

Biotic homogenization or riparian refugia? Urban and wild land snail assemblages along a subtropical precipitation gradient

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Abstract

A noted impact of urbanization is the tendency for biotic homogenization, or the increase of similarity of geographically disparate communities. On the other hand, some urban habitats harbor biodiversity native to their region, a role potentially important in xeric landscapes, with irrigation increasing the coverage and availability of mesic habitats in an otherwise water-limited landscape. We assessed the relative importance of urban yards as agents of biotic homogenization or riparian refugia by characterizing community composition of Tamaulipan thornforest land snail assemblages across a pronounced precipitation gradient in far south Texas, USA. We quantified α - and β -diversity and assessed whether the land snail fauna of urban yards are more similar to each other across a precipitation gradient than they are to their wild counterparts, as well as determined the significance of moisture in driving Tamaulipan thornforest β -diversity, both in terms of turnover (changing species composition) and nestedness (species loss). Sites with both the wild and wet conditions had the highest values of species richness and abundance. Urban land snail communities were significantly homogenized, outweighing the influence of the precipitation gradient. We did not find urban yards served as a refuge for native, moisture-dependent, riparian snails. Our analyses find that turnover, not nestedness, is the largest contributor to β -diversity in these assemblages. Studies of urbanization should address regional spatial scales to quantify how urbanization modifies regional biodiversity arising from background environmental gradients. Such an approach could lead to improved understanding of how large metroplex areas could be used to maintain and even promote biodiversity.

Key words: terrestrial snails, β -diversity, urban refuge, residential yards

Introduction

Biotic homogenization occurs when the similarity of geographically disparate communities is increased through human activity, often by the replacement of native (e.g. Baeten et al. 2012) with non-native human adapted/tolerant species (McKinney

and Lockwood 1999). Consequently, a stereotypical group of exotic species have become widely established across urban areas of the globe (McKinney and Lockwood 1999). Even though a significant proportion of urban biodiversity represents these weedy species, the fauna can also contain a surprising number of widespread native edge and even some locally endemic

species (McKinney and Lockwood 1999; McKinney 2006; Bergéy and Figueroa 2016). The importance of urbanized habitats, specifically, urban yards in harboring native biodiversity could become even more pronounced in xeric landscapes, with irrigation by landowners increasing the coverage and availability of mesic habitats in an otherwise highly water-limited landscape (Bergéy and Whipkey 2020). To test this hypothesis, we compare urban yard and wild Tamaulipan thornforest land snail assemblages across a pronounced precipitation gradient in far south Texas, USA.

An ideal context in which to explore biotic homogenization is along environmental gradients. Ecologists have long explored the consequences of environmental gradients for promoting and maintaining species diversity at local and regional scales, which manifests as increasing degrees of dissimilarity, or β -diversity, with increasing distance along or steepness of the gradient (Whittaker 1960; Jost 2007; Tuomisto 2010; Carvalho, Cardoso, and Gomes 2012; Legendre 2014; Baselga and Leprieur 2015; Bergéy and Whipkey 2020). Comparably fewer studies, however, have quantified the effects of human activity and subsequent biotic homogenization on background β -diversity.

Prior work on snail β -diversity was conducted across climatic gradients, i.e. temperature (Lososová et al. 2011; Horsák et al. 2013, 2016) or precipitation (Hoffmann et al. 2011; Hettenbergerová et al. 2013) or urbanization gradients (Horsák et al. 2009; Lososová et al. 2011; Hodges and McKinney 2018). One study examined both precipitation and urbanization jointly across cities selected to cover a broad precipitation regime (Lososová et al. 2011); however, none of these studies extends the urbanization gradient to include wild/relatively unmodified habitats. The study by Horsák et al. (2016) incorporates the influence of a regional fauna on urban fauna by inclusion of literature records of the regional species pool, omitting minute snails. However, to our knowledge, joint analyses of precipitation and urbanization, including examination of the regional context by sampling native communities, have not been explored across the same climatic gradient.

Although considerable effort has been expended on investigating highly modified urban habitats such as vacant lots, gardens and vegetated verges surrounding pavement (McDonnell 2011), less modified residential yards—even though representing a large proportion of the urban landscape (Loram et al. 2007)—remain relatively understudied because they are thought to be biologically depauperate and hard to access (Dyson et al. 2019). The limited research which has been conducted on these sites, however, suggests that they can serve as an important refuge for native fauna (Everette et al. 2001; Adams 2005; Merola-Zwartjes and DeLong 2005; Rutz 2008), especially riparian species (Rosenberg, Terrill, and Rosenberg 1987). This is likely the result not only of an increase in resource levels through irrigation and fertilization (Bergéy and Figueroa 2016) but also the establishment of more diverse vegetation cover via ornamental plants (Falk 1976; Cavender-Bares et al. 2020).

We begin by testing whether urbanization generates significant β -diversity. We characterize the impact of urbanization on α - β -diversity and community composition to address whether urban yards are more similar to each other across a precipitation gradient than they are to their wild counterparts (biotic homogenization hypothesis). If urban yard snail assemblages are homogenized, then urban communities, regardless of precipitation regime, should look more like each other than their respective wild communities. We also address whether urban yards in an arid environment act as refugia for moisture-demanding species (riparian refugia hypothesis). If urban yards act as

refugia for moist-affiliated species, then urban communities in the dry region should look more like wild communities in the wet region than they do wild communities within their same (dry) region. Finally, we ask how significant moisture is in driving Tamaulipan thornforest β -diversity, both in terms of turnover and nestedness (in the framework of Baselga 2010; Baselga and Orme 2012; Baselga and Leprieur 2015). The presence of diverse, relictual riparian habitats (uncleared palm forest) in the wet region drove our expectation that land snails are most diverse and abundant in the wet, riparian habitats and less so in the dry habitats. These observations led us to predict that nestedness is the major component of β -diversity in the region.

