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Resource and Landscape-Scale Habitat Availability Shape Insectivorous Bat Assemblages in a High-Altitude Andean City

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Abstract

The response of biodiversity to urbanization may be mediated by context, being important to study it in restrictive environments, such as high-elevation and semi-arid regions, where urban studies are scarce. La Paz, Bolivia, represents a good example of a city situated at high elevation (3,600 m a.s.l.), in a semi-arid environment, with poor urban planning and an accelerated urbanization rate. We evaluated how local environmental variables, landscape-scale habitat availability, and insect availability impacted insectivorous bat richness and species in this city. We surveyed 29 sampling sites using active acoustic monitoring and quantified vegetation cover, artificial light at night, insect availability, distance to natural remnants, and habitat availability within 200, 500, and 1,000 m donut buffers. Insect availability received the strongest support for both species richness and total acoustic activity, and landscape structure received secondary support for richness. Species-specific responses differed among the three dominant detected species: *Myotis oxyotus* activity was best supported by local greenness and artificial light at night (ALAN) variation, although insect availability and spatial structure models were also competitive. *Tadarida brasiliensis* was best explained by spatial structure rather than the measured environmental variables. *Histiotus montanus* was most strongly associated with insect availability. These results indicate that trophic resources and landscape context could be shaping insectivorous bat assemblages in this high-Andean urban ecosystem, but species-specific responses are influenced by a combination of local environmental conditions, resource availability, and spatial processes.

INTRODUCTION

Urbanization does not affect biodiversity uniformly, as ecological responses are mediated by the biome in which cities are embedded (Filloy et al. 2019; Diamant et al. 2025). This variation may be especially important in restrictive environments, such as high-elevation and arid or semi-arid regions. In drylands, water limitation and low productivity constrain species richness, and thus urbanization could have an oasis effect on certain functional groups (Leveau et al. 2022). High-elevation ecosystems, which present drastic temperature declines and atmospheric pressure changes (Körner 2007), naturally constrain functional and taxonomic biodiversity (Chakravarty et al. 2021).

Among urban wildlife, bats have received increasing attention because of their varied responses to urbanization (Russo and Ancillotto 2015; Rega-Brodsky et al. 2022; Saldaña-Vázquez et al. 2025), which are shaped by environmental factors working at both local and landscape scales (Gallo et al. 2018; Callas et al. 2024). At the immediate scale, vegetation cover, green area size, and vegetation structure support the richness of insectivorous bat assemblages (Tena et al. 2020; Callas et al. 2024). Also at a local scale, Artificial Light at Night (ALAN) can diminish bat diversity and activity, but can improve foraging opportunities for urban-tolerant species (Lacoeuilhe et al. 2014; Mena et al. 2022; Li et al. 2024). Furthermore, insect availability can act as a constraint, having a bottom-up effect in certain scenarios (Jung and Threlfall 2018). At broader spatial scales, natural urban remnants and habitat connectivity may play an important role in supporting bat diversity within cities, particularly by increasing habitat availability for disturbance-sensitive species (Tena et al. 2020). Although urban bats and their

response to urbanization have been studied before, most research has been conducted in temperate and lowland tropical ecosystems (Threlfall et al. 2012a; Jung and Threlfall 2018; Voigt et al. 2021), and there are comparatively few studies of urban bats in drylands and mountainous environments (Rosero-Taramuel et al. 2023; Dwyer et al. 2024; Salas-Salinas et al. 2026).

Environmental constraints are unlikely to affect species equally, because species-specific traits respond differently to urbanization (Jung and Kalko 2011; Rodríguez-Aguilar et al. 2017); functional traits such as roost specialization, wing loading related to flight maneuverability, foraging habitat, and echolocation call characteristics can shape their presence within cities (Jung and Threlfall 2018; Marsden et al. 2023). In general, bats that forage in open spaces, emit long quasi-constant frequency (QCF) or constant frequency (CF) calls, and are roost generalists are more associated with these ecosystems (Jung and Threlfall 2018; Villarroya-Villalba et al. 2021). Phylogenetically, free-tailed bats (Molossidae) possess most of these traits and are the most frequently recorded family in urban environments (Marsden et al. 2023).

La Paz city represents an unusual setting for urban bat ecology because it combines very high elevation (mean 3600 m a.s.l.) with semi-arid conditions, limited surface water, and scattered vegetation. Moreover, a historical lack of urban planning has resulted in highly fragmented natural remnants within the urban matrix, and dysfunctional green areas that remain threatened by accelerated urban expansion (Carlsson 2021). Bat diversity is also naturally limited at these elevations, with only nine species currently reported for the La Paz valley (Aguirre 1998; Moya et al. 2015). Despite this distinctive environmental context, urban bat ecology in Bolivia's arid ecosystems remains poorly understood, with previous studies focusing on species inventories (Aguirre 1998; Moya et al. 2015), roosts (Siles et al. 2005), or responses to local environmental variables (Peñaranda-del Carpio et al. 2016). Thus, bat responses to urbanization in mountainous semi-arid ecosystems at different scales remain unknown.

Our study aims to evaluate how both local and large-scale variables, as well as resource availability, influence the insectivorous bat assemblage and individual species in the high-Andean city of La Paz, to better understand their responses in this specific environment. Based on previous studies, we expect that bat responses to urbanization will vary across spatial scales. Consistent with other studies (Dwyer et al. 2024), we expect that vegetation will have a strong positive effect on both richness and activity, as it provides important resources (Suarez-Rubio et al. 2018), while artificial light should influence bat diversity negatively (Li et al. 2024). At the landscape scale, we expect the availability of and proximity to patch remnants to strongly influence the bat assemblage, particularly given the high degree of fragmentation within the city. At the species level, we expect species-specific responses due to substantial variation in urban tolerance functional traits among the insectivorous bats present in the La Paz valley. We expect clutter-space foraging species such as *Myotis oxyotus* and *Histiotus montanus* to be more sensitive to urbanization, whereas *Tadarida brasiliensis*, a well-known urban-tolerant species, will be more resistant to urban variables. Finally, due to low productivity and high temperature variation of high-elevation environments, combined with the fact that green urban areas are small, scarce, and

generally degraded in La Paz (Carlsson 2021), we expect an overall sensitivity to urbanization across all species in the city.

METHODS

STUDY AREA

The city of La Paz is located in the western Andean region of Bolivia. It covers ≈ 90 km² and harbors ≈ 750,000 inhabitants. The city is situated in a deep inter-Andean valley between 3,200 and 4,100 m a.s.l. The average temperature ranges between 10 and 14°C, with high daily temperature fluctuations of 15 to 25°C, and the mean annual precipitation is between 500 and 600 mm, with a rainy season from November to March (Beck et al. 2015). The urban matrix is highly fragmented, with natural remnants threatened by illegal construction, and publicly designed or managed green areas are very small and highly isolated (Villegas and Garitano-Zavala 2010; Carlsson 2021).

We selected 29 sampling sites between 3,150 and 3,800 m a.s.l., each covering 4-ha and separated by at least 250 m. Each sampling site was selected based on previous citizen-science urban bat recordings to increase the probability of detection in a city where bat activity is generally low. Nevertheless, sampling sites showed substantial structural variation among one another, including highly urbanized sites downtown with scarce to absent green areas (n = 10), moderately urbanized areas with large green spaces and private gardens (n = 9), and peri-urban areas with low gray infrastructure and extensive vegetation (n = 10) (Fig. 1).

Acoustic survey

We conducted acoustic surveys across 15 nights per month between December 2019 and March 2020, and between October and November 2020. This period corresponds to the warmer, more humid season of the year, when higher bat activity and species richness have been reported in our study area (Moya et al. 2015). Each of the 29 sites was surveyed on four separate nights during the study period. On each survey night, two observers simultaneously monitored two sites, with each observer using an Echo Meter Touch 2 Pro detector (Wildlife Acoustics®). The detectors were configured with an audio division ratio of 1/20, a 2-second trigger window, and high gain to ensure detection of low-frequency bat calls and long-distance calls. Recordings were conducted during the first three hours after dusk, which corresponds to the peak period of bat activity (Le Roux et al. 2014).

