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No evidence that novel resource availability drives bill shape divergence in urban

dark-eyed juncos (*Junco hyemalis*)

A thesis submitted in partial satisfaction of the requirements for the degree Master

of Science in Biology

by

Sara Elizabeth Freimuth

2023

ABSTRACT OF THE THESIS

No evidence that novel resource availability drives bill shape divergence in urban

dark-eyed juncos (*Junco hyemalis*)

by

Sara Elizabeth Freimuth

Master of Science in Biology

University of California, Los Angeles, 2023

Professor Pamela J. Yeh, Chair

Urbanization is rapidly changing landscapes worldwide, driving phenotypic divergence in

numerous urban wildlife populations. However, the strength and direction of this divergence may

vary across and within cities. Here, we investigated the influence of fine-scale environmental

variation on the morphological divergence of dark-eyed juncos (*Junco hyemalis*) across three

Southern California cities. We explored how bill shape varies across three urban populations and

one non-urban population, and we tested whether bill shape varies with fine-scale changes in

resource availability across urban Los Angeles. Bill shape differed between urban and non-urban

populations, but we did not observe expected patterns of bill shape divergence across cities. Bill

shape variation also was not associated with fine-scale variation in resource availability within

urban Los Angeles. Our findings suggest urban junco bill shape may be driven by non-adaptive

processes, other environmental factors, or a more complex suite of urban selection pressures.

The thesis of Sara Elizabeth Freimuth is approved.

Michael Edward Alfaro

Morgan Winn Tingley

Pamela J. Yeh, Committee Chair

University California, Los Angeles

2023

To my brother, for telling me years ago to try fieldwork.

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Introduction

Urbanization is rapidly changing landscapes around the world. Defined as the replacement of natural elements (soil, hydrologic system, vegetation, and fauna) by human-made ones, urbanization is a process of environmental change that can create novel and complex ecosystems (Dansereau, 1957; Szulkin et al., 2020). These new environmental conditions constitute driving forces of ecological and evolutionary change in cities (Shochat et al., 2006). In many cases, phenotypic divergence of urban populations from non-urban counterparts can occur more rapidly and be much more pronounced than divergence between pairs of non-urban populations (Darimont et al., 2009; Hendry et al., 2008, 2017). Thus, cities have the unique potential to serve as natural experiments for exploring organisms' responses to environmental change (Alberti, 2015; Donihue & Lambert, 2015; Gruber, 2019; Hahs & Evans, 2015).

Research has revealed cases of phenotypic divergence between urban and non-urban populations across numerous taxa (Johnson & Munshi-South, 2017). Birds, in particular, have been studied in cities for over a century and have shown divergence in numerous traits (Marzluff, 2017; Seress & Liker, 2015), including morphology (Liker et al., 2008), plumage (Yeh, 2004), physiology (Meillère et al., 2015), behavior (Atwell et al., 2012), song (Newman et al., 2008), and life history (Sepp et al., 2018). While most studies have explored phenotypic divergence between single-city pairings of urban and non-urban populations, evidence from studies of multiple cities suggests that urban traits do not always converge across different cities (Evans et al., 2009; Miller et al., 2018), but rather, the strength and direction of divergence may vary with the local ecological pressures involved.

Habitat structure and resource availability, in particular, may be key ecological drivers of phenotypic divergence in urban bird populations across cities. Habitat variation and

corresponding changes in foraging strategy have played a key role in the adaptive radiations of multiple avian taxa (e.g., Grant & Grant, 2007; Reddy et al., 2012). Intraspecific divergence of bill morphology in response to changes in vegetation and resource availability is well-documented in birds in natural habitats (Grant & Grant, 2002). There is evidence of dietary shifts driving morphological divergence in urban populations as well (Badyaev et al., 2008; Bosse et al., 2017). Notably, populations of birds can show adaptive differences in morphology consistent with differences in habitat structure and foraging ecology at microgeographic scales, even in the presence of gene flow (Langin et al., 2015; Milá et al., 2009; Senar et al., 2006). Thus, understanding the fine-scale heterogeneity of urban habitat structure and resource availability may be critical to understanding variation in the strength and direction of morphological divergence in birds across cities.