Methods

Taxonomic system

Our model group for this study is land snails (excluding slugs), because:

(1) They are taxonomically diverse and well described, especially for invertebrates. Terrestrial gastropods are believed to represent 35 000 global species and are the second most diverse molluscan group (Barker 2001). At the same time, their taxonomy is relatively mature with the description of new species having slowed in North America to <1% of the total fauna per decade (Nekola 2014b). Both continental (e.g. Pilsbry 1948) and regional (e.g. Cheatum, Fullington, and Pratt 1974) identification resources extend back over 70 years and arguably represent the earliest whole-fauna treatments produced for any non-lepidopteran invertebrate group in North America.

(2) Obtaining large samples is relatively simple due to high population densities, sometimes exceeding 5000 individuals/m² (Coles and Nekola 2007); in combination with the accumulation of shells for up to a decade following death (Pearce 2008). This greatly increases the encounter rate for rare and uncommon species (Rundell and Cowie 2004; Pearce 2008; Coppolino 2010). Additionally, accurate species level identification is usually possible via use of shell features alone (Nekola, Coles, and Horsák 2015; Nekola et al. 2018).

(3) The potential for significant changes in community structure is possible given that assemblages vary greatly across environmental gradients (Nekola 2014a; Barbato et al. 2017), with almost complete turnover being noted from xeric uplands to subaerial wetlands (Nekola 2002), and from base-rich to base-poor habitats (Nekola 2010). As a result land snail assemblage data are commonly used as environmental indicators in anthropology, archaeology, and paleoclimatic reconstructions (Fortunato 2015).

(4) Although land snails are poor active dispersers (Örstan, Sparks, and Pearce 2011), they are among the most adept passive dispersers, being able to move across 7000 km barriers typically via vertebrate vectors (Gittenberger et al. 2006). As a result, relatively low levels of dispersal limitation can be expected within a local region, making it more likely that observed pattern is related to ecological process and not historical contingency. The excellent passive dispersal abilities of land snails have also helped them rapidly spread through the global anthropogenic landscape (Robinson 1999), with their typical entry into urban yards (Hodges and McKinney 2018; Bergéy 2019) by the horticultural trade (Cowie et al. 2008; Bergéy and Figueroa 2016).

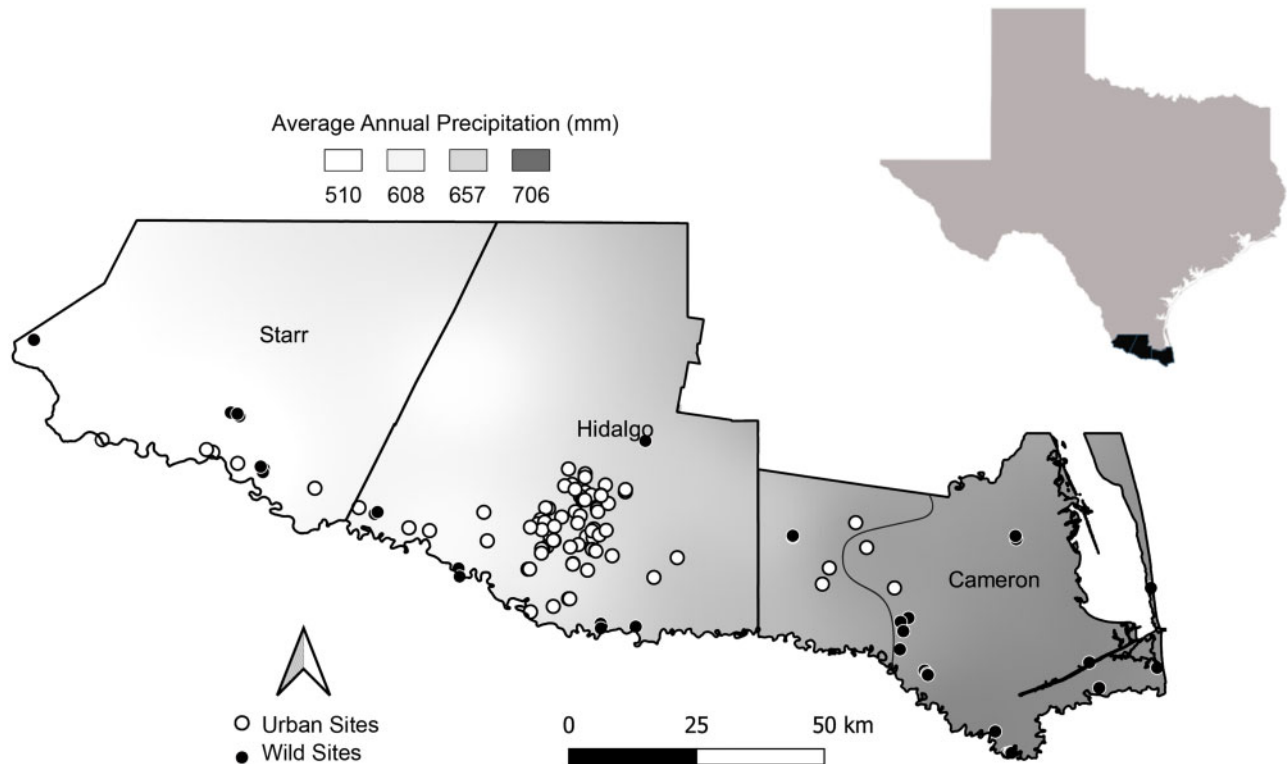


Figure 1: Map of wild ($n=49$) and urban ($n=81$) sites examined in the LRGV. The filled circles are wild sites and empty circles are urban sites. Urban sites excluded due to under or over sampling are not figured. The counties of the LRGV are labeled. Average annual precipitation illustrates the regional precipitation gradient with a wet-dry demarcation line in western Cameron county indicating exactly where the sites are categorized (wet or dry). Inset map of TX, USA shows the region of the study.