During each sampling hour, the observer completed one standardized sampling round. Each round included five 10-minute recording points: four located along the edges of the 4-ha sampling site and one point at its center. As transit between recording points took approximately 2 minutes, one sampling round took one hour to complete. The sampling design was created for this specific study.

Local-scale variables

At each sampling site, we measured local vegetation cover and artificial light at night (ALAN) intensity. Vegetation cover was estimated using the Normalized Difference Vegetation Index (NDVI) derived from low-cloud-cover Sentinel-2 satellite imagery (10 m spatial resolution) acquired in March 2020. The image was processed in QGIS to calculate NDVI values and subsequently clipped to each 4-ha sampling site. For each site, we extracted the mean NDVI value as a proxy for vegetation cover (Li et al. 2023).

ALAN was measured using a HOBO® data logger positioned in the area most exposed to artificial lighting. The logger was active during the three-hour acoustic survey period, recording light intensity (in lux) once per minute, to obtain a mean value for each site (Lacoeuilhe et al. 2014).

Landscape variables

We considered three landscape variables: 1) distance to the nearest natural remnant to understand accessibility to resources; 2) area of the nearest natural remnant to understand the effect of the nearest habitat resource; and 3) remnant availability within 200, 500, and 1,000 m in donut buffers, excluding the habitat available contained within the local sampling site, to measure overall habitat availability within the landscape. Natural remnants were defined as areas larger than 1 ha, composed of native or semi-natural vegetation, clearly distinct from urban parks, private gardens, or ornamental landscaping.

For each sampling site, we calculated the distance to the nearest natural remnant and the area of that remnant (in ha). We conducted spatial analyses in R using the *landscapemetrics* package, with Sentinel-2 satellite imagery (10-m spatial resolution) as the raster base. We manually digitized the natural remnants shapefile using the La Paz Municipal Protected Areas database (Gobierno Autónomo Municipal de La Paz -Secretaria de Ciudad Verde, unpublished data) as a base, which shows the initial area of Protected Areas polygons from the date each was created. Due to substantial discrepancies between the original surface and current remnants of the protected areas, the polygons were digitized using the March 2020 Sentinel imagery used for the NDVI calculation. We also estimated remnant area availability within 200 m, 500 m, and 1,000 m buffers around each sampling site using spatial intersections.

Insect availability

We estimated insect availability using a black light trap placed at each sampling site. We acknowledge that black light traps attract specific insect taxa and do not capture insect availability at greater heights, which has been demonstrated to be important for certain bat species (McCracken et al. 2021). However, this method is considered a reliable proxy for relative insect availability. Although light traps can affect bat activity (Froidevaux et al. 2018), the mobile sampling design used minimized potential bias. The trap consisted of a UV light source installed inside a box with a white cloth surface to attract and retain insects. It was activated during the three-hour acoustic survey period, and photographs were taken at one-hour intervals. As insects accumulated over time and remained on the cloth surface, only the final photograph was used for analysis. Images were processed in the ImageJ software, using a color threshold to calculate the proportion of the surface area covered by insects (Kesavaraju and Dickson 2012).

Acoustic analysis

All bat calls were classified manually using the Kaleidoscope software (Wildlife Acoustics). First, recordings were screened to separate bat calls from noise or non-bat calls. We included only recordings featuring distinctive calls with more than three consecutive pulses for further analysis. We measured bat pulses for maximum frequency, minimum frequency, pulse duration, inter-pulse interval, bandwidth, characteristic frequency (Fc), and characteristic slope (Sc). We compared acoustic parameters against a local reference library (Saravia Jiménez 2018) and verified them with regionally published acoustic references for the target species (Ugarte-Núñez 2020).

Bat activity was quantified as the number of passes recorded per total survey hours. A bat pass is defined as a sequence of three or more search-phase pulses. Feeding buzzes were quantified but were excluded from the analysis due to low representation in the dataset.

Sampling effort and rarefaction analysis

To evaluate whether the sampling effort was sufficient to characterize the detectable insectivorous bat assemblage, we performed an incidence-based rarefaction test and generated extrapolation curves in R using the *iNEXT* package.

Data Analysis

We evaluated the effects of habitat availability on species richness, acoustic activity, and species activity at different spatial scales (200, 500, and 1,000 m from our sampling points) using Generalized Linear Models (GLMs) with a Poisson distribution for richness and a negative binomial distribution with an offset of survey hours per site for species activity. We used the corrected Akaike Information Criterion (AICc) for small sample sizes (Burnham and Anderson 2004).

We fitted separate models for local variables (NDVI and ALAN), resource availability (insects), and landscape variables (distance to the nearest remnant, area of the nearest remnant, and habitat availability at the selected scale), and a complete model combining predictor groups. We implemented either GLMs or Generalized Additive Models (GAMs) depending on the linearity of response relationships and dispersion patterns. The performance of each model was compared using the AICc to identify the most relevant predictors. We performed the same analyses for bat activity and species-specific responses, using a negative binomial distribution with an offset of the hours of sampling effort. For species responses, we restricted analyses to the three most dominant species, as the models could not support the rarest sonotype data due to excess zeros. All analyses were conducted in R using the packages *MASS, MuMIn, spdep*, and *mgcv*. OpenAI's ChatGPT was used to assist with debugging and refinement of portions of the R code. All analyses were executed, reviewed, interpreted, and validated by the authors.

Model adequacy was evaluated using residual diagnostics, Pearson dispersion, and simulated zero counts. For GAM, we performed basis dimension checks and concurvity. Cook's distance was calculated

(Cook 1977), and a distance greater than 4/n was treated as potentially influential as an additional diagnostic. Model diagnostics and their interpretation are available in Supplementary Material S1.

We assessed spatial autocorrelation using Moran's I (Moran 1950) calculated from models' Pearson residuals. Spatial weights were defined using k-nearest neighbor networks. We evaluated k = 4 as the principal analysis, and k = 3 and k = 5 as complementary sensitivity tests (see S2). We performed 999 Monte Carlo permutations and used permutation p-values as the inferential criterion. For models with a detected spatial autocorrelation, we added a smooth of Universal Transverse Mercator (UTM) coordinates to account for spatial structure.

RESULTS

We completed 11.68 hours of survey per site, accumulating 339 hours of sampling and recording 1,593 passes. We identified three species, *Histiotus montanus, Myotis oxyotus*, and *Tadarida brasiliensis*, and an unidentified vespertilionid, hereafter referred to as Vesp. The sites with the highest number of bat passes were Lipari (944), the Municipal Zoo (193), Ciudadela (151), and Bolognia (114), whereas no recordings were obtained from Sopocachi, Riosinho, Camacho, San Luis, and Irpavi II (Fig. 2). The most frequently recorded species was *M. oxyotus* (935), followed by *H. montanus* (270), *T. brasiliensis* (267), and the least common was Vesp (121) (Fig. 2).

The incidence-based rarefaction curve showed that the sampling effort was sufficient to characterize the acoustically detectable species of the insectivorous bat assemblage. The analysis showed an asymptotic richness estimate, with observed richness (Sobs = 4; estimated richness = 4), and complete sample coverage (SC = 1.00). The rarefaction curve reached an asymptote well before the total sampling effort (Fig. S1).

Effects of habitat availability across spatial scales on bat assemblage and species responses

Both species richness and assemblage activity responded more strongly to habitat availability at broader scales (1,000 m). For total acoustic activity, the 1,000-m scale was retained over the 500-m scale because both had comparable AICc support, but the 1,000-m model had better diagnostic adequacy. At the species level, the best-supported spatial scale for habitat availability was 1,000 m for *H. montanus* and 500 m for both *M. oxyotus* and *T. brasiliensis*. For *T. brasiliensis*, the 500 m model had better diagnostic adequacy and a competitive support with the 1,000 m model, so it was retained for further analysis (Table 1).