Nevertheless, the fine-scale heterogeneity of urban habitats is often generalized or overlooked in studies exploring phenotypic divergence in urban populations (McDonnell & Hahs, 2013; Shochat et al., 2006). Vegetation structure and composition, for example, are habitat features implicated in avian foraging ecology that can vary greatly across and within urban environments according to the spatial scale and resolution at which they are classified (Blinkova & Shupova, 2017; Grimm et al., 2008; Holmes & Recher, 1986). While cities are often characterized by reduced vegetation cover and greater percentages of built-up land area relative to their non-urban counterparts, vegetation cover can also vary greatly across and within cities (Grimm et al., 2008; Magle et al., 2019). Beyond the general amount or density of vegetation, its structure and composition can vary greatly across and within cities as well. Residential neighborhoods and urban parks, for instance, can host more exotic plant species and less understory structural complexity than golf courses and patches of remnant vegetation (Threlfall

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et al., 2016). Not only can these changes in vegetation alter the types of fruits and seeds available to birds, but they also can impact insect availability (Mata et al., 2021; Narango et al., 2018). In Los Angeles, for example, urban and suburban backyards with native and drought-tolerant plants support a wider array of insects than those without (Adams et al., 2020). Thus, fine-scale urban-induced changes in vegetation structure and composition may more accurately reflect shifts in avian foraging strategy than broader changes in overall vegetation amount or extent.

Similarly, the availability of novel anthropogenic food sources can vary across and within urban environments. While urban environments are generally characterized as providing abundant supplemental food, such as anthropogenic food sources (Jones & James Reynolds, 2008), their availability is not always consistent across cities. The proportion of households engaging in bird feeding can differ at a broader scale between countries and at the local scale depending on house type and household size (Davies et al., 2012; U.S. Department of the Interior, Fish and Wildlife Service et al., 2006). Similarly, common sources of anthropogenic food waste birds may consume can vary spatially within cities (Brown et al., 2022). This has been shown not only to affect bird communities (Brown et al., 2022), but also may impact individual species, as some birds incorporate more anthropogenic food sources into their diets when they are more available in their local environments (Stofberg et al., 2019). Thus, changes in anthropogenic food source availability at local scales may influence the degree to which foraging shifts drive morphological divergence across and within cities.

Testing for hypothesis-driven associations between urban environmental features and phenotypes can offer insight into evolutionary processes and responses to urbanization (Santangelo et al., 2020). Here, we characterized environmental variation in urban habitats at a fine spatial scale and resolution to test adaptive hypotheses for morphological divergence of

dark-eyed juncos (*Junco hyemalis*). The dark-eyed junco (hereafter: "junco") presents an interesting case study for exploring if and how fine-scale environmental variation influences the strength and direction of phenotypic responses to urbanization across cities. Multiple populations of this generalist, ground-foraging passerine have colonized cities throughout Southern California in relative proximity to migratory non-urban populations (Bressler et al., 2020; Nolan Jr. et al., 2020; Yeh, 2004; Yeh & Price, 2004). Within cities, juncos occupy diverse habitats, from small parks in highly urbanized areas, to golf courses, to college campuses, to tree-lined city streets (eBird, 2021). A recent study found evidence for both convergent and non-convergent morphological evolution in Southern Californian urban juncos such that urban juncos in three cities were smaller than non-urban juncos, but different urban populations varied in patterns of divergence in other morphological traits. Specifically, urban juncos in Los Angeles and Santa Barbara had shorter, wider bills than non-urban juncos, but urban San Diego juncos did not (Diamant, 2023).

In this investigation we further explored these patterns of bill shape divergence in urban junco populations. We hypothesized that urbanization would drive bill shape divergence in urban populations of juncos, and we expected to observe patterns in bill shape across cities consistent with those observed by Diamant (2023). Specifically, we expected urban juncos in Los Angeles and Santa Barbara would have shorter, wider bills than non-urban juncos, but urban San Diego juncos would not. To explore potential drivers of these patterns of convergence and non-convergence across cities, we first examined potential drivers of bill shape related to foraging ecology within the city of Los Angeles. We hypothesized that changes in vegetation and anthropogenic food waste availability and corresponding shifts in foraging strategy drive bill divergence in urban juncos within Los Angeles. We predicted that differences in the availability

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and type of these novel resources at a small spatial scale will spatially covary with differences in bill shape within the city. In such a case, we would expect to see variation in these environmental features across cities covary with differences in bill shape across cities. Therefore, differences in the availability of these resources—and the juncos' ability to exploit them—might explain the lack of morphological convergence seen previously across cities.

