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RESEARCH ARTICLE

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Convergent niche shifts of endangered parrots (genus *Amazona*) during successful establishment in urban southern California

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Abstract

Aim: Introduced species offer insight on whether and how organisms can shift their ecological niches during translocation. The genus *Amazona* offers a clear test case, where sister species Red-crowned (*A. viridigenalis*) and Lilac-crowned Parrots (*A. finschi*) have established breeding populations in southern California following introduction via the pet trade from Mexico where they do not coexist. After establishment in the 1980s, introduced population sizes have increased, with mixed species flocks found throughout urban Los Angeles. Here, we investigate the differences between the environmental conditions of the native and introduced ranges of these now co-occurring species.

Location: Southern California and Mexico.

Methods: Using environmental data on climate and habitat from their native and introduced ranges, we tested whether Red-crowned and Lilac-crowned Parrots have divergent realized niches between their native ranges, and whether each species has significantly shifted its realized niche to inhabit urban southern California. We also analysed data from Texas and Florida introductions of Red-crowned Parrots for comparative analysis.

Results: There are significant differences in the native-range niches of both parrot species, but a convergence into a novel, shared environmental niche into urban southern California, characterized by colder temperatures, less tree cover and lower rainfall. Texas and Florida Red-crowned Parrots also show evidence for niche shifts with varying levels of niche conservatism through the establishment of somewhat different realized niches.

Main Conclusions: Despite significant niche shifts, introduced parrots are thriving, suggesting a broad fundamental niche and an ability to exploit urban resources. Unique niche shifts in different U.S. introductions indicate that *Amazona* parrots can adapt to diverse environmental conditions, with cities offering a resource niche and the timing of introduction playing a crucial role. Cities can potentially serve as refugia for threatened parrot species, but the risk of hybridization between species emphasizes the need for ongoing monitoring and genetic investigations.

KEYWORDS
Amazona parrots, anthropogenic influence, citizen science, exotic species, niche differentiation, niche shift, reciprocal species distribution model, sister species, species introduction, urban ecosystems

1 | INTRODUCTION

How introduced species establish themselves is a crucial question for predicting the impacts of invasive species on native ecosystems (Blackburn et al., 2011). Climate matching appears to be important to some species introductions (Liu et al., 2020; Strubbe et al., 2013), but there are also numerous cases of introduced species making remarkable niche shifts (Atwater et al., 2018; Hill et al., 2017; Wiens et al., 2019). If the fundamental niche describes the set of conditions where a species *could* thrive, while the realized niche describes the subset of conditions where a species actually occurs, given constraints like competition (Hutchinson, 1957), then niche shifts imply the filling of a new portion of the fundamental niche (a realized niche shift) or an expansion of the fundamental niche through adaptation or plasticity. In either case, niche shifts challenge the idea of niche conservatism (Wiens & Graham, 2005), which forms the basis for species range forecasting with climate change (e.g. Bellard et al., 2012; Nuñez-Penichet et al., 2021). Recently, new methods and data sources are allowing niche shifts to be detected and quantified with higher accuracy (Bates & Bertelsmeier, 2021).

Parrots are an emerging model group for studying species introductions, especially in urban areas. Cities have become refuges for many species by providing the necessary resources to survive and thrive (Luna et al., 2018a; Van Heezik et al., 2008), with many of these introduced species facing extinction in their native ranges (Luna et al., 2018b; Sawyer, 2005; Soanes & Lentini, 2019; Wang et al., 2018). Parrots show high urban tolerance (Neate-Clegg et al., 2023) and have become established in cities around the globe over the last 50 years (Lockwood, 1999; Menchetti & Mori, 2014; Uehling et al., 2019). In doing so, they have become emblematic of urban biodiversity and the ability of persecuted, non-native species to adapt and thrive in human-modified landscapes (Shaffer, 2018). Yet, it remains unclear how parrots have managed to insinuate themselves into the urban landscape. Some introduced parrot populations appear to exist well outside the conditions of their native source populations (Ancillotto et al., 2016; Strubbe et al., 2015) while others appear to have retained their native niches (Mori et al., 2020). The global endangerment of many parrot species in their home ranges provides special urgency to understanding how parrots acclimatize and thrive under novel environmental conditions.

We focus on two parrot species that were introduced to southern California from Mexico: the Red-crowned Parrot (*Amazona viridigenalis*) and the Lilac-crowned Parrot (*Amazona finschi*). They are sister species, and are allopatric in their native range, occurring on opposite coastal slopes of Mexico (Figure 1). In 1963, Bill Hardy, then curator of the Moore Laboratory of Zoology at Occidental College, first documented several pairs of Red-crowned Parrots in Los Angeles during a survey of introduced bird species (Hardy, 1973). By the 1970s, the population had grown to around 50 birds (Froke, 1981) and by the 1990s that number had swelled to over 1000 (Garrett, 1997). The current estimate places the number of Red-crowned Parrots at over 3000 birds in all of southern California (Garrett, 2020), but this number is likely conservative. Lilac-crowned Parrots became established somewhat later, perhaps in the 1980s, and now number around 800 birds (Garrett, 2020). Both species are considered endangered in their home ranges in Mexico, with evidence for population decline due to habitat loss and trapping for the pet trade (Forshaw & Knight, 2017). Thus, even in their introduced ranges, their numbers and ecological circumstances are of keen conservation interest.