Effects of urban variables on bat assemblage structure

Insect availability received the strongest support for richness. Even though landscape was not the best-supported model, it had relevant support for understanding bat species richness (W = 0.231). For bat assemblage activity, the resource model was also the best supported, with the complete model also

receiving important support (W = 0.300). The landscape and local models received substantially less support and thus were not considered (Table 2; Fig. 3).

Effect of urban variables on species response

Three species were considered for the analysis: *H. montanus, M. oxyotus*, and *T. brasiliensis*. Sonotype 4 (Vesp.) was excluded from further analysis due to low occupancy across sites, which made the models unstable and difficult to interpret. These three species possess distinct functional traits related to urbanization response and sensitivity (Siles et al. 2005; Jung and Threlfall 2018; Marsden et al. 2023), which can help explain their responses to the assessed urban variables (Table 3).

For *Myotis oxyotus* and *Tadarida brasiliensis*, we detected significant residual spatial correlation using a Moran's I test, and thus we incorporated spatial smooths of UTM coordinates into the candidate models. After this correction of models, we found that species-specific responses differed among the three dominant species. For *M. oxyotus*, the local +spatial model received the greatest support, but the resource availability and spatial baseline models were also competitive (ΔAICc < 2). For *T. brasiliensis*, the spatial baseline model was the best supported, with markedly greater support than the other models. In contrast, *Histiotus montanus* was best supported by the resource model (Fig. 4).

DISCUSSION

Habitat availability on insectivorous bat assemblage

At the assemblage level, both species richness and activity responded to habitat availability at broader scales. For species richness, the 1,000 m scale received the strongest support, while for total acoustic activity, the 500 m and the 1,000 m scales were competitive for the top-ranked models. Together, these results highlight that, when only habitat availability is considered, broader scales are more important than the immediate surroundings of sampling sites. Previous urban studies have shown the importance of evaluating multi-scale effects of urbanization in bat assemblages. In Montreal, Fabianek et al. (2011) found greater importance of local scales (100–500 m) in different species, whereas studies in Sydney demonstrated the importance of broader landscape context for bat activity (Threlfall et al. 2012a).

Insect availability received the strongest support for both richness and total activity, highlighting the critical importance of trophic resources for insectivorous bat assemblages in this urban context. However, it is important to note that our insect availability survey only captured a subset of the available prey assemblage, mainly phototactic, low-flying insect taxa. Some open-space aerial insectivorous bats, such as *T. brasiliensis*, are known to forage at high altitudes up to 3,000 m above ground level (McCracken et al. 2021). Whether such foraging behavior occurs in La Paz remains unknown and should be considered for further studies of bat ecology in high-altitude mountain ecosystems.

Furthermore, insect resources may also be influenced by landscape. The secondary support received by landscape for species richness suggests that matrix configuration could also contribute to bat species

alongside trophic resources. Other studies similarly showed that food availability and urban variables could play an equal role in shaping insectivorous bat communities (Threlfall et al. 2012b; Villarroya-Villalba et al. 2021; Miguel-Méndez et al. 2026). In semi-arid ecosystems, trophic resources may represent an important constraint linking environmental conditions to bat activity. Studies in arid environments such as Arizona (Hagen and Sabo 2014) and the Arava Desert (Hackett et al. 2013) show that water availability and primary productivity alter primarily prey availability and thus bat activity as well. A recent study in Tacna, Peru, reported a comparable pattern, with high bat richness and evenness found in a peri-urban area characterized by the presence of agricultural areas, where the authors suggested the concentration of insects and habitat heterogeneity could contribute to maintaining bat diversity (Salas-Salinas et al. 2026). In La Paz, the primary effect of resource availability, with the secondary support of landscape structure, could be consistent with this possibility.

Natural remnants may also provide potential roosting habitat to bats. In La Paz, only two natural bat roosts are known to the authors, and to our knowledge, no use of artificial roost structures has been documented. Natural remnants and surrounding areas in La Paz feature rock crevices suitable for bat roosting, as seen for *Histiotus montanus* (Carvalho et al. 2013) and *Tadarida brasiliensis* (Allen et al. 2009), potentially explaining part of the relationship between native remnants and bat richness or activity. However, because roost availability was not evaluated in this study, their direct influence on bats remains hypothetical.

Vegetation greenness received little support as an explanatory variable for richness. This contrasts with previous studies where urban green areas support bat diversity (Threlfall et al. 2012a; Rodríguez-Aguilar et al. 2017; Callas et al. 2024). In Australia, vegetation composition, tree height, and tree density strongly influenced insectivorous bat assemblages (Threlfall et al. 2016). In the study by Threlfall et al. (2016), a positive relationship was found between native vegetation and bats, possibly due to the importance of plant composition for insect availability, although that was not assessed. In arid urban ecosystems, urban green areas and water accessibility shape urban bat habitat use, enhancing activity (Dwyer et al. 2024). In the city of La Paz, the local model containing NDVI received little support at the assemblage level. This may partly reflect the semi-arid nature of the ecosystem, where native remnants do not necessarily exhibit high greenness. Moreover, vegetation greenness may only become ecologically important for bats when it is sufficiently large (Tena et al. 2020) and structurally complex enough (Threlfall et al. 2017) to support prey, foraging, and roosting conditions. This suggests that urban parks, ornamental gardens, and planted greenery may not offer sufficient habitat quality (Carlsson 2021) or resource availability to attract bat presence in the city. In contrast, native remnants may be important because they could be providing a combination of habitat structure, resources, and roosting opportunities that are not captured by vegetation greenness alone.

Contrary to our expectations, ALAN showed no support for any of the assemblage variables. Previously, ALAN has been documented to negatively affect bat assemblages, likely limiting movement and reducing accessibility to foraging patches within the urban matrix (Haddock et al. 2019; Mena et al. 2022; Li and Wilkins 2022). Although previous literature indicates that fast-flying species' activity may be

positively affected by ALAN (Haddock et al. 2019; Barré et al. 2022), studies such as Barré et al. (2022) show that ALAN's effect may interact with land use.

Bat species-specific responses

The three dominant species showed markedly different responses to the environmental variables evaluated. *Myotis oxyotus* and *Tadarida brasiliensis* responded better to habitat availability at the 500-m scale, while *H. montanus* responded to the 1,000-m scale. For *Tadarida brasiliensis*, the 1,000-m model had the lowest AICc, but the 500-m scale model was retained because it remained competitive and showed better diagnostic adequacy. These differences indicate that the spatial extent relevant to habitat availability is species-specific and may reflect differences in movement, foraging behavior, and use of the urban landscape, but broader habitat availability, and not immediate habitat, may be shaping bat species activity.

For *Myotis oxyotus*, the local + space model received the greatest support, with the secondary resource availability and spatial baseline models in competition (ΔAICc < 2). This suggests that *M. oxyotus*, as an edge-space forager, could take advantage of greener urban areas. However, because the spatial baseline and resource models were also competitive, the apparent influence of NDVI should be interpreted cautiously rather than as an isolated dominant effect. Also, *M. oxyotus* showed a possible negative effect on ALAN, which was included in the local model. Previous studies have shown that edge and clutter foraging species could have a greater sensitivity to ALAN, affecting their presence and activity (Haddock et al. 2019).

Tadarida brasiliensis, which has been described as an urban-tolerant species (Avila-Flores and Fenton 2005; Salas-Salinas et al. 2026), showed a predominantly spatial response in our study. After taking into account the residual spatial autocorrelation, none of the environmental models was supported by the model selection. This suggests that there are processes and patterns influencing *T. brasiliensis* that were not captured in the study and may be influenced by spatial distribution. Given the frequent dominance of *T. brasiliensis* in urban environments and its high mobility (Krauel and LeBuhn 2016), it could be possible that roost availability could be shaping its activity in La Paz.

Histiotus montanus showed a different response to habitat availability, responding to the largest scale assessed in the study. *H. montanus* has previously been identified as sensitive to habitat fragmentation due to its low wing loading and slow, maneuverable flight (Rodríguez-San Pedro and Simonetti 2015). Nevertheless, the final model comparison supported the resource model as the top-ranked model, with greater support than the landscape one, indicating that prey availability is more associated with its activity than habitat availability.