We observed differences in bill shape between urban and non-urban birds, but we did not observe the patterns in bill shape we predicted across cities. We also did not find significant support for the ecological associations with bill shape we predicted. Thus, we consider the possibility that other adaptive or non-adaptive processes may instead be driving urban bill shape divergence.

Methods

Study sites

We conducted fieldwork across Southern California by sampling urban juncos at three University of California campuses in Los Angeles (UCLA), Santa Barbara (UCSB), and San Diego (UCSD) and one non-urban mountain site in Angeles National Forest (ANF). All three campuses are low elevation coastal areas that broadly share differences compared to nearby non-urban mountain habitats in terms of vegetation greenness, amount of human traffic, and climate (Diamant, 2023). In addition to these three urban sites, we sampled individuals across the Los Angeles urban core to explore potential drivers of bill shape within a single urban population of juncos as well. These sites included Occidental College and urban parks of varying sizes and locations through the city that vary in pollutants, greenspace access, and climate (Zeise et al., 2021).

Field methods

We captured adult juncos during three consecutive breeding seasons between January and July from 2021 to 2023. The initiation of the breeding season was signaled by the onset of singing and territorial behavior by male juncos, typically observed in mid- to late-January in Los Angeles and San Diego, mid-February in Santa Barbara, and late-May to June in non-urban mountain sites. Individuals were lured into mist-nets using audio playbacks of junco calls and songs recorded at UCLA and other regional sites. Each junco was fitted with a federal metal band and a unique combination of three different colored leg bands. We aged individuals using molt limits such that second-year birds retain their juvenile secondary flight feathers and secondary coverts, and we sexed individuals using sex-based plumage differences and/or primary sex characteristics (cloacal protuberance and/or brood patch) (Pyle, 1997). We scored birds for fat content, checked for active molt, and recorded the following morphometrics: wing length, tail length, tarsus length, bill dimensions, and body mass. Wing length was measured as unflattened wing chord (Ralph et al., 1993) and tail length from the posterior end of the uropygial gland to the posterior tip of the longest rectrix. Bill dimensions included bill length measured from the distal edge of the nares to the tip of the upper mandible and bill width and depth at the base of the beak.

To characterize the juncos' local environments, we followed a modified version of the combined Rapid Assessment Protocol (CNPS-RAP) developed by the California Native Plant Society and California Department of Fish and Wildlife. In its original format, CNPS-RAP has been utilized to assess how changes in environmental elements, physical processes, and other natural or human-made disturbances influence the distribution of plants or patterning of vegetation (California Native Plant Society (CNPS), 2022). Several modifications were made to

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the CNPS-RAP to make it applicable for capturing ecological variation among urban junco habitats. First, sampling was conducted at junco capture locations, regardless of whether they fell within the CNPS-RAP definition of a vegetation stand. Rapid assessments were conducted in circular plots with a 50-meter radius around each individual's capture location. This area of habitat presents a reasonable approximation of the space used by small territorial passerines, including juncos (Sottas et al., 2020; Wood et al., 2016; Yeh & Price, 2004). Additionally, unlike CNPS-RAP's emphasis on dominant native species, we placed equal weight on cataloging dominant native and non-native species, including planted ornamentals. We catalogued 346 plants across all plots that we identified to the genus or species level. We also counted the number of trash cans within the assessment plot as a proxy for anthropogenic waste availability (Mazué et al., 2023).

Surveys of capture locations were conducted in the 2022 and 2023 field seasons. However, because the urban park and campus habitats are highly managed and maintained, cultivated landscapes, we included urban juncos measured in 2021 in our analysis if they were captured within a 15-meter radius (one mist-net length) of the center of any assessment plot surveyed in the 2022 field season. Similarly, we included some juncos captured in 2023 without reassessing the capture location if the individual was captured within a 15-meter radius of the center of a 2022 assessment plot.

In total, we measured and characterized the capture sites of 170 adult juncos, including 63 at UCLA, 40 in other urban Los Angeles habitats, 20 at UCSB, 31 at UCSD, and 16 in Angeles National Forest. All animals were cared for and tested according to institutional guidelines and approval (IACUC #ARC-2018-007).