We tested for niche shifts in Red-crowned and Lilac-crowned Parrots using environmental data (e.g. climate and habitat variables) associated with community science records. What is known about the natural ecologies of these species in Mexico suggests they have different native niches, with Lilac-crowned Parrots inhabiting tropical dry forests (Renton, 2001) and higher elevation coniferous forests (Allen et al., 2016; Moore, 1937), while Red-crowned Parrots occupy lowland sub-deciduous tropical forest (Enkerlin-Hoeflich & Hogan, 1997). The two species are sometimes seen in mixed species flocks in urban southern California, suggesting niche overlap. There are anecdotal reports that Lilac-crowned Parrots use natural forests in mountains near urban valleys and at least one confirmed nest of a Lilac-crowned Parrot from 1700 m elevation in the San Gabriel Mountains near Los Angeles (Allen et al., 2016). While conditions in southern California seem quite different from their native range, introduced populations of *Amazona* parrots across the United States also appear to cluster in southern latitudes (e.g. Texas and Florida), suggesting some environmental constraints on their establishment (i.e. niche conservatism).

We sought to address several questions about the realized niches of native and introduced Red-crowned and Lilac-crowned

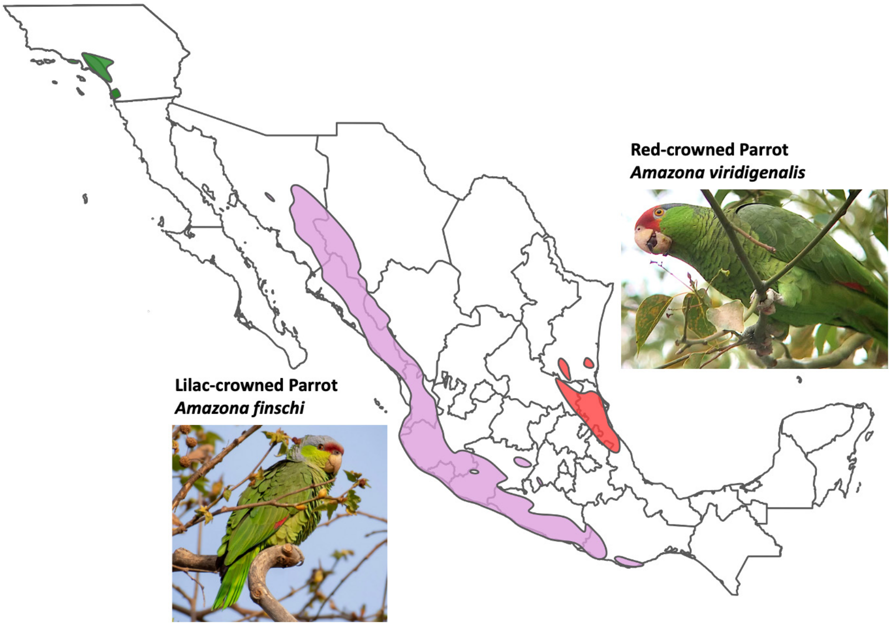

FIGURE 1 Native Mexican range for Lilac-crowned Parrot (purple) and Red-crowned Parrot (red) and introduced range for both species (green) in southern California. Data for species ranges were drawn from eBird status and trends data. Red-crowned Parrot photographed by B. Ramirez at Occidental College, Los Angeles, California. Lilac-crowned Parrot photographed by M. Mutchler in Los Angeles, California.

Parrots in southern California: (1) Do the two species have different environmental niches in their native ranges in Mexico? (2) Are any differences in their native niches mirrored in their introduced, urban niche in southern California? (3) Do introduced parrots show evidence of a niche shift resulting from their introduction to cities in southern California? (4) Can the environmental niches of two other extralimital populations of Red-crowned Parrots in Texas and Florida point to any unifying explanations behind successful parrot introductions in the mainland United States? To test for and quantify any niche shifts, we used a variety of the latest techniques (Bates & Bertelsmeier, 2021), including both species distribution models as well as ordination approaches that visualize the realized niche in multidimensional environment space (E-space; sensu Soberón & Nakamura, 2009) compared to the total range of environments available within the dispersal distance of the occurrence records. For our environmental data, we focused on temperature, rainfall, and habitat features like greenness and tree cover, which are known to be important to the seasonal ecology and life history of these species.

2 | METHODS

2.1 | Georeferenced observations

Community science data are an effective way to collect large-scale species abundance data (Chandler et al., 2017; Dickinson et al., 2010; Lee et al., 2020). Our dataset was compiled from two large community-science databases, eBird (Sullivan et al., 2014) and iNaturalist. Despite the large scale of community science data, it is crucial to consider the challenges associated with the raw data quality including uneven sampling, spatial bias, temporal bias, and variation in observer skill level (Geldmann et al., 2016; Isaac et al., 2014). As described below, we accounted for these factors by filtering and processing observations from each database to create a more consistent observation method and an overall more unbiased high-quality dataset (Johnston et al., 2021; Kosmala et al., 2016).

To collect locality information from the native range, we downloaded observations from eBird for both Red-crowned and Lilac-crowned Parrots in their respective ranges over the last 20 years. We removed points outside of the native distributions because they have been introduced to several urban centres in Mexico as well as the U.S. and also filtered the observations to only include those with the native exotic code. This resulted in a final dataset with 6534 native *Amazona* observations (748 Red-crowned Parrots and 5786 Lilac-crowned Parrots).