Regional ecology and urban context

The study was conducted within the floodplain of the Lower Rio Grande Valley (LRGV; Fig. 1) of Texas representing approximately 250 km of riparian habitat along the international border (Leslie 2016). This region is rapidly urbanizing (Huang and Fipps 2006). Small, protected areas, part of the National Wildlife Refuge system, have been established to preserve the last remnants of endangered Tamaulipan thornforest (Leslie 2016), a xeric, subtropical, vegetative community (>1200 plant species; Saghatelyan 2017). This assemblage is characterized by drought-tolerant and spiny plants (e.g. prickly-pear cactus—*Opuntia engelmannii* var. *lindheimeri* and honey mesquite—*Prosopis glandulosa*; Lonard and Judd 2002). Tropical trees (e.g. Sabal Palm—*Sabal mexicana* and Montezuma Cypress—*Taxodium mucronatum*) are concentrated in the wetter (715 mm per year annual precipitation) portion of the valley with semitropical xeric scrub (e.g. Guajillo Acacia—*Senegalia berlandieri* and Blackbrush Acacia—*Vachellia rigidula*) dominating in the drier (549 mm per year) region (Leslie 2016). Although prior land snail community composition and/or urbanization effects studies have been conducted in temperate forest or grassland environments, subtropical thornforest habitats have been rarely examined.

Sample sites

Our samples were taken in either urban yards or non-urban “wild” habitats. Urban sites were private, residential yards sampled by students as part of an undergraduate, course-based, participatory research experience. Students obtained permission to sample private yards, an often challenging endeavor

(Dyson et al. 2019), expanding urban sampling reach. However, this also introduced a geographic bias as more of the students lived in the central part of the study region (addressed later). After initial training and collection standardization experiences, students each sampled 5 private yards that they received permission to access. This allowed targeted surveying of yards across the urban region ($n=81$; Fig. 1). There is evidence that private front yards are different than backyards so sampling in this study took place across the entire parcel combining both front and backyard samples (Locke et al. 2018).

Sampling sites in non-urban, less human-impacted habitats, which we call ‘wild’ in this article, was chosen based on literature review of the Rio Grande Valley and by the expertise of two local botanists, Dr. Andrew McDonald and Raziel Flores with the aid of US Fish and Wildlife Service personnel. Our aim was to sample all remaining patches of primary thornforest (never cleared, minimally human impacted) and to sample each subtype of thornforest twice each across the region. The subtypes of thornforest and projected locations were determined from the Texas Ecosystem Analytical Mapper (<http://tpwd.texas.gov/gis/team/>; TPWD [Texas Parks and Wildlife Department] 2019) followed by adjustment of habitat choice on-site. We prioritized $n=49$ sites on public land (or where we could obtain landowner permission) that have never been cleared; however, it must be recognized that all Tamaulipan Thornforest is human impacted to some degree.

Annual precipitation data for each site was retrieved from WorldClim (Hijmans et al. 2005). Average annual precipitation across the region was found to be bimodal, therefore we categorized sites as wet (653–706 mm) or dry (510–614 mm; illustrated in Fig. 1).

Sampling strategy

A targeted sampling strategy was used for both wild and urban habitats. Targeted sampling methods included collecting shells of large-bodied snails by hand, retention of leaf litter and the organic layer of the soil, and brushing/shaking moss and bushes over sieves.

Utilized land snail microhabitat is profoundly different between wild and urban habitats therefore sampling targets varied. In wild habitats, snails were most often found in decomposed leaf litter accumulations and coarse woody debris while in urban sites they preferred undecomposed leaf litter and graminoid thatch, hard substrates (building foundations, bricks, cement blocks and other building materials), as well as coarse woody debris. We thus adopted the approach advocated by Cameron and Pokryszko (2005) in which we standardized sampling to roughly equivalent areas and search times, but use a variety of sampling strategies to optimally sample the most important microsites within a given site. We freely admit that by using different approaches to encounter the maximum number of individuals per site that urban and wild samples were collected in different ways. However, if sampling had been strictly standardized, fewer individuals would have been encountered (especially in urban sites), leading to data with low statistical power and lacking the ability to robustly test the observed pattern.

To debulk samples, soil and leaf litter was passed through a 2.0 mm mesh sieve followed by a 0.65 mm mesh sieve. The remaining leaf litter was dried in the laboratory at room temperature for 1–3 days, depending on the initial moisture level of the sample. Leaf litter samples were then sieved again to remove additional soil. Shells and shell fragments were picked from the leaf litter and soil under a dissecting microscope. Shells were identified to species (or the lowest taxonomic level possible based on shell morphology) by a team of snail taxonomic experts: Jeffrey C. Nekola, Kathryn E. Perez and Benjamin T. Hutchins. Slugs were excluded due to difficulty with preservation and identification. We also ignored members of the snail family Succineidae because they cannot be identified to species by shell. Both live and dry/dead shells were counted. Including dead shells increases the likelihood of encountering rare or seasonal taxa or those with a very fast decay rate, especially in the wet region where shell decay of small shells occurs at a higher rate (Říhová et al. 2018). If differential shell decay drives the patterns observed, we would expect to find lower shell abundances and richness in the wet region, particularly in minute and small snails.

Statistical analyses

Despite efforts to standardize urban sampling, some student collected samples did not meet expectations. Therefore, we used a standard scaling factor in JMP (JMP, Version 11 1989–2019) to screen sampling sites and exclude those grossly over or undersampled, with bias values ranging from 0.11 to 2.00. With the wild samples, we were concerned that a single site at the wet extreme of the region, the Sabal Palm Sanctuary which contained the only primary palm-dominated riparian forest in the region, would overly influence test results. We assessed this issue by conducting all subsequent analyses both with and without the Sabal Palm Sanctuary samples to determine if results were driven by this site.

Kolmogorov–Smirnov tests for normality were conducted in SPSS (IBM SPSS 2017). Due to a significant departure from normality in the data, we performed a Kruskal–Wallis test in SPSS

(IBM SPSS 2017) to examine species richness and abundance by habitat type (i.e. wild-dry, wild-wet, urban-dry and urban-wet). Dunn's tests were conducted where necessary as non-parametric post hoc tests with a Bonferroni-adjusted significance level. We first conducted these tests on the unaltered dataset, which revealed significant differences among habitats for both abundance and richness. However, because of the imbalanced sampling across habitats, we used a resampling approach ($n=1000$) in which sample size was standardized at $n=5$ sites in each of the four habitats, and we conducted the Kruskal–Wallis (followed by Dunn test, when appropriate) within each iteration. We reasoned that if a majority of Kruskal–Wallis tests from the 1000 samples were significant at the $\alpha = 0.05$ level, then the conclusions based on the original dataset would be warranted. The converse would suggest that some degree of caution should be used in drawing conclusions depending on the similarity of resampled and original distributions.