Our results highlight a potential value of insectivorous bats as bioindicators of ecological conditions in the city of La Paz, as their richness was associated with resource availability and landscape context. In a semi-arid ecosystem such as the La Paz valley, the conservation of natural remnants may play an important role in sustaining bat biodiversity and its associated ecosystem services. Therefore, urban

planning in La Paz should consider a shift beyond the creation of green areas to include ecological functionality and connectivity. To maintain bat diversity within the city, protecting native remnants and restricting urban expansion onto unstable soils where wildlife resides represent key activities that should be integrated into the municipal agenda.

Although active monitoring remains an efficient tool for acoustic bat studies (Russo et al. 2025), and we followed the standard protocol for bat monitoring in the first hours after sunset, when there is a greater probability of species detection, we acknowledge the importance of passive acoustic monitoring to ensure a better comprehension of urban bat activity and composition. Nevertheless, rarefaction analysis indicated that the sampling effort was sufficient to characterize the most frequently acoustically detectable species included in our analysis. Other species are less detectable acoustically (Corcoran and Weller 2018), and others could be less frequent or have a difference in activity spans. Future research and long-term monitoring should consider 12-hour acoustic surveys to try to detect the rest of the species and understand activity patterns and temporal use of urban spaces.

Some typical urban variables likely affecting bat activity were not evaluated, such as local noise, habitat heterogeneity, and socioeconomic variables that may vary across urban contexts (Li et al. 2019). Nonetheless, the variables assessed capture several dimensions relevant to bat activity within the context of La Paz city. Finally, while water availability is important for bats in urban environments (Russo and Ancillotto 2015; Lehrer et al. 2021) and was initially considered in this study, only three sampling sites presented water bodies. Consequently, the statistical power to assess its influence on the bat assemblage would be insufficient, and this variable was excluded from the analyses.

CONCLUSIONS

Our results partially supported our initial expectations regarding the effects of urbanization on the insectivorous bat assemblage in La Paz. As predicted, responses varied across spatial scales, with broader-scale habitat availability (500 and 1,000 m buffer) more important for assemblage and species responses. However, contrary to what we expected, local vegetation greenness and ALAN received little support at the assemblage level. Prey availability was the strongest predictor for both richness and total bat activity, and landscape structure received secondary support. These results may indicate that, in this high-altitude semi-arid context, resource availability may be a stronger constraint for insectivorous bat assemblages than other environmental urban characteristics.

As we expected, species-specific responses differed among species. *Myotis oxyotus* activity was best supported by the local model that included vegetation greenness and ALAN, but resource availability and spatial baseline were also competitive. *Tadarida brasiliensis* response was best explained by spatial structure and received no support for the environmental variables assessed, which may be consistent with its urban tolerance, and its activity may be influenced by roost distribution. On the other hand, *Histiotus montanus* responded best to insect availability. Although we could not clearly identify which species were more sensitive to urbanization, the results indicate that bat responses in La Paz are shaped

by species-specific combinations and an influence of resource availability and landscape at the assemblage level.

Declarations

COMPETING INTERESTS

The authors do not have any financial or non-financial conflicts of interest to report.

ETHICS STATEMENT

Not applicable, as no animal was captured or collected.

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Author Contribution

S.T.P. contributed to the conceptualization, experimental design, fieldwork, data analysis, and manuscript redaction. L.F.A. and I.M. contributed to conceptualization, supervision of results, and revision of the manuscript. L.F.P. contributed to conceptualization, assessment of interpretation of results, and substantial revision of initial drafts and later versions of the manuscript. All authors have reviewed and approved the final version of the manuscript.

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Data Availability

Database, R script, and supplementary material are available in Zenodo at the following link: 10.5281/zenodo.22982579

References

1. Aguirre LF (1998) Breve nota sobre Nyctinomops macrotis (Chiroptera: Molossidae) para La Paz. 91–92
2. Allen LC, Turmelle AS, Mendonça MT et al (2009) Roosting ecology and variation in adaptive and innate immune system function in the Brazilian free-tailed bat (Tadarida brasiliensis). J Comp Physiol B 179:315–323. https://doi.org/10.1007/s00360-008-0315-3
3. Avila-Flores R, Fenton MB (2005) Use of spatial features by foraging insectivorous bats in a large urban landscape. J Mammal 86:1193–1204. https://doi.org/10.1644/04-MAMM-A-085R1.1
4. Barré K, Vernet A, Azam C et al (2022) Landscape composition drives the impacts of artificial light at night on insectivorous bats. Environ Pollut 292:118394. https://doi.org/10.1016/j.envpol.2021.118394
5. Beck SG, García E, Thompson Baldivieso LN et al (2015) Paisajes, eco-regiones y vegetación. In: Moya MI, Meneses RI, Sarmiento J (eds) Historia Natural de un valle en Los Andes: La Paz, 2nd edn. Museo Nacional de Historia Natural, La Paz, pp 113–158
6. Burnham KP, Anderson DR (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociol Methods Res 33:261–304. https://doi.org/10.1177/0049124104268644
7. Callas M, Lumsden LF, Rendall AR, Yokochi K (2024) More trees and fewer roads: the importance of local and landscape features for insectivorous bats in open urban green spaces. Wildl Res 51:WR23079. https://doi.org/10.1071/WR23079
8. Carlsson M Exploring the potential of Green Infrastructure to enhance urban resilience as part of the 2040 Development Plan La Paz, Bolivia., Tesis (2021) KTH ROYAL INSTITUTE OF TECHNOLOGY SCHOOL OF ARCHITECTURE AND THE BUILT ENVIRONMENT
9. Carvalho WD, Martins MA, Dias D, Esbérard CEL (2013) Extension of geographic range, notes on taxonomy and roosting of *Histiotus montanus* (Chiroptera: Vespertilionidae) in southeastern Brazil. mamm 77:341–346. https://doi.org/10.1515/mammalia-2012-0012
10. Chakravarty R, Mohan R, Voigt CC et al (2021) Functional diversity of Himalayan bat communities declines at high elevation without the loss of phylogenetic diversity. Sci Rep 11:22556. https://doi.org/10.1038/s41598-021-01939-3
11. Cook RD (1977) Detection of Influential Observation in Linear Regression. Technometrics 19:15–18. https://doi.org/10.1080/00401706.1977.10489493
12. Corcoran AJ, Weller TJ (2018) Inconspicuous echolocation in hoary bats (*Lasiurus cinereus*). Proc R Soc B Biol Sci 285:20180441. https://doi.org/10.1098/rspb.2018.0441
13. Diamant ES, Oswald KN, Awoyemi AG et al (2025) The importance of biome in shaping urban biodiversity. Trends Ecol Evol 40:601–612. https://doi.org/10.1016/j.tree.2025.03.014
14. Dwyer JM, Moore MS, Lewis JS (2024) Trade-offs in habitat use and occupancy of bats across the gradient of urbanization and seasons. Ecosphere 15:e4884. https://doi.org/10.1002/ecs2.4884