In their non-native southern California range, the two species are often found together, making identification more difficult. We thus focused on photo-vouchered observations in iNaturalist. To collect photo-vouchered observations with precise GPS locations, we started a project on the community science platform iNaturalist called the Free-Flying Los Angeles Parrot Project (FLAPP), which collected parrot records with unmasked locations from Los Angeles, Orange, Riverside, San Bernardino, San Diego, and Santa Barbara counties. Observations from 2001 to 2022 were ingested into FLAPP for a total of 2330 *Amazona* observations (some photos contained multiple individuals). Because the two species are similar and hard to identify, even with good photos, we supplemented the iNaturalist identifications with our own determination based on diagnostic phenotypic characters (Renton, 2020) of cere and orbital colour (dark in Lilac-crowned), iris colour (darker orange in Lilac-crowned), crown colour and extent (maroon and short in Lilac-crowned), and breast feathering scalloping (very scalloped in Lilac-crowned). The final species identification was determined when two researchers on our team independently agreed after evaluating the phenotypic characters, and we updated the species ID on iNaturalist. We removed 37 hybrids, resulting in a final dataset with 517 Red-crowned Parrots and 372 Lilac-crowned Parrots.

For comparative analysis, we also collected and filtered observations from eBird for introduced populations of Red-crowned Parrots in Texas ($n=1136$) and Florida ($n=193$; Epps, 2007). We used eBird data for these populations to increase sample size and because Red-Crowned Parrots are the overwhelmingly dominant species in these areas. There is debate whether the Texas population in the Lower Rio Grande Valley is of native or introduced origin, but it seems likely that human introductions were at least partly responsible for its establishment (Kiacz et al., 2021). To account for variability in detectability, for all eBird data, we filtered observations based on effort variables for more consistent observation methods. Following eBird best practices, checklists were restricted to less than 5 h long and 5 km in length (Strimas-Mackey et al., 2020). Additionally, only observations with media were kept to avoid potential misidentifications.

2.2 | Geospatial environmental data

Our environmental data consisted of 24 variables at a resolution of 1 km^2. These variables included: 19 temperature and precipitation variables collected and extrapolated from weather stations (http://www.worldclim.org; Fick & Hijmans, 2017) plus elevation, which are used to assess the climatic variability in a region and are frequently used in habitat suitability models. Many organisms are limited by temperature extremes, especially outside the tropics (Khaliq et al., 2017), and prior field studies have suggested an important role for seasonality of rainfall to the ecology of these species (Renton & Salinas-Melgoza, 2004). To supplement climate data, we included four habitat variables derived from orbiting satellites over the years 2001–2005 as potential measures of vegetation required for foraging, nesting, and roosting of parrots: (1) the normalized difference vegetation index (NDVI), which describes vegetation greenness; (2) NDVI annual standard deviation (NDVI_std), which describes greenness seasonality; (3) percentage tree cover (tree) from the Moderate Resolution Imaging Spectroradiometer (MODIS); (4) and a variable collected by the Quick Scatterometer (QuikSCAT), a low Earth-orbiting satellite designed to measure sea winds from microwave backscatter. Terrestrial QuikSCAT data can relate to tree canopy structure and moisture content (Frolking et al., 2006), but in the context of this study QuikSCAT most likely relates to urbanization, with larger values (more backscatter) in urban areas compared to natural areas (Nghiem et al., 2009; Sorichetta et al., 2020).

2.3 | Tests for niche divergence and niche shifts

We first visualized niche shifts in all univariate climate and habitat variables with box plots. We tested for shifts by assessing the best-fit general linear model of divergence with the Akaike Information Criterion (AIC) using R 4.2.1 (R Core Team, 2022). Models tested include an effect of species (Red-crowned vs. Lilac-crowned), range (native vs. introduced), species + range, species + range + an interaction (species × range), and the null model of no shift. For PCA and species distribution models, we tested for correlations among climate and habitat variables and retained only one variable from groups of variables with greater than 70% correlation (Dormann et al., 2013). For our map-based method, we ran reciprocal species distribution models by implementing Maxent through the R package 'ENMeval' (Kass et al., 2021). We created sets of models for both native ranges in Mexico using the following Maxent feature classes and combinations: linear, quadratic, hinge, linear quadratic, linear hinge, quadratic hinge, and linear quadratic hinge. The regularization multiplier was also set from 0.5 to 4 in half steps and from 5 to 10 to incorporate a penalty for adding additional parameters to the model. To control for spatial autocorrelation, we used block spatial cross-validation to partition our presence and background data into four groups based on longitude and latitude and we removed duplicate observations from the same grid cell before running the models to avoid duplicate sampling of the same data (Muscarella et al., 2014). From each set, the model with the highest Continuous Boyce Index (CBI) value was chosen as the best-fit and each was used to calibrate the projection of suitable habitat into southern California. We calculated the total area of habitat suitability per model by using the minimum training presence (MTP) of the native Mexican ranges, which uses the lowest suitability value of an actual observation point as a lower threshold and creates a binary model (suitable or not) to calculate the total suitable area.