All analyses of β -diversity were carried out in R v. 3.6.0 (R Core Team 2019) using modifications to functions included in the 'betapart' package v 1.5.1 (Baselga et al. 2018) and a Jaccard index. The betapart package was developed to partition total dissimilarity across sites (beta diversity) into two additive terms: species replacements from one site to the next (species turnover) and species loss from one site to the next (nestedness; Baselga and Orme 2012). These three estimates (total, nestedness and turnover) can be made between a single pair of sites or for a collection of sites. In our case, the question of whether nestedness or turnover dominate transitions from urban to wild habitats or from wet to dry regions dictated that we use a hybrid approach. We modified the functions beta.multi and beta.sample (Baselga et al. 2018) to restrict pairwise site comparisons to two sites of contrasting type (wet vs. dry, or urban vs. wild). This effectively excluded any dissimilarity within a given habitat or region from the multiple-site measures, allowing us to make inferences regarding the two ecological processes strictly with respect to our habitat or climate transitions of interest. As with analyses of abundance and richness, we controlled for large differences in the number of sites in each habitat + climate combination by resampling a prespecified number of sites ($n=5$, equal to number of sites in the urban habitat in the wet region) 1000 times, and estimating means and standard deviations from the sample. As a methodological check, we first verified that the dissimilarity within urban and wild communities was significantly less than the dissimilarity across these two types of habitats, which should be the case if our urban-wild distinction is valid.

Non-metric multi-dimensional scaling (NMDS) analysis was conducted in PRIMER 6 (Clarke and Gorley 2006) on the presence-absence dataset, excluding sites with less than four species. A resemblance matrix was calculated using Jaccard similarity, followed by NMDS using 1000 restarts, minimum stress of 0.01 and Kruskal stress of 1. Analysis of Similarity (ANOSIM in Primer 6) on the same (presence-absence) resemblance matrix was used to assess differences among wet vs. dry and urban vs. wild factors using a two-factor with replicates layout and 999 permutations. Additionally, we tested for the existence of a significant difference between one or more groups following a permutational multivariate analysis of variance (PERMANOVA) using distance matrices approach (on abundance data), using the adonis function (Anderson 2001) in the R vegan package (Oksanen et al. 2019). We assess the significance of two factors: disturbance type (urban vs. wild) and moisture regime (wet vs. dry).

Results

From an initial dataset of 120 student collected urban sites, 81 (76 in the dry region and 5 in the wet region) were retained as they possessed similar sampling effort per site to wild sampling (not over or undersampled at each site). We sampled 49 wild sites, 21 in the dry region and 28 in the wet. Comparison of richness \times total encountered shells (live and dead) across all sites (Supplementary Fig. S1) shows that site richness asymptotes at around 75 shells in urban and 100 shells in wild sites, with the number of species at a given number of shells being least in urban and greatest in wild sites. Statistical results were not impacted by inclusion of sites from the singular Sabal Palm Sanctuary; therefore, all reported statistics and figures include this site.

Table 1 lists the species present and number of sites in which each taxon was observed across habitat types. We encountered 35 871 individuals of 32 land snail species. The highest species richness occurred in wild-wet habitats (mean \pm SD: 9.71 ± 2.41), lower in urban-wet (6.60 ± 2.14) and least in urban-dry (4.83 ± 2.03) and wild-dry (4.81 ± 3.79). Abundances were highest in wild-wet habitats (835.54 ± 753.85), were lower in wild-dry (245 ± 358.09) and least in urban-dry (92.34 ± 81.99) and urban-wet (62.60 ± 31.43). Higher shell abundances in wet habitats and minute snails only found in those habitats indicate that inclusion of both live and dead shells are not driving our

results. Abundance and species richness were found to not be normally distributed (abundance: Kolmogorov-Smirnov statistic = 0.292, $df = 130$, $P < 0.0001$; species Richness: Kolmogorov-Smirnov statistic = 0.182, $df = 130$, $P < 0.0001$). Using the original dataset, non-parametric Kruskal-Wallis tests followed by pairwise Dunn's tests (with Bonferroni correction applied) found both species richness and abundance were significantly affected by precipitation (species richness: $n = 130$, $\chi^2 = 29.194$, $df = 1$, $P < 0.0001$; abundance: $n = 130$, $\chi^2 = 23.209$, $df = 1$, $P < 0.0001$) and urbanization (species richness: $n = 130$, $\chi^2 = 8.375$, $df = 1$, $P = 0.004$; abundance: $n = 130$, $\chi^2 = 12.436$, $df = 1$, $P < 0.0001$). Post hoc comparisons (i.e. Dunn's test) found significant differences between wild-dry compared with wild-wet ($P < 0.0001$; Fig. 2) and urban-dry vs. wild-wet for both measures of diversity ($P < 0.0001$).

Using a resampled dataset controlling for sample size ($n = 5$ sites across all habitats), the majority of Kruskal-Wallis tests were not significant at the $\alpha = 0.05$ level for both abundance and richness (30.2% and 20.1%, respectively). However, the distributions of abundance and richness within each habitat were similar between the original and resampled datasets (Fig. 2). Controlling for sample size, the wild-wet habitat remained as the largest in terms of both abundance and richness, and for the 30% and 20% of resamples with significant differences (respectively), wild-wet habitat was significantly greater than one or more other habitats (post hoc Dunn test at

Table 1: The number of sites ($n = 130$) each species was sampled from in each habitat category

