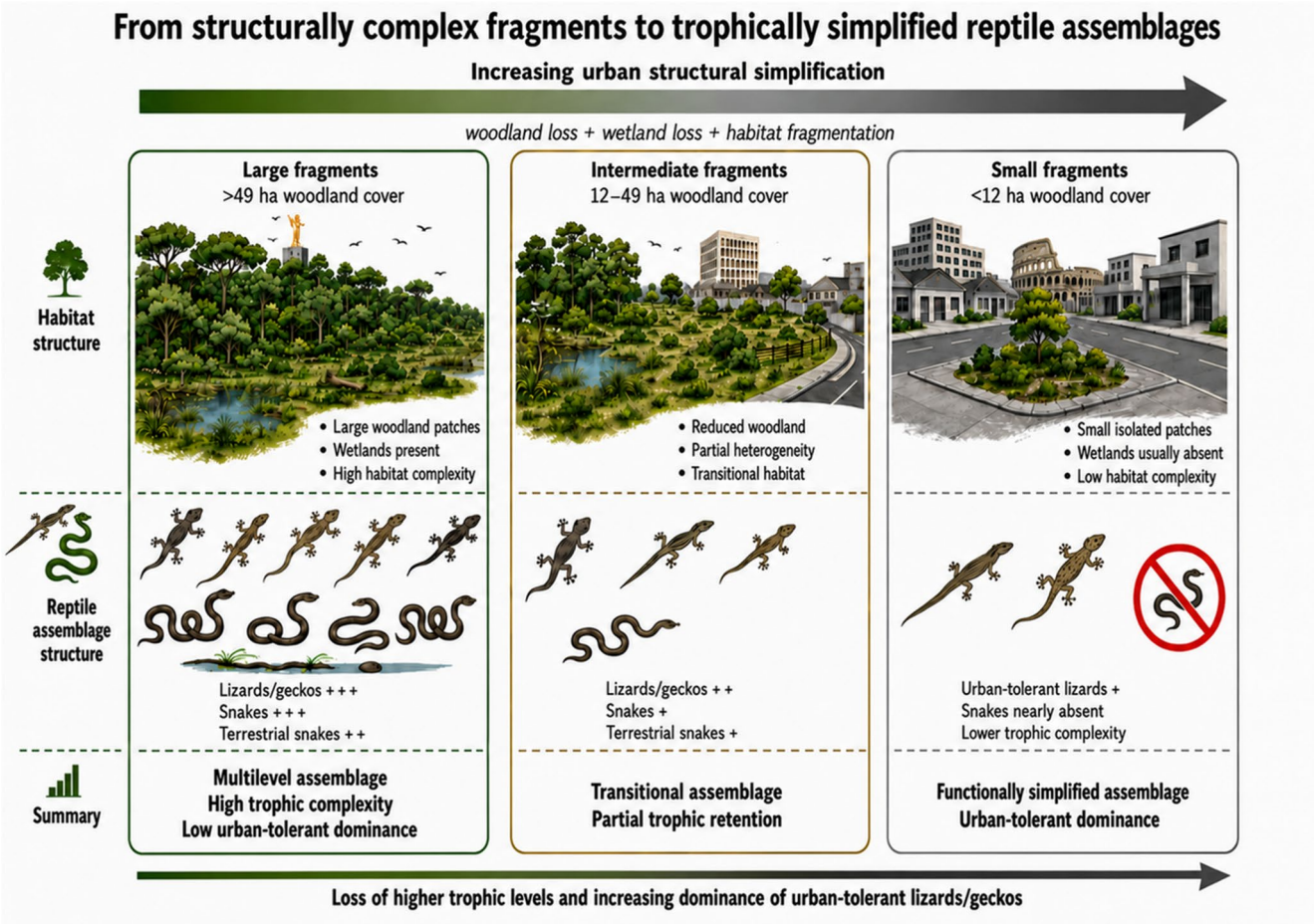

Fig. 3 Conceptual model of trophic simplification in reptile assemblages along an urban structural gradient. Urbanization-related habitat loss and fragmentation reduce woodland cover, wetland availability and habitat heterogeneity within green-space fragments. Large and structurally complex fragments retain diverse reptile assemblages comprising lizards, geckos and snakes, with greater representation of higher trophic components. Intermediate fragments show partial trophic retention, whereas small, woodland-poor fragments are dominated by urban-tolerant lizards and geckos and almost entirely lack snakes. The resulting pattern is not merely a decline in species richness, but a taxon-linked functional simplification involving the erosion of the higher trophic component of the reptile assemblage

2018). In this sense, urbanization does not eliminate reptiles uniformly, but selectively removes ecological functions associated with higher trophic positions.