To conduct quantitative tests for niche overlap between both regions for each species, we ran a PCA-env (Broennimann et al., 2012) using the R package 'ecospat' (Di Cola et al., 2017), which conducts a PCA with presence and background environmental conditions from both ranges. We created buffered regions that represented typical dispersal distances for the *Amazona* parrots to capture a realistic representation of the environmental conditions the parrots encounter in each population. To encompass all the parrot observations in each region, our buffer was 105 km in the native ranges and 60 km in the shared introduced range. Within our buffered regions of dispersal capacity, we created 10,000 randomly sampled pseudo-absences to help delimit the realized niche denoted by the presence points. PCA scores were found for the native and introduced ranges and were compared using occurrence density grids of 100 × 100 km cells. A kernel density function was applied to these cells to avoid any inaccurate estimates of species densities. An occurrence density was found for both the native and introduced ranges for both parrot species and was used to assess the environmental overlap between these ranges.

Using environmental space to measure these niche dynamics is beneficial because it takes climate availability and analogy into account better than geography in space would (Di Cola et al., 2017). The observed niche overlap was then evaluated using Shoener's *D*, and niche conservatism was tested using a niche equivalency test and a similarity test. The niche equivalency test assesses whether the niche overlap is constant between random niches that are created by reallocating pooled species occurrences. The niche similarity test determines whether the native niche is more similar to the introduced niche than a random niche created within the introduced range. Niche dynamics were also quantified by finding the proportions of the non-overlapping native niche (unfilling), non-overlapping introduced niche (expansion), and the overlapping of both (stability) for each species between both regions. For comparative analysis of southern California *Amazona* with Red-crowned Parrots in Florida and Texas, we created additional PCA plots and univariate box plots including all four mainland US populations.

3 | RESULTS

3.1 | Native ranges are divergent and introduced ranges overlap in environmental niche space

A PCA of 12 retained, uncorrelated environmental variables indicated that the first two principal component axes (PC1 and PC2) could explain 56% of the total environmental variation across all occurrence points from the native ranges and southern California introduced populations of Red-Crowned and Lilac-crowned Parrots (Figure 2a). The variables with the highest (absolute value) loadings on PC1 were temperature, greenness (NDVI), precipitation, and tree cover, while PC2 was primarily associated with precipitation and temperature (Table S1). Visualizing both occurrence and background (i.e. geographically accessible) points for native and introduced populations of both Red-crowned and Lilac-crowned Parrots revealed that the two species have divergent and non-overlapping environmental niches in their native ranges (Figure 2a). The niches of the introduced populations overlap, are divergent from both native niches, and occupy a much smaller portion of environmental space.

Univariate differences provide a finer-grained view of environmental divergence between species and between native and introduced niches (Figure 2b; Figure S1). For example, the range of values for vegetation greenness, annual mean temperature, and temperature of the wettest quarter that are experienced by the introduced southern California populations are almost entirely non-overlapping with the range of these environmental variables experienced in the native ranges of both Red-crowned and Lilac-crowned Parrots (Figure S1). Additionally, there are less severe differences between the native and introduced ranges in environmental variables such as temperature seasonality, isothermality and mean temperature of the driest month. In contrast, there are no significant differences between the inhabited environmental conditions for the two species in the introduced southern California populations. Testing these observations with a model-based approach, the species + range + (species × range) interaction model was the best fit for 20 out of 24 individual climate and habitat variables and both retained PC axes. This interaction term (species × range) means that species are not only shifting their niche values in the move from their native to introduced ranges, but values for the two species are also becoming more similar in their introduced range. The species + range model best explained 3 variables, and the region model best explained one variable (Figure S1).

3.2 | Native distribution models fail to predict occupancy in the introduced ranges

Projecting habitat suitability from the native range of each species onto southern California revealed little predicted suitable habitat in the urban Los Angeles area, where thousands of parrots have now become established (Figure 3). There was high model performance for the species distribution models, with CBI values greater than 0.9 for both the Red-crowned and Lilac-crowned Parrots (Table S2). After thresholding based on the minimum suitability value of the native ranges, the Red-crowned Parrot native model had 145,786 km^2 (36%) above the MTP of 0.035 (i.e. the lowest suitability value where a parrot was found in the native range) and 20,384 km^2 (3.3%) in the southern California projection (Figure 3a). The Lilac-crowned Parrot native model had 473,773 km^2 (17.3%) above the MTP (0.003) and 15,048 km^2 (2.5%) in the southern California projection (Figure 3b). Despite each of these projections having large areas above the MTP, none of these values were greater than 0.25 and 0.16 suitability for Red-crowned and Lilac-crowned Parrots respectively, indicating that the introduced environment was deemed much less suitable than the native environment with 0.24 and 0.23 mean suitability respectively. Niche models for the native ranges of the two species also failed to predict large amounts of high suitability in the other species' range, suggesting that the niches of the two species are divergent (Figure S3).

3.3 | Quantitative tests for niche shifts

There was no observed overlap between the native and introduced niches of the Red-crowned Parrot (Schoener's $D = 0$), rejecting the hypothesis that the niches are the same (Figure S2a). The test of niche similarity (Figure S2a) showed that observed environmental differences between the inhabited native and introduced niches for Red-crowned Parrots failed to reject the null hypothesis of background environmental differences between these areas (the peak of the null distribution also centred near zero, resulting in the failure to reject the null hypothesis; $p = 1$). There was no overlap between native and introduced niche space (Figure 4a). For the Lilac-crowned Parrots, the native and introduced niches also had no overlap (Schoener's $D = 0$), allowing us to reject the hypothesis of niche equivalency (Figure S2b). For the test of niche similarity (Figure S2b), the native and introduced niches, though highly divergent, were again similar to the differences between their background areas, reflected in the failure to reject the null hypothesis ($p = 1$). There was no overlap between native and introduced niche space (Figure 4b).