Species	Urban-wet ($n = 5$)	Urban-dry ($n = 76$)	Wild-wet ($n = 28$)	Wild-dry ($n = 21$)
<i>Allopeas gracile</i> *	1	28	1	0
<i>Cecilioides acicula</i> *	0	6	0	0
<i>Euconulus trochulus</i>	0	0	4	0
<i>Euglandina texasiana</i>	0	0	16	3
<i>Gastrocopta contracta</i>	0	0	12	1
<i>Gastrocopta cristata</i>	0	6	0	0
<i>Gastrocopta pellucida</i>	2	36	24	16
<i>Gastrocopta riograndensis</i>	0	0	7	1
<i>Gastrocopta riparia</i>	5	43	9	0
<i>Gastrocopta rupicola</i>	2	6	0	0
<i>Gastrocopta servilis</i> *	1	17	0	0
<i>Gastrocopta sterkiana</i>	0	0	0	1
<i>Gastrocopta tappaniana</i>	0	0	6	1
<i>Glyphyalinia umbilicata</i>	0	0	13	4
<i>Guppya gundlachi</i>	0	0	16	4
<i>Hawaiiia minuscula</i>	3	18	22	6
<i>Helicina orbiculata</i>	1	1	21	7
<i>Helicodiscus (Lucilla) singleyanus</i>	1	5	3	6
<i>Huttonella (Gulella) bicolor</i> *	0	4	8	0
<i>Linisa texasiana</i>	5	45	15	11
<i>Polygyra cereolus</i>	1	18	5	0
<i>Praticolella mexicana</i> *	5	64	7	5
<i>Praticolella salina</i>	0	0	6	0
<i>Praticolella trimatris</i>	0	0	0	3
<i>Pupisoma dioscoricola</i>	0	0	18	8
<i>Pupisoma macneilli</i>	0	0	1	0
<i>Pupoides albilabris</i>	3	27	5	1
<i>Rabdotus alternatus</i>	3	40	8	17
<i>Strobilops hubbardi</i>	0	0	5	0
<i>Thysanophora hornii</i>	0	0	18	5
<i>Thysanophora plagioptrycha</i>	0	0	14	1
<i>Zonitoides arboreus</i>	0	1	7	0

Introduced species indicated with *, designated according to Najev et al. (forthcoming) and Robinson (1999).

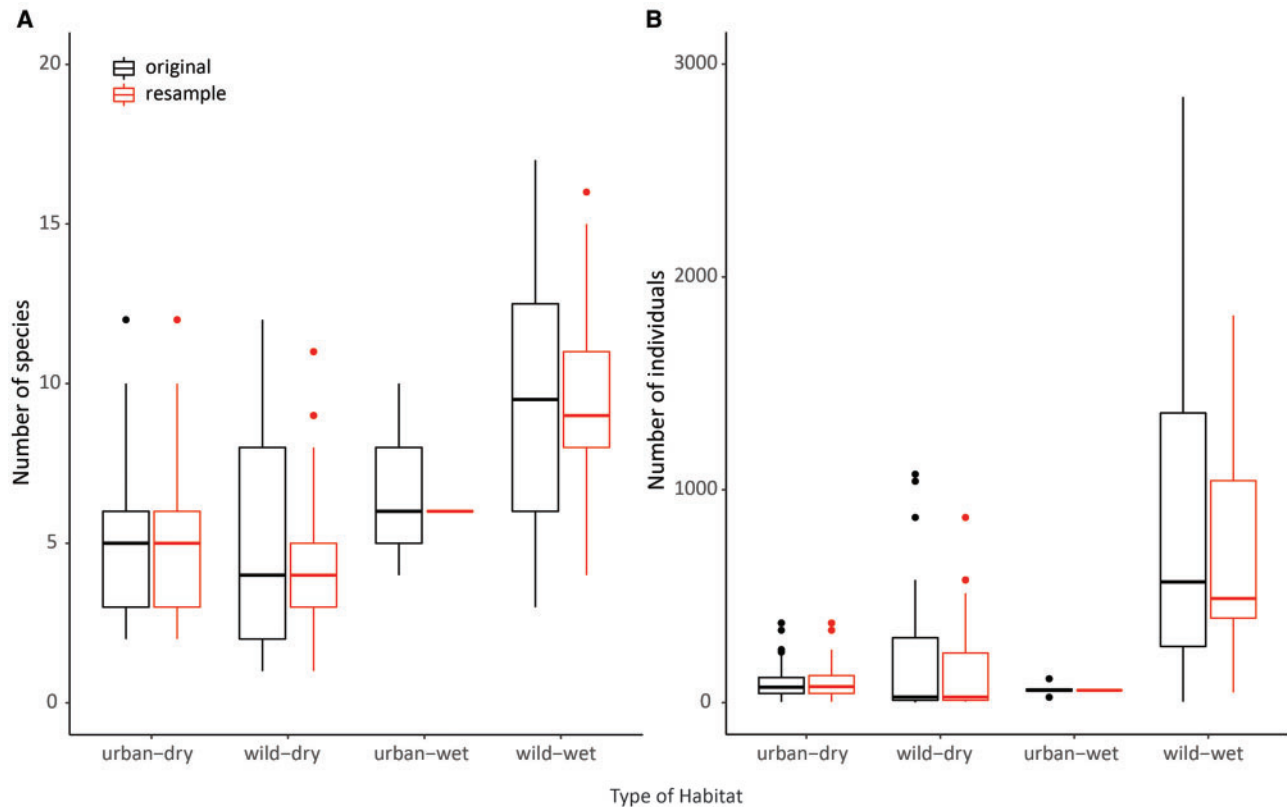


Figure 2: Describing snail species richness (A) and abundance (B) in urban and wild areas in dry and wet regions of the LRGV. Original and resampled datasets are presented, the latter controlling for sample size ($n=5$ sites resampled in each habitat 1000 times). A majority of the 1000 Kruskal-Wallis tests were not significant for both abundance and richness (30.2% and 20.1%, respectively). Urban sites are not significantly different from each other. Urban-dry areas are not a refugia for snails from wild-wet areas.

$\alpha=0.05$ level). In neither the original and resampled dataset were urban-wet and wild-wet sites significantly different from each other. Urban sites are not significantly different from each other for both measures of diversity across the precipitation gradient. Urban-dry areas are also not a refugia for snails from wild-wet areas.

As an initial check that our β -diversity measures were useful to compare these snail assemblages, we asked whether our two habitat distinctions (wild vs. urban) result in distinct communities. We found that in terms of β -diversity, urban communities are more like other urban communities than they are to wild communities (Supplementary Fig. S2, one-sided two-sample Mann-Whitney U test statistic [MWU] = 85 833, $P < 0.001$), as are wild communities to each other relative to urban communities (MWU = 286 290, $P < 0.001$). This holds for both the wet and dry regions. Therefore, our two habitat distinctions ('wild' vs. 'urban') are indeed distinct in terms of species composition, reinforcing the significant main effect of urbanization on species richness and abundance.