The positive associations of woodland cover with trophic complexity and the community trophic index provide additional support for the interpretation of trophic and functional simplification in small fragments. Even when some reptile species persist, the loss of snakes reduces the representation of the higher trophic component and leaves assemblages increasingly dominated by insectivorous and generalist taxa. However, this evidence should be interpreted cautiously. The relationship between woodland cover and trophic complexity remained positive under most alternative scoring schemes and after the exclusion of reptile-free fragments, but weakened under the most conservative classification and became marginal when all snakes were collapsed into a single trophic category in the analysis restricted to occupied fragments. Trophic complexity should therefore be regarded as corroborative rather than stand-alone evidence of functional downgrading. By contrast, the community trophic index remained positively associated with woodland cover under all alternative scoring schemes. Taken together with the strong patterns in snake occurrence, snake richness and urban-tolerant dominance, these results indicate a consistent reorganization of reptile assemblages along the woodland-cover gradient. Such simplification could potentially alter predator–prey interactions and top-down processes, although these consequences cannot be evaluated using the present occurrence dataset. Comparable changes in interaction structure have been reported in broader urban food-web studies (Shochat et al. 2006; Start et al. 2020).

A central limitation of our interpretation is that trophic position is strongly associated with taxonomic affiliation in this assemblage. Snakes represent the vertebrate-predator component of the reptile fauna, whereas most lizards and geckos are primarily arthropod feeders (Simbula et al. 2019, 2022). Therefore, the observed pattern cannot be interpreted as evidence that trophic position alone causes snake loss from small fragments. Other taxon-linked traits are likely to contribute to the same pattern, as reptile responses to urbanization often vary among species according to habitat requirements, behaviour and life-history traits (French et al. 2018). Many urban-tolerant lizards and geckos can exploit walls, buildings, gardens and other vertical or anthropogenic substrates, including in the urban landscape of Rome (Simbula et al. 2019). By contrast, snakes are generally more dependent on structurally complex ground habitats, suitable refuges, permeable substrates and prey fields; snake sensitivity to human land use is also associated with traits such as vertebrate-feeding and aquatic-habitat use (Todd et al. 2017). More broadly, habitat structure can be a key determinant of reptile assemblages in urban remnants (Garden et al. 2007), and snake persistence may depend on the availability and quality of retreat sites with suitable structural and thermal properties (Webb and Shine 1998; Webb et al. 2004). Ground compaction, soil sealing and paving, together with reduced litter cover and loss or disturbance of refuges, may therefore affect snakes more strongly than wall- and building-associated lizards, independently of trophic position (Pike et al. 2010). For this reason, we interpret trophic downgrading here as a taxon-linked functional pattern: the loss of snakes simultaneously represents the loss of a taxonomic group with specific habitat requirements and the erosion of the higher trophic component of the reptile assemblage. Claims concerning the relative magnitude of group responses should therefore be considered suggestive rather than conclusive. Future studies combining abundance data, occupancy modelling, prey availability, microhabitat structure and independent functional traits will be needed to separate trophic mechanisms from lineage-specific ecological constraints.

Our results also align with growing evidence that urbanization promotes functional homogenization. The strong dominance of urban-tolerant lizards and geckos in small fragments indicates that urban reptile communities are increasingly composed of a narrow set of species capable of exploiting anthropogenic habitats. The classification of *P. muralis* as urban-tolerant deserves some caution because this species is generally less synanthropic than *P. siculus* and may show different responses to urbanization in other geographic contexts (Maune et al. 2025), although it is widespread in gardens, walls and highly urbanized green spaces in Rome (Vignoli et al. 2009, 2013; Maura et al. 2011; Simbula et al. 2019). We therefore repeated the urban-tolerant dominance analysis using a stricter classification that excluded *P. muralis* and retained only *Hemidactylus turcicus*, *Tarentola mauritanica* and *P. siculus*. The decline in urban-tolerant dominance with increasing woodland cover remained strong and significant under this stricter classification, showing that the pattern was not driven solely by the inclusion of *P. muralis*. This sensitivity analysis supports the robustness of the functional homogenization pattern while also highlighting that urban-tolerance classifications should be context-dependent and explicitly tested when species show flexible habitat use. This mirrors findings in other taxonomic groups where urban environments favor generalist species while filtering out specialists (McKinney 2006; Aronson et al. 2016; Ducatez et al. 2018). In reptiles, this process may be reinforced by the strong habitat specificity and sensitivity of many snake species to human land use and habitat modification (Todd et al. 2017; French et al. 2018).