3.4 | Florida and Texas populations show different kinds of niche shifts

PCA plots and univariate box plots including two other introduced populations of Red-crowned Parrots in Texas and Florida

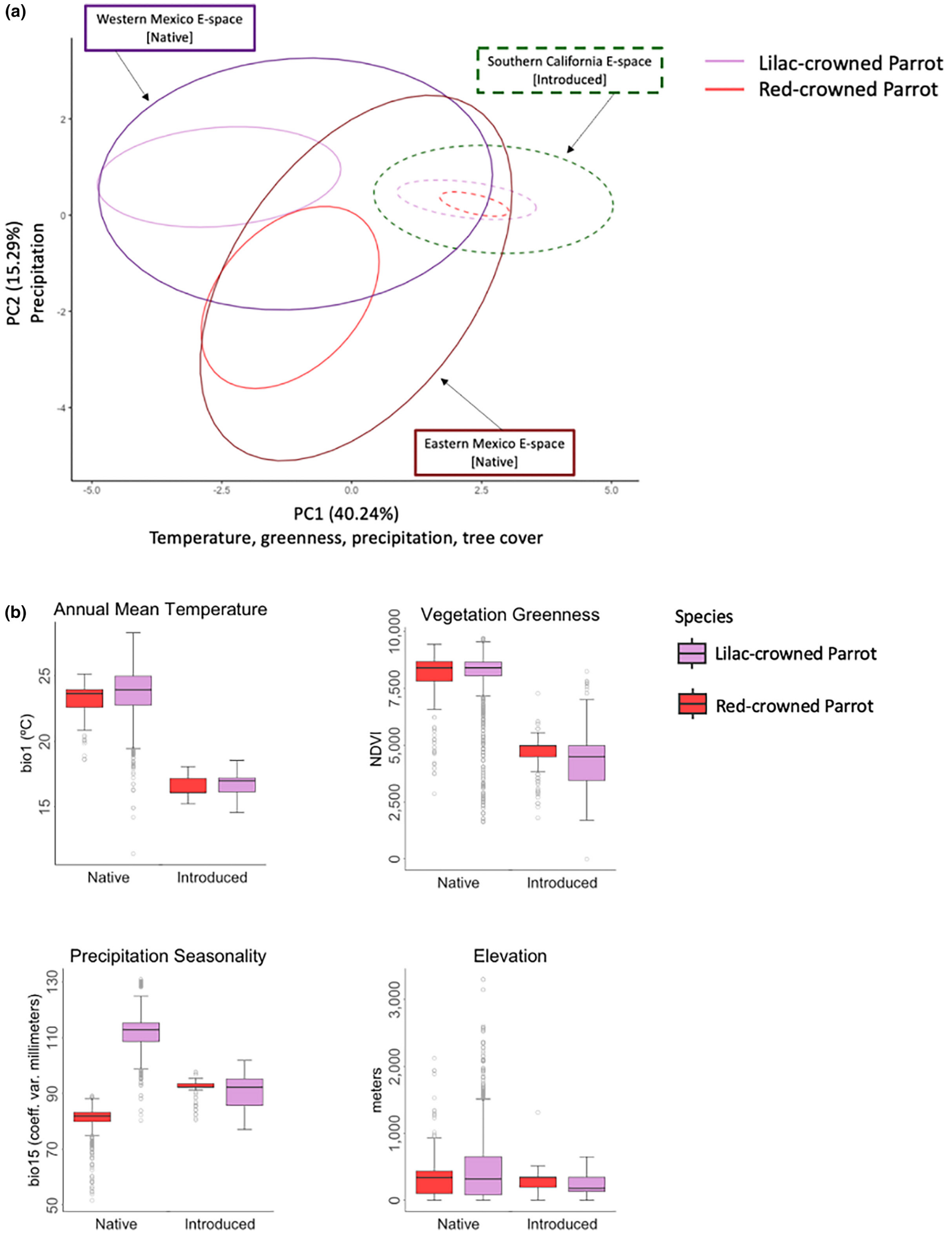

FIGURE 2 Environmental niche divergence between Red-crowned and Lilac-crowned Parrots in their native and introduced ranges. (a) Plot of divergence in environmental space (E-space) for the first and second principal component (PC) describing 56% of the total variation. Biological interpretations of the PC axes are derived from variable loadings in Table S1. Ovals represent the 95% confidence ellipse of the occurrence points (red and purple lines) and the background points, which reflect the available environmental space in the flying distance of the occurrence records. (b) Comparing the distributions of inhabited conditions by introduced and native populations. For each panel, the standard interpretation of the given BioClim variable is the plot title.