We tested several hypotheses on the effect of urbanization on β -diversity. We found urbanization does generate more β -diversity than what exists in wild habitats alone (Fig. 3A). Urban-wild β -diversity is significantly greater than wild habitats both across a precipitation gradient and overall (MWU = 827 925, $P < 0.001$ and $W=707\ 800$, $P < 0.001$, respectively). In fact, β -diversity at the urban-wild interface is the greatest among all possible comparisons (Supplementary Fig. S3). We found that urbanization has a homogenizing effect on land snail

species composition (Fig. 3B). Urban yards are more similar to each other across a precipitation gradient than to their wild counterparts within the same precipitation range (MWU = 278.5; $P < 0.001$ and $W=2200$; $P < 0.001$, relative to urban-wild transition in the dry and wet regions, respectively). We found that urban yards do not act as a refugia for moisture-affiliated snail species (Fig. 4A). Urban yards in the dry region are not significantly less dissimilar to wild communities in the wet region than they are relative to wild communities in the dry region (Fig. 4A; MWU = 598 818; $P < 0.001$).

Although β -diversity across the precipitation gradient is greater than that found within the wetter region, β -diversity within drier climates is comparable with that across the precipitation gradient (Fig. 4B; MWU = 212 451; $P < 0.001$, and $W=483\ 398$; $P=0.099$, respectively). We found that urban-wild β -diversity is greater in the dry region relative to the wet region (Fig. 4C; MWU = 235 919; $P < 0.001$). We found that the largest contribution to β -diversity across all habitats was turnover, with a much smaller contribution by nestedness (Table 2 and Supplementary Fig. S3). In wild habitats, turnover made up 78% of the total Jaccard dissimilarity. However, in the drier region, nestedness made up a comparatively larger fraction of the total dissimilarity compared with the wetter region (39% vs. 19%, respectively). Turnover was even more important at the urban-wild transition, making up 88% of the total dissimilarity (86% and 90% in drier and wetter region, respectively).

NMDS resulted in the best configuration with a stress of 0.12 (Fig. 5). This analysis of community composition finds the

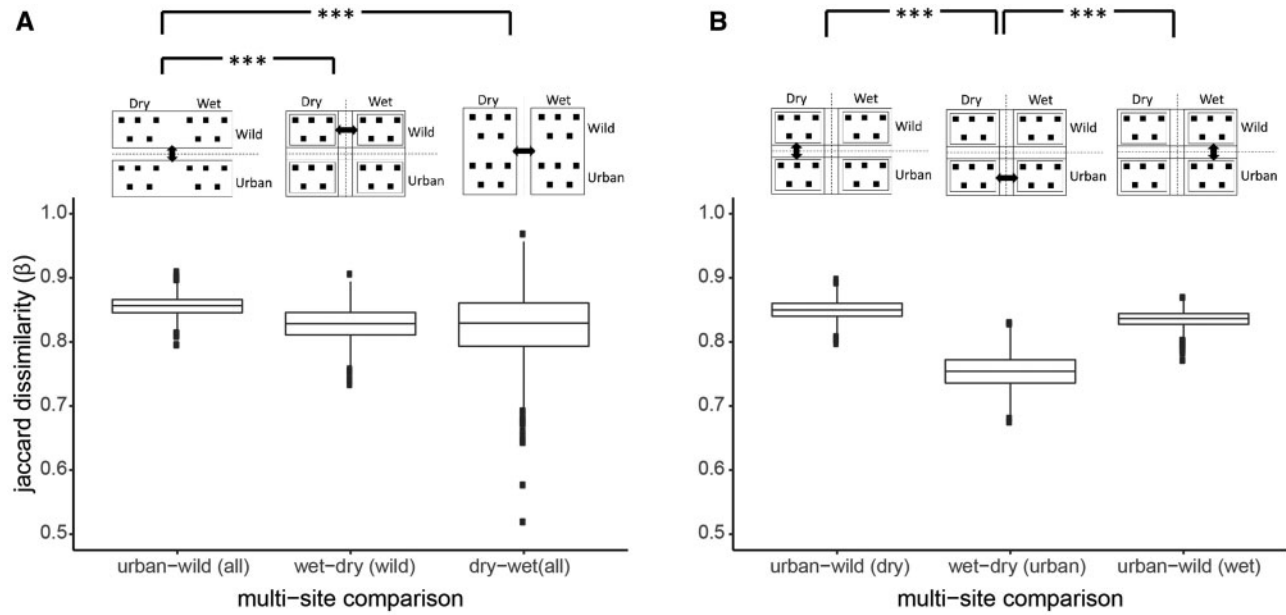


Figure 3: (A) Comparing dissimilarity (β -diversity) of the urban-wild transition to that of wild habitats both along a precipitation gradient (wet-dry [all] and overall (wild-wild [all])). (B) Comparing dissimilarity of urban habitats across the wet-dry transition (urban dry to urban wet) to that of their corresponding wild communities. Results of MWU are shown above. Significance codes: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