Statistical Analysis

Bill shape across populations

We determined bill shape by principal component analysis (PCA) using bill length, bill width, and bill depth from juncos across all sites. The first principal component described variation in bill size, while the second component described variation in bill shape (Table 1). We compared bill morphology across the three urban campus populations (UCLA, UCSB, UCSD) and one non-urban mountain population (ANF) using a linear mixed model (LMM). We used bill PC2 as the response variable and included population and sex as fixed effects. To account for any researcher measurement differences, we also included bander as a random effect. Using the *emmeans* package, we then calculated *post-hoc* estimated marginal means and determined pairwise contrasts and effect sizes (Lenth, 2023; R Core Team, 2021). Pairwise contrasts were considered statistically significant when the 95% confidence intervals for an effect size did not overlap with zero.

Ecological associations with bill shape

We then explored how bill shape varied with fine-scale vegetation and human food waste availability. We considered both the origin and structure of vegetation in our analysis, as both these factors are linked to foraging ecology in birds through their provision of fruits and seeds, as well as their associations with the diversity and abundance of insects (Blinkova & Shupova, 2017; Loesberg & Meyer, 2021; Mata et al., 2021; Narango et al., 2018; Wilson et al., 1999).

We assigned the plant species found in each survey plot to the following vegetation groups based on origin and structure: native trees, native midstory, non-native trees, non-native midstory, and turf grasses. The origin of each plant was described as native or non-native to

California, where possible, using Calflora and the United States Department of Agriculture

PLANTS database (Calflora, 2023; USDA, NRCS, 2023). We determined the origin of 340 of

the 346 dominant plants we identified to the genus or species level in rapid assessments and

classified them further into structural groups for inclusion in our analysis. Tree groups consisted

of overstory, and understory confers, hardwoods, and palms. Midstory groups consisted of

shrubs, forbs, succulents, lilioids, and graminoids. Turf grasses consisted of communities of

introduced turf-forming grass species, typically planted and maintained as lawns.

To account for the percent cover of all vegetation types being lower in plots dominated

by built cover, we analyzed variation in the cover of each vegetation type relative to the cover of

all types of vegetation, rather than as a percent cover of the overall area of the assessment plot.

We determined the relative cover of each vegetation group by dividing its percent cover in a

given assessment plot by the sum of the percent cover of all vegetation groups in that plot. For

example, the relative cover of native trees was calculated as the sum of the percent cover of all

individual native tree species within a capture location's assessment plot divided by the sum of

the percent cover of all vegetation groups. We then performed a PCA with the relative cover of

non-native trees, non-native midstory, turf grasses, native trees, and native midstory. PC1

described differences in vegetation origin, where higher scores were associated with greater

introduced vegetation cover and lower scores were associated with greater native tree vegetation

cover (Table 2). PC2 largely described introduced understory structural differences, where

higher scores were associated with greater relative cover of turf grasses and lower scores are

associated with greater relative cover of introduced midstory species.

For human food waste availability, we counted the number of trash cans in the

assessment plot of each junco's capture location as a proxy for human food waste availability

(García-Arroyo et al., 2023; Katlam et al., 2018; Mazué et al., 2023). We expected that any effect of trash cans on bill shape would diminish as the number of trash cans increased. Thus, trash can counts were log transformed prior to analysis by taking the log of one plus each count.

Our final LMM included bill PC2 as a response variable with vegetation PC1, vegetation PC2, and log of trash cans as predictors. We also included sex as a fixed effect and bander as a random effect.

Results

Bill shape across populations

Bill shape diverged between urban and non-urban populations, and we found evidence for convergence across cities (Figure 2). In pairwise comparisons, the non-urban mountain population in Angeles National Forest had significantly longer, narrower, and shallower bills than the UCLA population (effect size (CI) = -1.41 (-2.27, -0.55), the UCSB population (effect size (CI) = -1.05 (-1.86, -0.25), and the UCSD population (effect size (CI) = -1.29 (-2.04, -0.54). All effect size confidence intervals in pairwise comparisons between urban populations overlapped with zero, demonstrating non-significance.

Ecological associations with bill shape

In urban juncos across Los Angeles, bill shape was not associated with any of the ecological factors implicated in foraging strategy (Figure 3; Table 4). Bill shape was not associated with either relative native and non-native vegetation cover (Vegetation PC1; $X^2 = 1.23$, p = 0.27; Figure 3A), introduced understory complexity (Vegetation PC2; $X^2 = 0.004$, p = 0.95; Figure 3B), or trash cans ($X^2 = 0.45$, p = 0.50; Figure 3B).