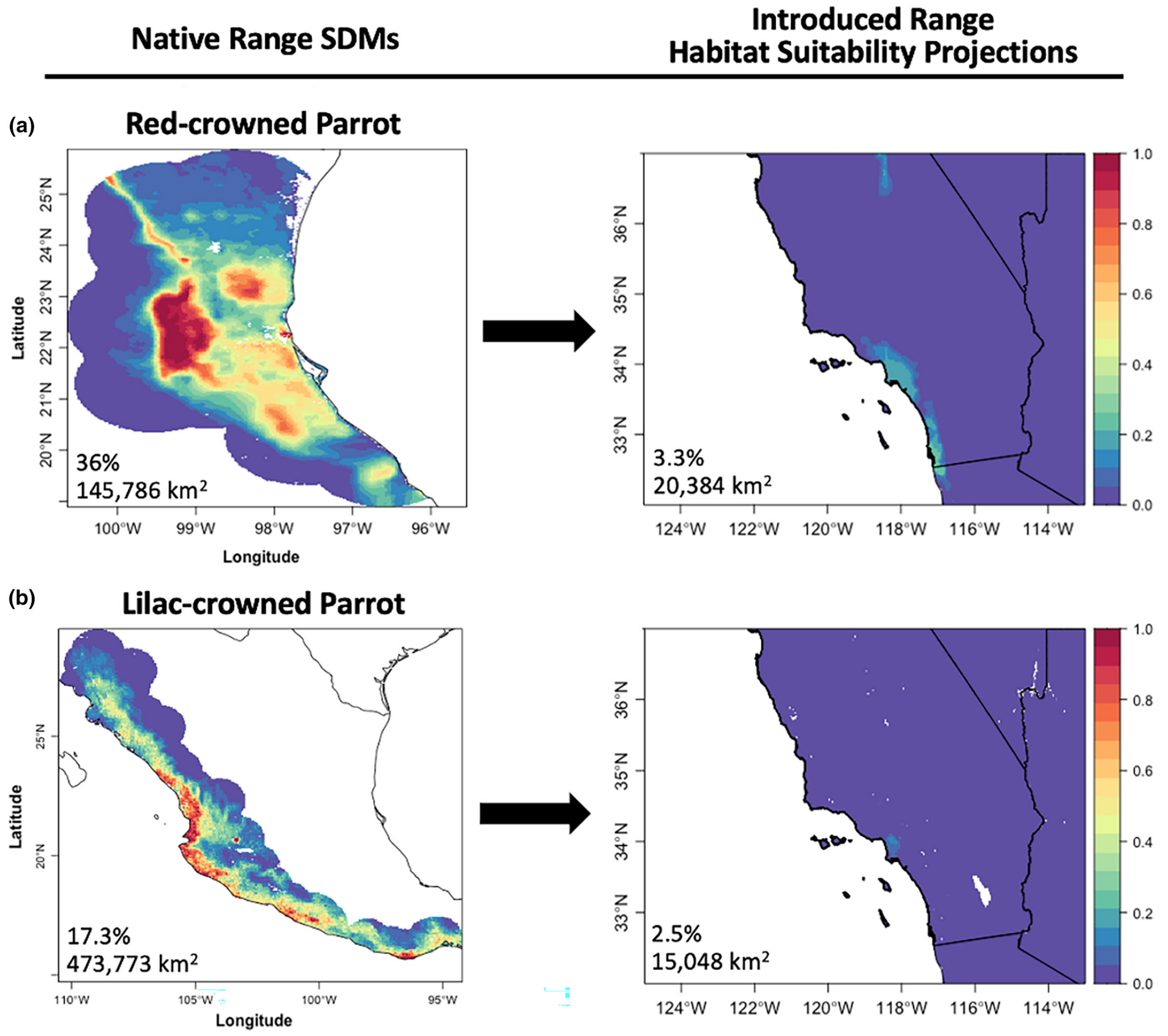

FIGURE 3 Reciprocal species distribution models for the (a) Red-crowned and (b) Lilac-crowned Parrots in their native ranges in Mexico, separately projected onto their introduced range in southern California. Percentages and the total area of suitable habitat quantified by thresholding with the minimum training presence (MTP) are listed for each respective model. Maximum suitability scores did not exceed 0.25 and 0.16 for the Red-crowned and Lilac-crowned Parrots respectively, showing much less suitable habitat in the introduced region.

also show evidence for niche shifts between their native and introduced populations (Figure 5a). Surprisingly, the Texas population, which is geographically proximate to the native population, shows evidence for a large niche shift. However, the portion of the available environmental space that is occupied by the Texas population is the most similar to the native environmental conditions, suggesting a measure of niche conservatism in the niche of this population. In contrast, the introduced Florida population inhabits conditions that are the most similar to the native range of Red-crowned Parrots. Despite the fact that Florida includes some environmental conditions that closely match the realized native niche, the introduced Florida parrots do not inhabit those areas, instead preferring places that fall mostly outside the realized niche of native Red-crowned Parrots.

Univariate box plots show that the niche of the introduced southern California parrots differs in several environmental characteristics from the introduced Texas and Florida populations (Figure 5b). For example, the annual mean temperature and the extreme minimum temperature experienced by the southern California parrots are much colder than the Texas and Florida populations, which are more similar to the native range. Also, the annual precipitation and extreme minimum precipitation experienced by the southern California population is much lower than Florida and Texas populations.