15. Fabianek F, Gagnon D, Delorme M (2011) Bat distribution and activity in Montréal Island green spaces: Responses to multi-scale habitat effects in a densely urbanized area. Écoscience 18:9–17. https://doi.org/10.2980/18-1-3373
16. Filloy J, Zurita GA, Bellocq MI (2019) Bird Diversity in Urban Ecosystems: The Role of the Biome and Land Use Along Urbanization Gradients. Ecosystems 22:213–227. https://doi.org/10.1007/s10021-018-0264-y
17. Froidevaux JSP, Fialas PC, Jones G (2018) Catching insects while recording bats: impacts of light trapping on acoustic sampling. Remote Sens Ecol Conserv 4:240–247. https://doi.org/10.1002/rse2.71
18. Gallo T, Lehrer EW, Fidino M et al (2018) Need for multiscale planning for conservation of urban bats. Conserv Biol 32:638–647. https://doi.org/10.1111/cobi.13047
19. Hackett TD, Korine C, Holderied MW (2013) The Importance of Acacia Trees for Insectivorous Bats and Arthropods in the Arava Desert. PLoS ONE 8:e52999. https://doi.org/10.1371/journal.pone.0052999
20. Haddock JK, Threlfall CG, Law B, Hochuli DF (2019) Responses of insectivorous bats and nocturnal insects to local changes in street light technology. Austral Ecol 44:1052–1064. https://doi.org/10.1111/aec.12772
21. Hagen EM, Sabo JL (2014) Temporal variability in insectivorous bat activity along two desert streams with contrasting patterns of prey availability. J Arid Environ 102:104–112. https://doi.org/10.1016/j.jaridenv.2013.11.016
22. Jung K, Kalko EKV (2011) Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization. Divers Distrib 17:262–274. https://doi.org/10.1111/j.1472-4642.2010.00738.x
23. Jung K, Threlfall CG (2018) Trait-dependent tolerance of bats to urbanization: a global meta-analysis. Proc R Soc B Biol Sci 285:20181222. https://doi.org/10.1098/rspb.2018.1222
24. Kesavaraju B, Dickson S (2012) New Technique to Count Mosquito Adults: Using ImageJ Software to Estimate Number of Mosquito Adults in a Trap. J Am Mosq Control Assoc 28:330–333. https://doi.org/10.2987/12-6254R.1
25. Körner C (2007) The use of 'altitude' in ecological research. Trends Ecol Evol 22:569–574. https://doi.org/10.1016/j.tree.2007.09.006
26. Krauel JJ, LeBuhn G (2016) Patterns of Bat Distribution and Foraging Activity in a Highly Urbanized Temperate Environment. PLoS ONE 11:e0168927. https://doi.org/10.1371/journal.pone.0168927
27. Lacoeuilhe A, Machon N, Julien J-F et al (2014) The Influence of Low Intensities of Light Pollution on Bat Communities in a Semi-Natural Context. PLoS ONE 9:e103042. https://doi.org/10.1371/journal.pone.0103042
28. Lehrer EW, Gallo T, Fidino M et al (2021) Urban bat occupancy is highly influenced by noise and the location of water: Considerations for nature-based urban planning. Landsc Urban Plan 210:104063. https://doi.org/10.1016/j.landurbplan.2021.104063

29. Leveau LM, Vaccaro AS, Bellocq MI (2022) Urbanization and bird diversity: does the relationship change in deserts and subtropical forests? Urban Ecosyst 25:1891–1900. https://doi.org/10.1007/s11252-022-01269-w
30. Li H, Allen P, Boris S et al (2024) Artificial light at night (ALAN) pollution alters bat lunar chronobiology: insights from broad-scale long-term acoustic monitoring. Ecol Process 13:13. https://doi.org/10.1186/s13717-024-00491-y
31. Li H, Parker KA, Kalcounis-Rueppell MC (2019) The luxury effect beyond cities: bats respond to socioeconomic variation across landscapes. BMC Ecol 19:46. https://doi.org/10.1186/s12898-019-0262-8
32. Li H, Wilkins KT (2022) Predator-Prey Relationship between Urban Bats and Insects Impacted by Both Artificial Light at Night and Spatial Clutter. Biology 11:829. https://doi.org/10.3390/biology11060829
33. Li S, Zhou Z, Ma R et al (2023) Extracting subpixel vegetation NDVI time series for evaluating the mixed pixel effect on GPP estimation in urban areas. Int J Digit Earth 16:3222–3238. https://doi.org/10.1080/17538947.2023.2246945
34. Marsden GE, Vosloo D, Schoeman MC (2023) Urban tolerance is phylogenetically constrained and mediated by pre-adaptations in African bats. Ecol Evol 13:e9840. https://doi.org/10.1002/ece3.9840
35. McCracken GF, Lee Y-F, Gillam EH et al (2021) Bats Flying at High Altitudes. In: Lim BK, Fenton MB, Brigham RM et al (eds) 50 Years of Bat Research. Springer International Publishing, Cham, pp 189–205
36. Mena JL, Rivero J, Bonifaz E et al (2022) The effect of artificial light on bat richness and nocturnal soundscapes along an urbanization gradient in an arid landscape of central Peru. Urban Ecosyst 25:563–574. https://doi.org/10.1007/s11252-021-01163-x
37. Miguel-Méndez RS, MacSwiney GMC, Rosas-Guerrero V et al (2026) Food or urbanization? assessing the diversity of urban insectivorous bats in a Neotropical city. Urban Ecosyst 29:194. https://doi.org/10.1007/s11252-026-02044-x
38. Moran PAP (1950) Notes on continuous stochastic phenomena. Biometrika 37:17–23. https://doi.org/10.1093/biomet/37.1-2.17
39. Moya MI, Aliaga-Rossel E, Rico A et al (2015) Mamíferos del valle de La Paz. In: Moya MI, Meneses RI, Sarmiento J (eds) Historia Natural de un valle en Los Andes: La Paz, 2nd edn. Museo Nacional de Historia Natural, La Paz, pp 671–716
40. Peñaranda-del Carpio M, Quiroz-Calizaya JM, Pérez-Zubieta JC, Aguirre LF (2016) Actividad relativa e intensidad de forrajeo de murciélagos en espacios abiertos de la ciudad de Cochabamba, Bolivia. Red Lat. Car Cons Murc 7:8–13
41. Rega-Brodsky CC, Aronson MFJ, Piana MR et al (2022) Urban biodiversity: State of the science and future directions. Urban Ecosyst 25:1083–1096. https://doi.org/10.1007/s11252-022-01207-w
42. Rodríguez-Aguilar G, Orozco-Lugo CL, Vleut I, Vazquez L-B (2017) Influence of urbanization on the occurrence and activity of aerial insectivorous bats. Urban Ecosyst 20:477–488.

https://doi.org/10.1007/s11252-016-0608-3

43. Rodríguez-San Pedro A, Simonetti JA (2015) The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? Landsc Ecol 30:1561–1572. https://doi.org/10.1007/s10980-015-0213-5
44. Rosero-Taramuel JL, Mejía-Fontecha IY, Marín-Ramírez A et al (2023) Urban and peri-urban bats (Mammalia: Chiroptera) in Manizales, Colombia: exploring a conservation area in sub-Andean and Andean ecosystems. Mammalia 87:545–556. https://doi.org/10.1515/mammalia-2022-0138
45. Russo D, Ancillotto L (2015) Sensitivity of bats to urbanization: a review. Mamm Biol 80:205–212. https://doi.org/10.1016/j.mambio.2014.10.003
46. Russo D, Soprano F, Cistrone L et al (2025) Precision foraging: Bats in organic desert palm plantations hunt where it is most needed. Glob Ecol Conserv 58:e03467. https://doi.org/10.1016/j.gecco.2025.e03467
47. Salas-Salinas M, Quispe-Huacca FL, Curo-Mamani JL et al (2026) Bats in the Urban Desert: Acoustic Diversity and Community Composition Along an Urban–Rural Gradient in Tacna, Peru. Urban Sci 10:474. https://doi.org/10.3390/urbansci10080474
48. Saldaña-Vázquez RA, Carballo-Morales JD, Hernández-Montero JR et al (2025) Bats in Tropical Cities: the Ecology in, of and for Cities. In: Angeoletto F, Tryjanowski P, Fellowes MDE (eds) Ecology of Tropical Cities, vol II. Springer Nature Switzerland, Cham, pp 235–264
49. Saravia Jiménez ER (2018) Patrones de actividad de murciélagos insectívoros en cultivos de maíz de los Valles Secos de La Paz-Bolivia. Bachelor's Thesis, Universidad Mayor de San Andrés
50. Siles L, Peñaranda D, Pérez-Zubieta JC, Barboza K (2005) Los murciélagos de la ciudad de Cochabamba. 51–64
51. Suarez-Rubio M, Ille C, Bruckner A (2018) Insectivorous bats respond to vegetation complexity in urban green spaces. Ecol Evol 8:3240–3253. https://doi.org/10.1002/ece3.3897
52. Tena E, Fandos G, De Paz Ó et al (2020) Size does matter: Passive sampling in urban parks of a regional bat assemblage. Urban Ecosyst 23:227–234. https://doi.org/10.1007/s11252-019-00913-2
53. Threlfall CG, Law B, Banks PB (2012a) Influence of Landscape Structure and Human Modifications on Insect Biomass and Bat Foraging Activity in an Urban Landscape. PLoS ONE 7:e38800. https://doi.org/10.1371/journal.pone.0038800
54. Threlfall CG, Law B, Banks PB (2012b) Sensitivity of insectivorous bats to urbanization: Implications for suburban conservation planning. Biol Conserv 146:41–52. https://doi.org/10.1016/j.biocon.2011.11.026
55. Threlfall CG, Mata L, Mackie JA et al (2017) Increasing biodiversity in urban green spaces through simple vegetation interventions. J Appl Ecol 54:1874–1883. https://doi.org/10.1111/1365-2664.12876
56. Threlfall CG, Williams NSG, Hahs AK, Livesley SJ (2016) Approaches to urban vegetation management and the impacts on urban bird and bat assemblages. Landsc Urban Plan 153:28–39. https://doi.org/10.1016/j.landurbplan.2016.04.011