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Discussion

Bill shape across populations

We found that across all cities, urban dark-eyed juncos had significantly shorter, wider, and deeper bills than non-urban dark-eyed juncos. Urbanization has driven bill shape divergence in other urban birds as well (Badyaev et al., 2008). Evidence for a stubbier urban bill shape, in particular, has also been found in the European black bird (*Turdus merula*) (Evans et al., 2009) and the New Zealand fantail (*Rhipidura fuliginosa*) (Amiot et al., 2022). Our observation of this shorter, wider, and deeper bill shape across multiple urban populations of juncos also offers evidence for convergent evolution of bill shape across cities. Given urbanization drives strong ecological change that can be broadly consistent across cities, it is often expected to drive predictable or repeatable evolutionary responses across different populations of urban species (Gould, 1989; Grimm et al., 2008). This has been observed in other urban dwellers, such as the white clover (*Trifolium repens*), which repeatedly evolved a potent antiherbivore defense across 20 cities of varying size (Johnson et al., 2018).

The evidence for bill shape convergence across cities here, however, was unexpected given that urban junco populations showed more complex patterns in bill shape divergence across cities in another recent study (Diamant, 2023). Consistent with this study, we found that urban juncos in Los Angeles and Santa Barbara had shorter and wider bills than the mountain population in Angeles National Forest. In contrast, we also found that urban juncos in San Diego had shorter and wider bills than non-urban juncos and did not significantly differ from either of the other cities' urban populations.

One explanation for why we observed convergence in bill shape across cities rather than the patterns observed by Diamant (2023) is that the urban San Diego juncos have rapidly evolved

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shorter, wider bills. Rapid evolution in response to extreme environmental change is not uncommon, especially in cities. The weed *Crepis sancta*, for example, evolved lower dispersal of seeds to facilitate dispersal success in habitats with increased impervious surface ground cover in as little as 5-12 generations (Cheptou et al., 2008). Rapid evolution has also been observed for other traits in this same population of San Diego juncos (Yeh, 2004), so it is possible that they are rapidly evolving shorter, wider bills as well. Of course, considering the smaller sample size in our study, we may not have completely captured bill shape variation within and across each population. However, further research could reveal if, how, and why bill shape has changed over time in the urban San Diego population.

Ecological associations with bill shape

Bill shape was not associated with vegetation or human refuse availability in urban Los Angeles juncos. One possible explanation for this is that bill shape divergence in urban populations may be the outcome of non-adaptive processes, like genetic drift. Urbanization can often lead to reduced gene flow between urban and non-urban populations (Miles et al., 2019). Loss of migratory behavior is also a common response to urbanization in birds, including juncos (Adriaensen & Dhondt, 1990; Møller et al., 2014; Warkentin et al., 1990; Yeh, 2004). It is possible that a reduction of gene flow resulting from urbanization and/or loss of migratory behavior in juncos has increased genetic drift in this population, and, in turn, led to bill shape divergence. This seems unlikely, however, because the urban Los Angeles juncos do not appear to be entirely isolated from nearby non-urban mountain populations. Multiple urban juncos banded at UCLA have been observed or recaptured at non-urban or peri-urban mountain sites,

suggesting there is likely active gene flow between the urban Los Angeles population and nearby non-urban mountain populations (Diamant, 2023).

This suggests that selection can still drive bill shape divergence in urban juncos, yet these selection pressures are still unknown. While our findings and those of additional studies suggest that novel resource availability, temperature, and song likely do not drive bill shape divergence in urban juncos, it is possible that other ecological factors exert selection pressures on bill shape in cities (Diamant, 2023; Wong et al., 2022). For example, Evans et al. (2009) hypothesized that the stubbier bills observed in urban European blackbirds might facilitate a switch in feeding technique from probing in deep soils to picking up items from shallow soils or hard surfaces in cities. This is consistent with the adaptive divergence seen in Darwin's small ground finches (*Geospiza fuliginosa*), where lowland individuals feeding mainly by picking and chipping at seeds on the ground had shorter and deeper bills than highland individuals gleaning insects in short vegetation (Kleindorfer et al., 2006). Stubbier bills, therefore, could be advantageous for urban ground-foraging birds like juncos if they are foraging more often on hard substrates. Additional studies of urban junco foraging behavior could offer insight into whether shifts in foraging technique select for shorter, wider bills in urban birds.