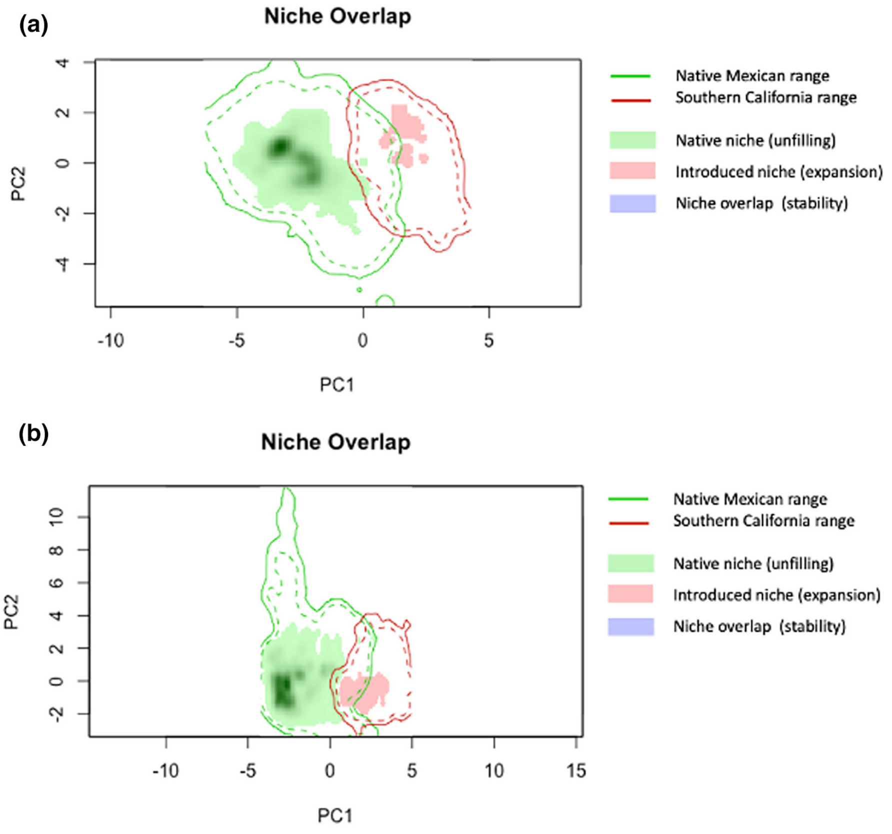

FIGURE 4 Observed area of niche unfilling (native range), expansion (introduced range), and stability (overlap) for the (a) Red-crowned and (b) Lilac-crowned Parrots. No niche overlap is observed for either species, dashed lines represent the extent of background environmental variation for each region and the grey shading represents the occurrence densities within the native range.

4 | DISCUSSION

As populations of introduced parrots appear and expand in cities around the world, it has not been clear whether these establishments typically involve niche shifts into novel conditions or whether parrots tend to establish in areas similar to their home ranges, consistent with niche conservatism. Because of these extensive introductions and the conservation concerns associated with many parrot species, characterizations of both their native and introduced niches are urgently needed. Our results show, first, that the native environmental niches of Red-crowned and Lilac-crowned Parrots, which are allopatric in their home ranges but now occur together in urban Los Angeles, differ significantly (Figure 2a; Figure S3). In their native ranges, Lilac-crowned Parrot habitat is more seasonal in its precipitation and greenness compared with that of Red-crowned Parrots. This is consistent with observations that Lilac-crowned Parrots also have seasonal movement patterns and diet-switching (Renton, 2001; Salinas-Melgoza & Renton, 2005). The link between our quantification of the native niches and observed differences between species habitats and life-histories provides a measure of confidence that at least some of the environmental characteristics we measured capture aspects of the habitat that are biologically meaningful to the parrots.

In contrast to the differences in their native ranges, the two species now inhabit a novel, shared environmental niche in urban southern California, which covers a narrower portion of total environmental space than the native range of either species. As we discuss in more detail below, this new realized niche space is both colder and has less tree cover and rainfall than the native niches. Nevertheless, introduced parrots appear to be thriving. While climate might pose some limits on where successful introductions occur (see below), it appears that *Amazona* parrots either have broad fundamental niches or have expanded their fundamental niche through an ability to exploit the novel resources offered in cities.

4.1 | Introduced southern California parrots have shifted into the same urban niche

Niche visualizations from species distribution models, ordination approaches in multidimensional environmental space, as well as univariate box plots, point to major environmental niche switches for both Red-crowned and Lilac-crowned Parrots upon their introduction to southern California. When projecting the native distribution model onto the landscape of southern California, there is very little identified suitable habitat in southern California, emphasizing the basic niche dissimilarity between regions. It is, however, interesting that the only areas with any predicted suitability are in parts of southern California where the parrots are found. We discuss evidence for niche conservatism in more detail below, but this result lends support to the theory that, even in cases where native and introduced niches do not match, the distance to the 'niche margin' might still be an important factor in the establishment of successful introductions (Broennimann et al., 2021).

Not only have the parrots' niches shifted in the transition to urban southern California, but the niches of the two species have