57. Ugarte-Núñez JA (2020) Clave de identificación por ecolocación de 20 especies de murciélagos del suroeste de Perú. Cienc Desarro 37–48. https://doi.org/10.33326/26176033.2020.27.996
58. Villarroya-Villalba L, Casanelles-Abella J, Moretti M et al (2021) Response of bats and nocturnal insects to urban green areas in Europe. Basic Appl Ecol 51:59–70. https://doi.org/10.1016/j.baae.2021.01.006
59. Villegas M, Garitano-Zavala Á (2010) Bird community responses to different urban conditions in La Paz, Bolivia. Urban Ecosyst 13:375–391. https://doi.org/10.1007/s11252-010-0126-7
60. Voigt CC, Dekker J, Fritze M et al (2021) The Impact Of Light Pollution On Bats Varies According To Foraging Guild And Habitat Context. Bioscience 71:1103–1109. https://doi.org/10.1093/biosci/biab087

Tables

Table 1. Effects of habitat availability at different spatial scales on bat species richness, total activity, and species-specific activity. Separate models were fitted using the total area of natural remnants within 200-, 500-, and 1,000-m donut buffers, alongside a model of local habitat within each sampling site. For each model, the corrected Akaike Information Criterion (AICc), the difference in AICc relative to the best-supported model (ΔAICc), and the Akaike weight (W) are reported. Bold values indicate the best-supported spatial scale for each response variable. *For total activity, the 1,000 m scale model was selected because it had comparable support to the 500 m model (ΔAICc = 0.40) and had better adequacy in the diagnostic checks. **For *Tadarida brasiliensis* response, the 500 m scale was retained because it had comparable support to the 1,000 m model (ΔAICc = 1.67) and better model adequacy. (See S1).

Response	Scale (m)	AICc	ΔAICc	W
Richness	Local scale	97.4	7.94	0.009
	200	92.5	3.06	0.104
	500	89.8	0.33	0.408
	1,000	**89.5**	**0.00**	**0.480**
Activity	Local scale	219.1	10.38	0.003
	200	214.8	6.12	0.025
	500	208.7	0.00	0.534
	1,000*	**209.1**	**0.40**	**0.438**
Tadarida brasiliensis	Local scale	154.8	12.55	0.001
	200	148.6	6.32	0.029
	500**	**143.9**	**1.67**	**0.294**
	1,000	142.3	0.00	0.676
Myotis oxyotus	Local scale	135.5	7.53	0.014
	200	130.3	2.42	0.179
	500	**127.9**	**0.00**	**0.601**
	1,000	130.1	2.15	0.205
Histiotus montanus	Local scale	132.9	6.00	0.035
	200	132.2	5.27	0.051
	500	129.4	2.45	0.207
	1,000	**126.9**	**0.00**	**0.707**

Table 2. Model comparison for detected bat species richness and total acoustic activity. Resource, landscape, local-scale, complete, and null models were compared using the Akaike Information Criterion corrected for small sample sizes (AICc). Resource models included insect availability; landscape models included distance to the nearest natural remnant and habitat availability at the selected spatial scale (1,000 m for both richness and activity); local-scale models included artificial light at night (ALAN) and vegetation cover (NDVI); complete models combined resource, landscape, and local predictors; and null models included only the intercept. For each model, the relation form (smooth or linear), the corrected Akaike Information Criterion (AICc), the difference in AICc relative to the best-supported model (ΔAICc), and the Akaike weight (W) are reported.

Richness	Relation form	AICc	ΔAICc	w
Resource	**Smooth**	**86.6**	**0.00**	**0.722**
Landscape	Linear	88.8	2.28	0.231
Complete model	Smooth	92.7	6.18	0.033
Local-scale variables	Linear	94.5	7.92	0.014
Null model	–	101.0	14.48	0.001
Bat activity	**Relation form**	**AICc**	**ΔAICc**	**W**
Resource	**Smooth**	**201.8**	**0.00**	**0.686**
Complete model	**Smooth**	**203.5**	**1.65**	**0.300**
Landscape	Linear	209.6	7.81	0.014
Local-scale variables	Linear	217.0	15.15	< 0.001
Null model	–	222.3	20.47	< 0.001

Table 3. Functional traits of the three bat species analyzed in this study. Variables commonly associated with urbanization tolerance are summarized according to previous literature (Siles et al. 2005; Jung and Threlfall 2018; Marsden et al. 2023)**.**

Species	Foraging space	Wing load	Call structure	Call duration	Roost selection specialization	Expected Urban tolerance
Tadarida brasiliensis	Open-space	High	Narrowband	Long	Low	High
Myotis oxyotus	Edge-space	N/A	Broadband	Short	High	Low
Histiotus montanus	Edge/clutter-space	Low	Broadband	Medium	Intermediate–high	Low

Table 4. Species-specific model selection for acoustic activity. Local, resource, landscape, complete, and null models were compared for *Myotis oxyotus, Tadarida brasiliensis,* and *Histiotus montanus* using the Akaike Information Criterion corrected for small sample sizes (AICc). For each model, the corrected Akaike Information Criterion (AICc), the difference in AICc relative to the best-supported model (ΔAICc), and the Akaike weight (W) are reported. For species in which residual spatial autocorrelation was detected using Moran's I, we refitted the presented models including a smooth of UTM coordinates as a proxy of spatial structure. Habitat availability was evaluated at the spatial scale selected for each species: 500 m for *M. oxyotus* and *T. brasiliensis*, and 1,000 m for *H. montanus* (see Table 1).

Species	Model	AICc	ΔAICc	Weight
Myotis oxyotus	**Local+space**	**121.9**	**0.00**	**0.439**
	Resource+space	122.9	1.01	0.265
	Spatial baseline	123.1	1.24	0.236
	Landscape+space	126.1	4.18	0.054
	Complete+space	130.8	8.90	0.005
Tadarida brasiliensis	**Spatial baseline**	**116.5**	**0.00**	**0.828**
	Resource+space	120.4	3.83	0.122
	Local +space	123.5	6.97	0.025
	Landscape+space	123.6	7.06	0.024
	Complete+space	134.5	17.95	< 0.001
Histiotus montanus	**Resource**	**125.3**	**0.00**	**0.763**
	Landscape	128.9	3.60	0.126
	Null	130.9	5.60	0.046
	Local	131.6	6.30	0.033
	Complete	131.7	6.37	0.032