Further studies of foraging in juncos also could offer additional insight into the potential role of urban dietary shifts as an adaptive driver of bill shape. We found that novel resource availability and inferred dietary shifts were not associated with bill shape in juncos. However, this finding does not rule out dietary shifts as a potential adaptive driver of bill shape. The juncos in our study have been observed feeding on insects, seeds, fruits, and human food waste in cities, but the relative contribution of each of these items to the urban junco diet is largely unknown. As

a result, it is possible that our measures of vegetation and human food waste do not sufficiently reflect the availability of novel resources as they relate to foraging.

The wider and deeper bills seen in urban juncos suggests they are consuming harder foods, given that bill width and depth are implicated in bite force (Badyaev et al., 2008; Herrel et al., 2005). Vegetation might be able to represent local changes in plant and insect availability (Blinkova & Shupova, 2017; Mata et al., 2021; Narango et al., 2018; Wilson et al., 1999), but it may not as effectively reflect shifts towards harder seeds or insects. Seed size and handling time, rather than biogeographic origin (native vs non-native) could also be more important for urban juncos in determining seed preferences, as seen in other studies of generalist birds (Loesberg & Meyer, 2021; Titulaer et al., 2018). Thus, future studies focusing on urban junco diet composition with respect to food item characteristics such as size and hardness might uncover how these changes in diet could select for bill shape.

Like vegetation, the number of trash cans in a habitat also may not reflect urban dietary shifts in juncos as well as we anticipated. Multiple studies have shown that birds often rely on visual cues such as increased human activity in the area or even human placement of refuse in trash cans, rather than the presence of trash cans alone, when foraging on human food waste (Coulson et al., 1987; Monaghan et al., 1986; Noreen & Sultan, 2021; Spelt et al., 2021; Stofberg et al., 2019). A recent study also showed that the type of openings of trash cans influenced the likelihood of birds foraging from them, which was not accounted for in our study (García-Arroyo et al., 2023). Thus, it is possible that increased consumption of anthropogenic waste drives bill shape in urban juncos but went undetected in our study. Further studies on junco foraging behavior and diet in cities may offer insight into patterns of human food waste consumption across urban junco populations and their potential influence on bill shape.

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Ultimately, the findings here and in other studies suggest selection pressures on bill morphology in juncos are likely complex and multifaceted. In a study investigating spatial and temporal variation in the bill shape of juncos from non-urban populations across California, no single environmental variable was consistently associated with variability in different aspects of bill morphology (LaBarbera et al., 2017). Rather, only measures of overall habitat type and long-term temperature variability were predictors for multiple bill traits (LaBarbera et al., 2017). Thus, numerous individual environmental factors may drive junco bill shape divergence in cities, albeit with weak or possibly even opposing selection pressures. Understanding the factors that shape variation in bill shape will ultimately require analyses of multiple environmental factors, their different effects on individual bill traits, and their composite effects on overall bill morphology.