The role of Mediterranean landscape structure is also central to interpreting these patterns. Unlike many more recently urbanized regions, Mediterranean cities such as Rome retain a heterogeneous mosaic of green spaces embedded within

a long-established urban matrix. Nevertheless, our findings show that this heterogeneity is not sufficient to maintain full trophic structure in small fragments. Instead, only larger woodland patches and wetlands support complete reptile assemblages including higher-level predators. This suggests that even historically complex urban landscapes can experience functional erosion if habitat patches fall below critical structural thresholds.

The lack of association between reptile richness and distance from the city centre further highlights the limitations of traditional urban gradient models. Rather than a simple radial decline in biodiversity, reptile assemblages in Rome are structured by local habitat configuration, particularly woodland cover, fragment size, and wetland presence. This supports previous work in Mediterranean urban systems showing that ecological patterns are better explained by habitat structure than by geographic position within the city (Battisti 2003; Vignoli et al. 2013b). Consequently, conservation strategies based solely on urban–rural distance are unlikely to capture the true drivers of biodiversity loss in such systems.

From a conservation perspective, the marked sensitivity of snakes has important implications. Snakes are often overlooked in urban biodiversity planning due to their cryptic nature and low detectability, yet they represent a critical component of vertebrate food webs. Their loss may indicate deeper ecological disruption than is evident from species richness alone. Maintaining snake populations therefore requires preserving sufficiently large and structurally complex green spaces, as well as ensuring the presence of wetlands and habitat connectivity.

A limitation of this re-analysis is that the original dataset is based on presence–absence records rather than standardized abundance or detection-corrected occupancy estimates. Snakes are generally less detectable than lizards and geckos, and this may partly influence comparisons among functional groups. However, the original dataset was based on repeated surveys and long-term knowledge of the study fragments, reducing the likelihood that the observed patterns merely reflect detectability differences. Moreover, the strong association between snake occurrence, fragment size, woodland cover and wetland presence is biologically consistent with the known spatial and habitat requirements of snakes. Future studies should explicitly combine occupancy modelling, abundance estimates and direct trophic-interaction data to test the mechanisms underlying urban trophic downgrading.

In conclusion, this study provides evidence that urbanization-related habitat simplification is associated not only with species loss, but also with trophic and functional simplification of reptile assemblages. Snakes emerge as key indicators of this process due to their sensitivity to habitat structure and their position at higher trophic levels. Urban green spaces that retain woodland complexity and wetland habitats are essential for maintaining functional reptile communities. Future research should further explore how these trophic changes influence ecosystem functioning and whether similar patterns occur across other vertebrate groups in urban environments.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11252-026-02092-3.

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Author contributions L.V. and L.L. jointly conceived the study, developed the conceptual framework, interpreted the results, and contributed to manuscript writing and revision. L.V. reconstructed and curated the dataset, designed and performed the statistical analyses, prepared the figures and tables, and wrote the first draft of the manuscript. L.L. contributed to the ecological interpretation of the results, the trophic and functional framing of the study, and critical revisions of the manuscript. Both authors approved the final version of the manuscript.

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Data availability The data supporting the findings of this study are available as Supplementary Material. The supplementary dataset includes the reconstructed site × species presence–absence matrix for reptile assemblages in green-space fragments of Rome, the associated environmental predictors, and the derived functional and trophic metrics used in the analyses. The R script used to reproduce the statistical analyses, model selection, tables and figures is also provided as Supplementary Material. The dataset derives from a re-analysis of field data originally collected for Vignoli et al. (2009). No additional data were generated during the present study.

Declarations

Ethics approval This study is based on a re-analysis of previously collected presence–absence data and did not involve new field sampling, animal handling, experimental procedures, or collection of biological material. Therefore, no new ethics approval was required.

Competing interests The authors declare no competing interests.

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