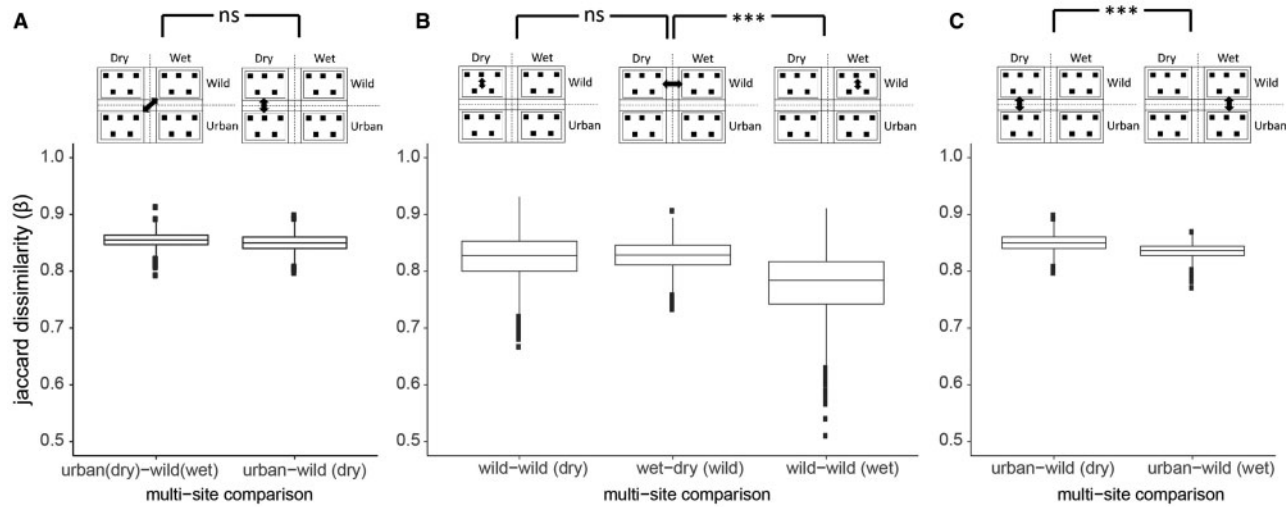


Figure 4: (A) Comparing urban yards in the dry region relative to wild habitats in the wet region vs. dry region. If urban yards act as refugia for moist-affiliated species, then urban communities in the dry region should look more like wild communities in the wet east than they do to wild communities within their same (dry) region. (B) Comparing dissimilarity (β -diversity) of wild habitats across the wet-dry transition (wild wet to wild dry) to that occurring within dry and wet regions. (C) Assessing whether urban yards in the dry region are more dissimilar to their wild counterparts than urban yards are to their wild counterparts in the wet region. Results of MWU are shown above. Significance codes: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

composition of most wild sites is separate from urban sites and the urban-dry sites are particularly distinct. The urban-wet sites are found entirely within the cloud of urban-dry sites. Comparison among factors using both ANOSIM and PERMANOVA found both urbanization and moisture regime were significant factors (PERMANOVA $F = 33.5$, $P < 0.001$; $F = 2.7$; $P = 0.013$, respectively) controlling species composition; however, their interaction ($F = 1.34$, $P = 0.20$) was not. Results for ANOSIM were in agreement, finding significant effects of moisture regime ($R = 0.025$; $P = 0.039$; 389 permutations \pm global R) and to an even greater degree, urbanization ($R = 0.648$; $P = 0.001$; 0 permutations \pm global R).

Discussion

Our investigation of the land snail assemblages of urban yards and native habitats in the LRGV provides insight into the nature of urban yard community assembly and how biodiversity is packed into a partially urbanized landscape.

Urban yards vs. native habitats: diversity, abundance and species composition

Species richness and abundance were highest in the wild-wet habitats and lowest in both dry urban and wild habitats, in both

Table 2: Bootstrapped estimates of the three Jaccard dissimilarity components for six different habitat or climate transitions

Habitat or climate transition	Turnover (beta.JTU)	Nestedness (beta.JNE)	Both (beta.JAC)
Urban-wild (wet)	0.754 ± 0.027	0.082 ± 0.018	0.835 ± 0.014
Urban-wild (dry)	0.734 ± 0.045	0.116 ± 0.039	0.85 ± 0.016
Urban-wild (all)	0.749 ± 0.04	0.106 ± 0.034	0.855 ± 0.017
Wet-dry (urban)	0.587 ± 0.051	0.165 ± 0.042	0.752 ± 0.027
Wet-dry (wild)	0.625 ± 0.06	0.202 ± 0.062	0.826 ± 0.026
Wet-dry (all)	0.722 ± 0.045	0.124 ± 0.041	0.846 ± 0.019

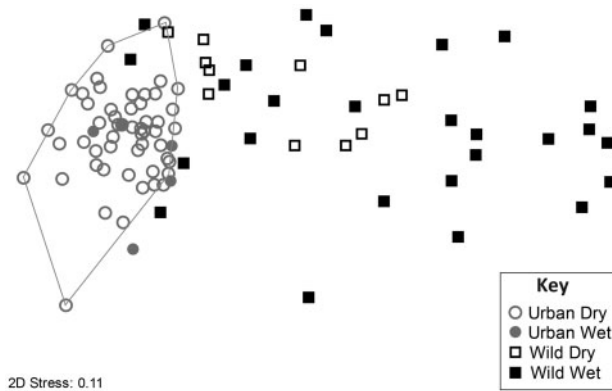


Figure 5: NMDS showing the difference in community composition across urban vs. wild and wet vs. dry comparisons. Each symbol represents a sampling site and proximity indicates similarity. The distinctive urban, dry community is highlighted. Both urbanization and precipitation regime were significant factors ($F=33.5$, $P<0.001$; $F=2.7$; $P=0.013$, respectively) controlling species composition.

the original and resampled dataset (Fig. 2), with abundance of the average wild site being an order of magnitude higher than urban yards. Both urbanization and regional climate appear to underlie these observed patterns. Despite the fact that we were unable to detect any significant differences in abundance or richness between habitats when controlling for sample size, the marked correspondence between the original and resampled datasets suggest that the wild-wet habitat does have significantly greater abundance and richness relative to other habitats, but our unbalanced sampling design was insufficient to capture such differences. Although wild and urban sites shared many species, urban yards appeared to support far more introduced and synanthropic species (Table 1), with the wild sites possessing a higher proportion of both native and rare snail species, such as *Praticolella trimatris* and *Gastrocopta riograndensis*. Urban-wild β -diversity is greater than that observed between wild habitats, indicating differentiation of the urban assemblages (Fig. 3A). These results are in agreement with prior studies showing that urban areas and early-successional habitats have lower snail diversity compared with older-successional forests (Horsák et al. 2009; Lososová et al. 2011; Najev et al. forthcoming). Similar results have been seen in strip-mined lands compared with relatively undisturbed areas (Watters, Menker, and O'Dee 2005).