Figures
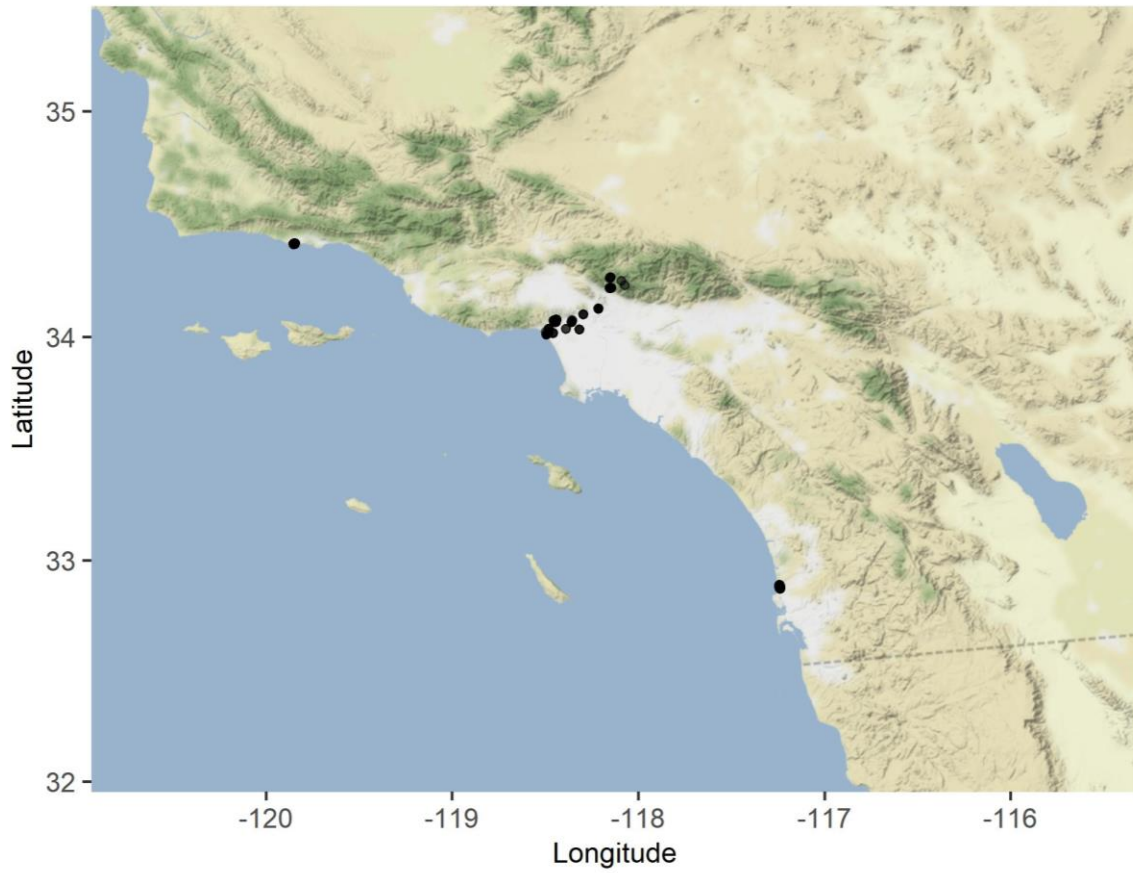
Figure 1. Map of junco banding locations across Southern California. Sites include urban University of California campuses, urban parks in Los Angeles, and non-urban locations in Angeles National Forest.
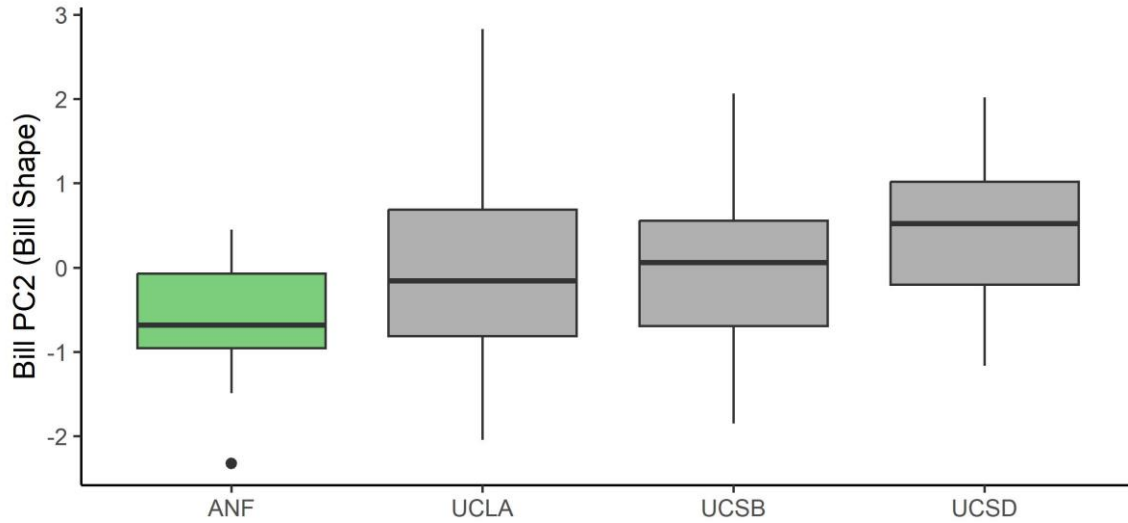
Figure 2. Bill shape differs significantly between urban (gray) and non-urban (green) populations of juncos, but not between different urban populations. Higher PC2 scores are associated with shorter, wider, and deeper bills (Table 1).
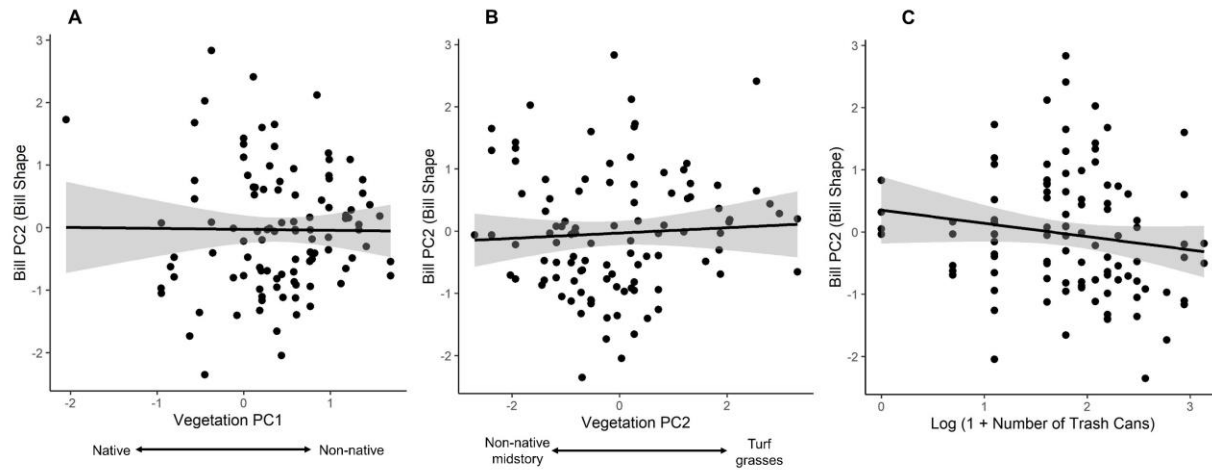
Figure 3. Within urban Los Angeles, bill shape is not associated with (A) vegetation origin ($p = 0.27$). Bill shape also is not associated with (B) introduced understory complexity ($p = 0.95$) or (C) human refuse availability ($p = 0.50$) across urban Los Angeles.