Figures

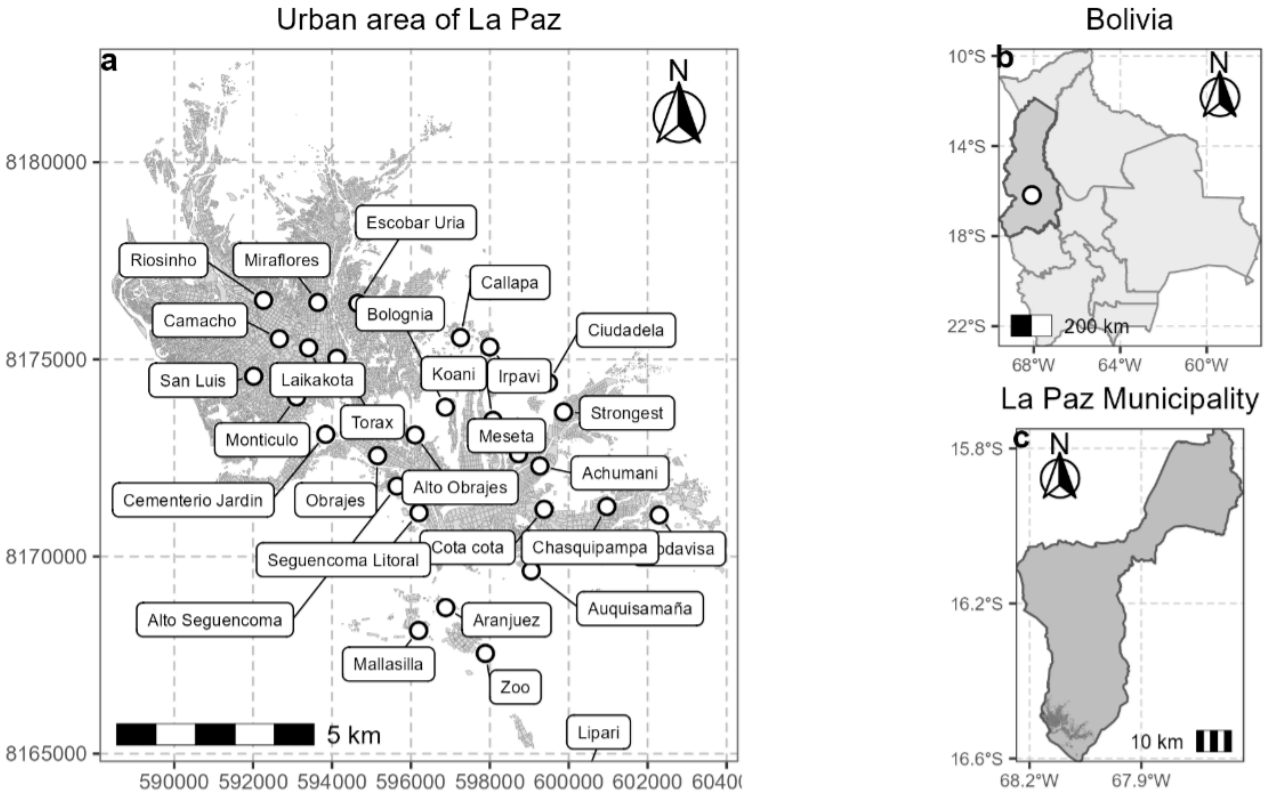


Figure 1

Study area. a) Map of the La Paz urban area showing the 29 sampling sites. b) Location of La Paz within Bolivia. c) Urban area in La Paz Municipality.

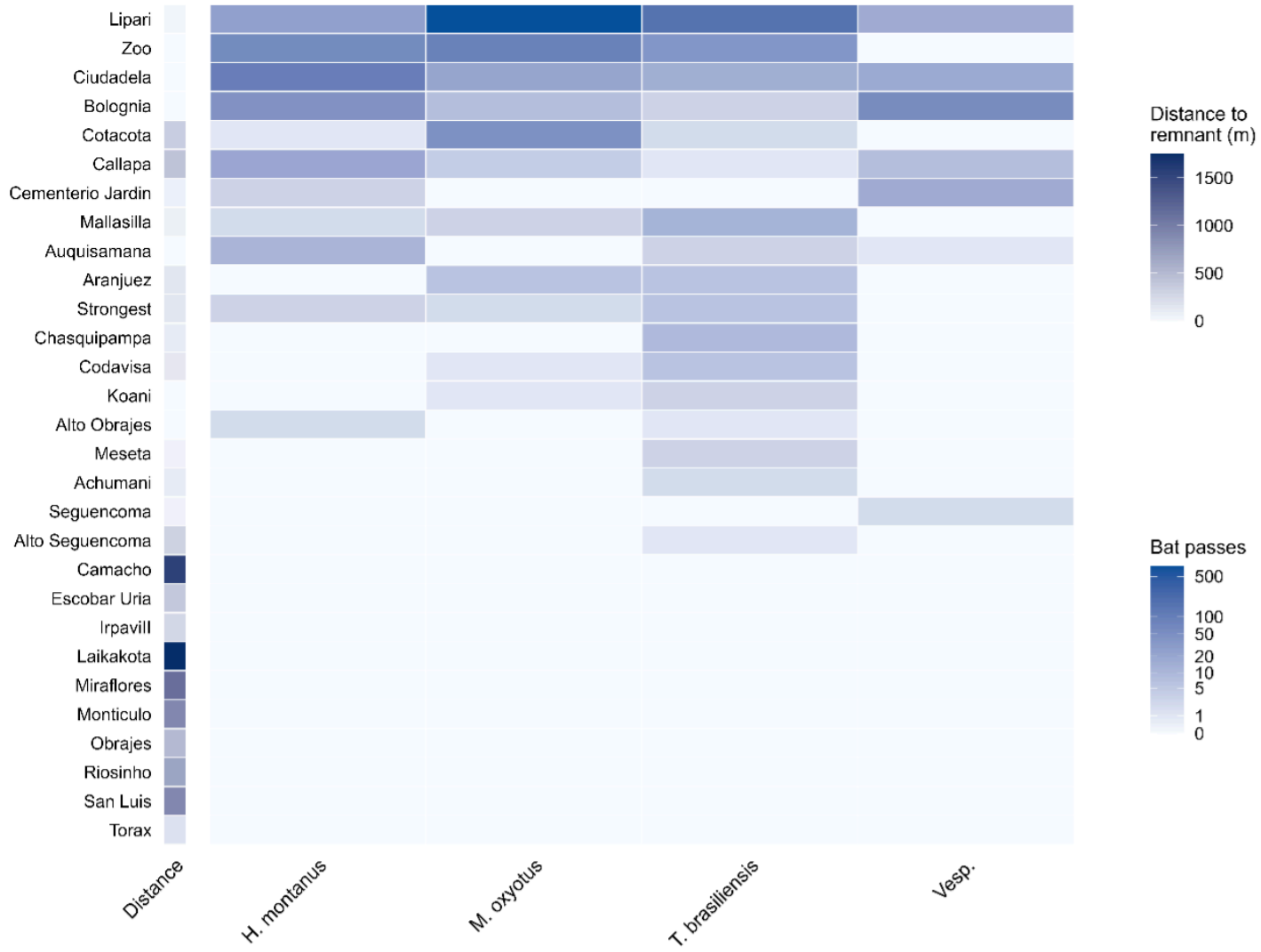


Figure 2

Heatmap of bat activity across sampling sites in the city of La Paz. Bat activity values were log (x + 1) transformed for visual clarity, while legend labels display original untransformed bat pass counts. Sites are ordered from highest to lowest total bat activity. The left annotation bar indicates the distance (in m) to the nearest natural remnant. Darker blue shades represent higher bat activity or greater distance to natural remnants.