Biotic homogenization, not urban refugia

These urban land snail communities appear homogenized, outweighing the influence of the precipitation gradient. The similarity in species richness between urban sites across the precipitation gradient (Fig. 2) supports this conclusion. Further

support can be seen in urban sites having the lowest levels of dissimilarity (β -diversity; Fig. 3B). Finally, analysis of snail communities (Fig. 5) found wild sites are more widely scattered, whereas urban sites are clustered, further indicating the broad similarity within urban sites.

Five introduced snail species were observed mostly in urban sites, with a notable species, *Praticolella mexicana*, found in all habitats and being the most frequently encountered species (occurring in 84% of sites). Urban habitats also harbored common cosmopolitan species able to tolerate high levels of anthropogenic activity (e.g. *Gastrocopta pellucida* and *Hawaiia minuscula*), native synanthropic (e.g. *Linisa texasiana*, *Polygyra cereolus*), introduced synanthropic (e.g. *Allopeas gracile*, *Gastrocopta servilis*) and a few disturbance tolerant native taxa (e.g. *Euglandina texasiana*). These results mirror other urban land snail studies (Bergey 2019).

Elevated avian diversity has been noted in golf courses and residential areas with detached housing (e.g., urban yards) in California oak woodlands (Blair 1996). Golf courses in a desert environment (Chihuahuan Desert in New Mexico, USA) also support increased native avian riparian species richness and diversity (Merola-Zwartjes and DeLong 2005). Therefore, we proposed that elevated watering by landowners could allow yards to provide refugia for moisture-dependent (riparian) snail taxa. Comparison of the urban-dry with the wild-wet (Table 1) reveals that they share the suite of a taxa common to all habitats, two introduced taxa, but only a single native species (*Zonitoides arboreus*) is unique to both urban-dry and wild-wet. *Zonitoides arboreus* is widely distributed in the human-altered habitats of the southeastern USA, wherever there is sufficient moisture. Measures of β -diversity further disprove the riparian-refuge hypothesis: Urban yards in the dry region are not significantly less dissimilar to wild communities in the wet region than they are relative to wild communities in the dry region (Fig. 4A). NMDS also highlights the lack of overlap among urban and wild communities (which are significantly different), particularly the wild-wet with urban sites. Urban yards, even with elevated watering, thus do not serve as refugia for moisture-dependent, riparian land snails in an arid environment. This contradicts prior findings that some urban habitats support riparian bird diversity and have been suggested to potentially mitigate native riparian vegetation loss (Rosenberg, Terrill, and Rosenberg 1987; Merola-Zwartjes and DeLong 2005). Our results caution that these findings may not be universal across all taxa groups. This could be due to differences in vagility, with these alternative habitats available in highly mobile animals with large foraging extents but less likely for a riparian snail to encounter. But, snails, at least for some species, are known to easily be spread by humans (Robinson 1999; Hodges and McKinney 2018; Bergey 2019; McKinney et al. 2019; Gladstone et al. 2020) so differences in vagility might not fully explain this discrepancy.

An avenue for future investigation is whether different types of urban yards could be better positioned to provide mesic refugia. Blair (1996), for instance, considered several types of urban and residential areas that are traditionally managed differently. In our current study, the residential yards surveyed were largely traditional lawns. However, there is movement among horticulturists in the region to plant more native thornforest plants to benefit butterflies and birds. It is possible that native land snails could also potentially benefit from this change. A careful study of long-established residential yards planted with native flora is required to eliminate the refugia hypothesis's potential.

β -diversity along the wild-to-urban gradient

Although β -diversity across the precipitation gradient is greater than that found across the wild to urban gradient in the wetter region, it is no greater than what is found across the wild to urban gradient in the drier region, as these two gradients express comparable levels of dissimilarity (Fig. 4B). However, gradient steepness between wild and urban habitats is greater in the drier region relative to the wetter region (Fig. 4C). This result can be readily explained by the increased differential between well-watered urban yards in the dry region vs. native habitats developed in the xeric regional climate. Urban yard land snail community composition in a temperate grassland and post oak woodland matrix found that elevated watering was one variable affecting species composition (Bergey and Figueroa 2016). Thus, it seems as though human activities, like irrigation, do in fact increase gradient length and influence community composition in xeric landscapes.

Finally, we considered the relative contributions of turnover and nestedness in producing observed β -diversity patterns. Our initial expectation was one of nestedness with most of the diversity being in the wet region and lower diversity and abundance in the dry habitats. However, we also noted that some species appeared restricted to a given precipitation regime. *Praticolellatrimatris* and *Gastrocopta sterkiiana* were limited to wild sites in the dry region and *G. riograndensis* and *Strobilops hubbardi* were restricted to a few wild sites in the wet region.

Our analyses show that, across the entire region, β -diversity within both wild areas and at the urban-wild interface is primarily driven by turnover. However, we found a role for nestedness in wild communities of the drier region (Supplementary Fig. S3). One possible explanation for this result is that community assembly in the dry region is primarily driven by moisture level, most species being able to persist in more humid riparian habitats and only a subset being able to tolerate the more xeric uplands. Such a pattern underscores the increasing importance of moist microhabitats within an otherwise xeric landscape, corroborating our findings at the urban-wild transition in the drier region. The predominance of turnover over nestedness for β -diversity at the urban-wild interface suggests that many species prefer either wild or urban sites, and that urban sites do not simply represent a subset of the native fauna that tolerates anthropogenic activities. Previous studies of land snail β -diversity, undertaken in temperate forest landscapes, tended to find a mix of native and non-native species in urban habitats (Horsák et al. 2009; Lososová et al. 2011; Hodges and McKinney 2018). These studies also found declines in species richness and an increasing proportion of non-native species with increasing urbanization.

In conclusion, we find strong biotic homogenization in urban land snail communities across a precipitation gradient. We did not find that urban environments, even with elevated moisture

levels, provided a refuge for native riparian snail taxa. Importantly, we argue that studies of urbanization should focus on intermediate (regional) scales to quantify how it modifies regional biodiversity arising from background environmental gradients. Such approaches are likely to lead to an improved understanding of how multi-city urban metroplex areas, which span large geographic regions, can be used maintain and even promote background biodiversity.

Supplementary data

Supplementary data are available at JUECOL online.

Data availability

The datasets used in the analyses are available as Supplementary Material (.xlsx file).

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