Tables

Table 1. PCA loadings and variance explained for bill variation across all juncos. PC1 explains size differences, while PC2 explains shape differences.

	Bill PC1	**Bill PC2**
Bill length (mm)	0.30	-0.95
Bill depth (mm)	0.68	0.18
Bill width (mm)	0.67	0.25
Proportion of variance explained	0.48	0.31

Table 2. PCA loadings and variance explained for variation in vegetation structure and origin across all junco capture sites. PC1 distinguishes capture locations dominated by introduced trees and turf grasses from capture locations dominated by native trees and midstory species. PC2 largely describes within-urban understory structural differences, where higher scores are associated with greater relative cover of introduced midstory species and lower scores are associated with greater relative cover of turf grasses. Variables listed represent the relative cover of each vegetation type.

	Vegetation PC1	**Vegetation PC2**
Non-native trees	0.48	-0.11
Non-native midstory species	0.05	-0.75
Non-native turf grasses	0.32	0.64
Native trees	-0.61	0.15
Native midstory species	-0.53	0.05
Proportion of variance explained	0.40	0.28

Table 3. Pairwise contrasts and effect sizes comparing bill shape across populations. All urban populations differ from the non-urban mountain population but not from one another. Effect sizes (95% CI) are shown and bolded where Cis do not overlap with zero. Direction is indicated for significant pairwise contrasts, the former being less than ("<") the latter. Bill PC2 scores for Angeles National Forest are less than those for UCLA, UCSB, and UCSD, indicating the urban populations all have shorter, wider bills.

	Bill PC2 (bill shape)
Angeles National Forest compared to UCLA	**-1.41 (-2.27, -0.55)** <
Angeles National Forest compared to UCSB	**-1.05 (-1.86, -0.25)** <
Angeles National Forest compared to UCSD	**-1.28 (-2.04, -0.54)** <
UCLA compared to UCSB	0.36 (-0.39, 1.10)
UCLA compared to UCSD	0.12 (-0.55, 0.79)
UCSB compared to UCSD	-0.23 (-0.92, 0.45)

Table 4. Linear mixed model of ecological associations with bill shape in 103 adult juncos across urban Los Angeles. Bill shape was not significantly associated with relative native and non-native vegetation cover (vegetation PC1; Table 2), introduced understory complexity (vegetation PC2; Table 2), trash cans, or sex.

	Estimate	**S.E.**	**p-value**
Intercept	0.046	0.446	0.92
Vegetation PC1	-0.156	0.140	0.27
Vegetation PC2	0.004	0.066	0.95
Log trash cans	0.093	0.139	0.50
Sex	0.008	0.181	0.96

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