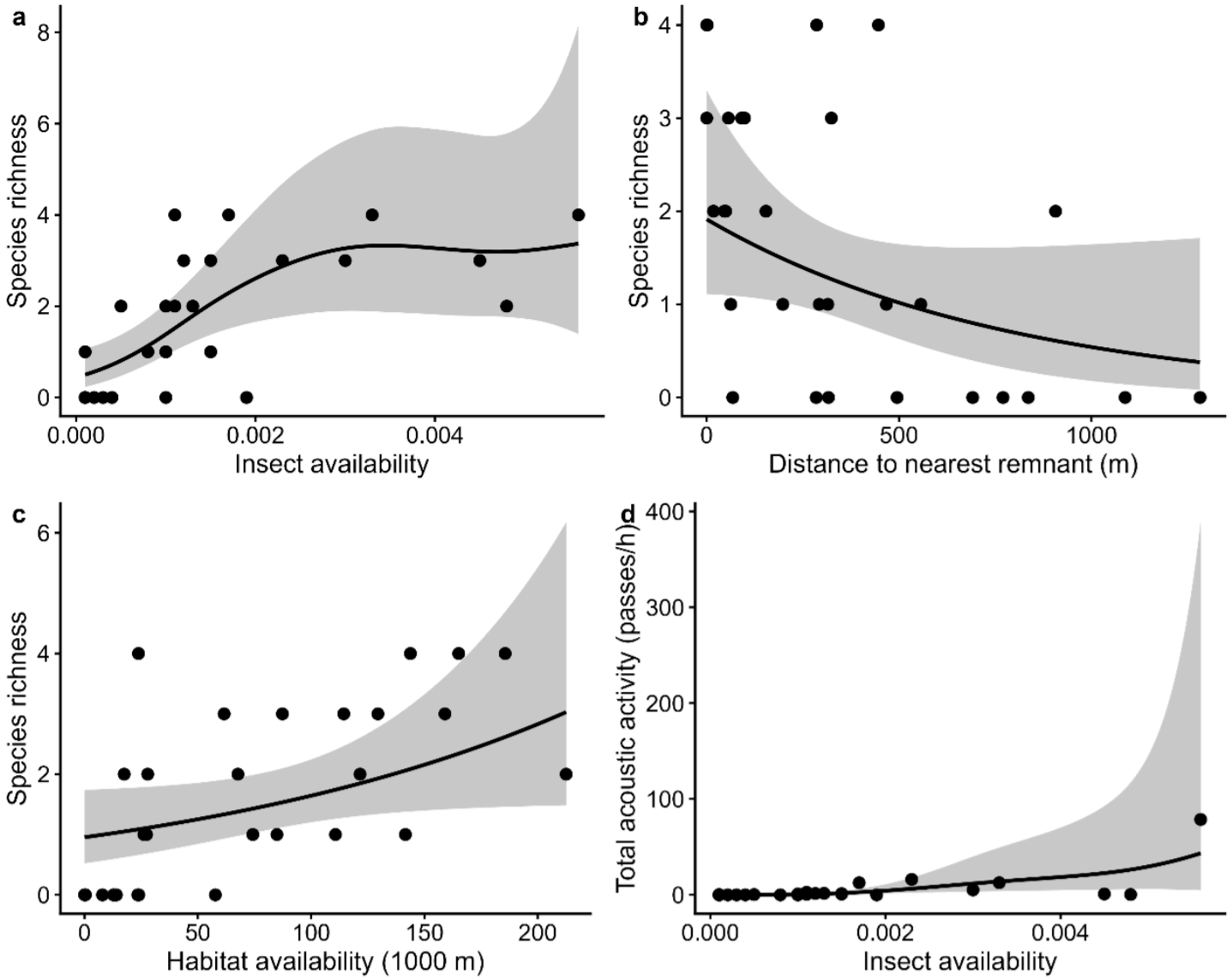


Figure 3

Relationships between environmental predictors and bat assemblage responses. (a) Species richness in relation to insect availability, based on the top-ranked resource model. (b) Species richness in relation to distance to the nearest natural remnant and (c) habitat availability within 1,000 m, based on the landscape model, which received secondary support (ΔAICc = 2.28). (d) Total acoustic activity in relation to insect availability, based on the top-ranked resource model. Solid lines represent model predictions, shaded areas indicate 95% confidence intervals, and points represent observed values. For models containing multiple predictors, predictions were generated while holding the other predictor at its median value.

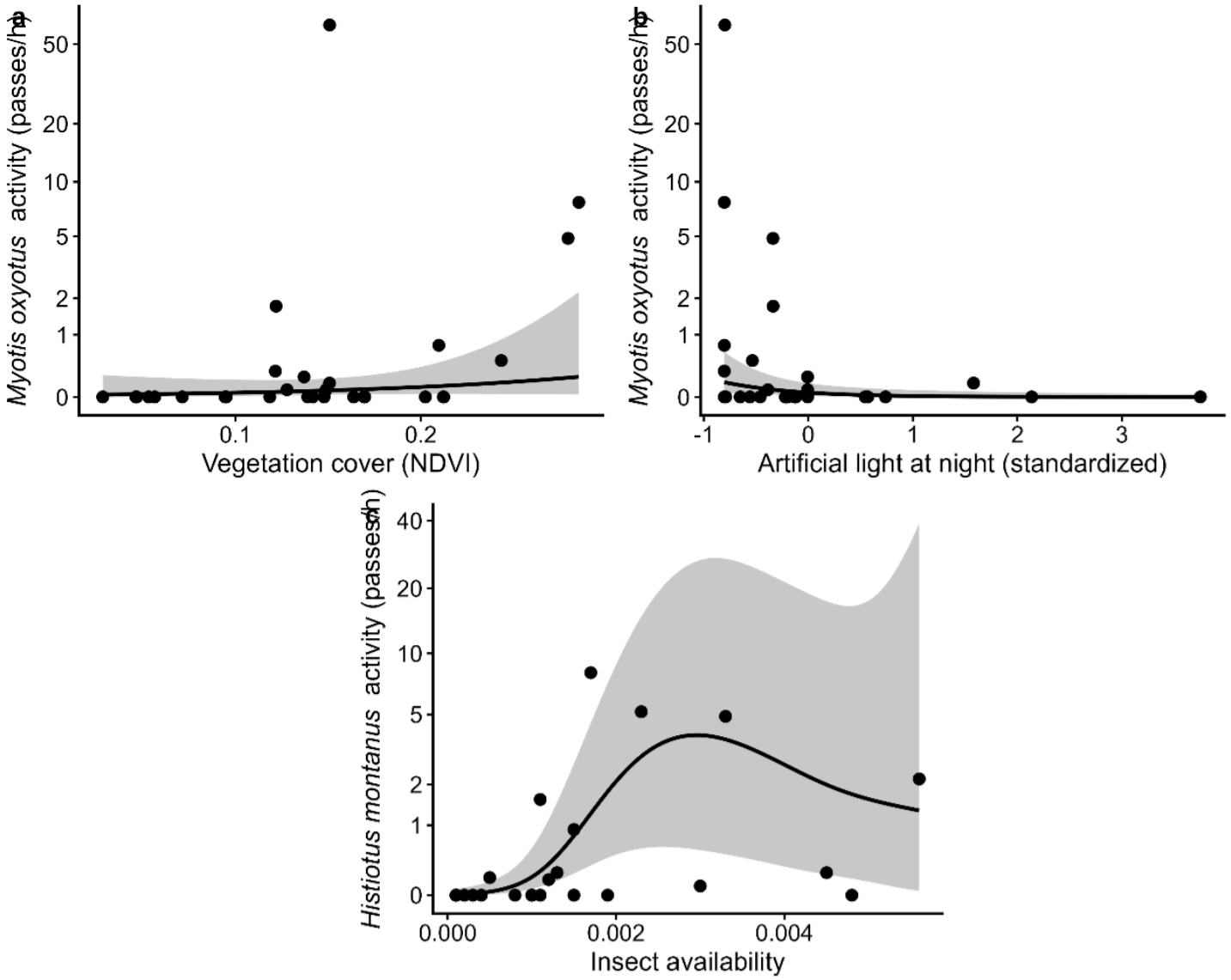


Figure 4

Species-specific relationships between environmental predictors and acoustic activity. (a) *Myotis oxyotus* activity in relation to vegetation cover (NDVI) and (b) artificial light at night (ALAN), based on the top-ranked local model including spatial structure. Displayed predictions represent the environmental component of the model after accounting for the spatial smooth. (c) *Histiotus montanus* activity in relation to insect availability, based on the top-ranked resource model. Solid lines represent model predictions, shaded areas indicate 95% confidence intervals, and points represent observed values. Acoustic activity is shown on a log (x + 1)-transformed scale for visualization, with axis labels expressed as untransformed bat passes per hour of sampling

Supplementary Files

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