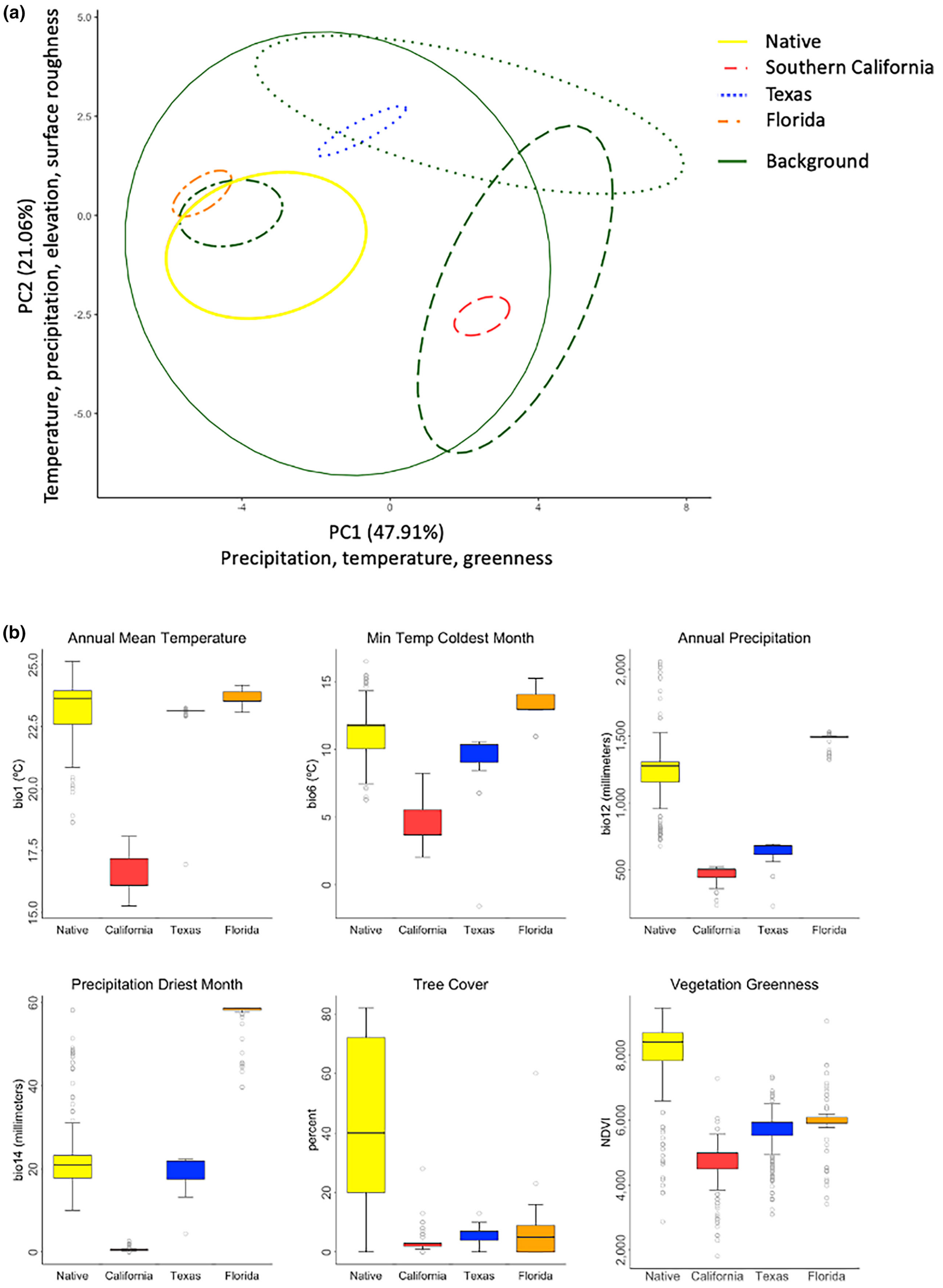

FIGURE 5 Comparison of niche shifts in various introduced Red-crowned Parrot populations. (a) Plot of divergence in environmental space for the first and second principal component (PC) describing 69% of the total variation. Ovals represent the 95% confidence ellipse of the points. Each green oval represents the breadth of environmental conditions (background) of each corresponding region shown by line type. (b) Univariate divergence of environmental variables between each region.

also converged across nearly every climate and habitat variable. This is not merely the result of being forced into the same set of environmental conditions in the introduced range due to lack of options. While the available background environment is narrower in southern California, it is still much wider than the realized niche of the introduced populations, meaning that there is much potential E-space in southern California left unoccupied (Figure 2; Figure S1). For example, there are forested mountains within easy flying distance of the cities. These mountains are in some ways more environmentally similar to the native ranges of both species, but they are infrequently used by the parrots. It has been suggested that Lilac-crowned Parrots might make greater use of natural forests in the mountains adjacent to urban valleys in Los Angeles (Allen et al., 2016), but we found no evidence for consistent habitat or elevational differences between species in southern California based on occurrence records.

Our results add to a growing body of evidence that introduced species can experience rapid niche shifts beyond what appears possible in their native ranges (Wiens et al., 2019). Yet, prior evidence for niche shifts by introduced parrots has generally been mixed (Ancillotto et al., 2016; Mori et al., 2020; Strubbe et al., 2015). Introduced parrots seem to do well in milder climates where the minimum January temperature does not dip below freezing (Uehling et al., 2019), although there are examples of introductions in colder climates (Postigo et al., 2019; Strubbe & Matthysen, 2009). Our study extends this conclusion by showing that introduced parrots are not simply experiencing a more benign subset of their native environmental niches, as has been shown in non-native European birds (Strubbe et al., 2013). Rather, some environmental conditions fall entirely outside of the range of variation they experience in their native ranges in Mexico. For example, for Red-crowned Parrots, the driest month in southern California is significantly drier than any portion of their native range. The timing of precipitation in southern California is also different, with low rainfall overall and a winter rainfall regime rather than summer rains. Artificial irrigation may help close the gap between native and introduced climates, allowing more year-round vegetation in southern California cities than expected given its natural precipitation levels. Further, an 'urban oasis' effect could partly explain why introduced parrots do not seem to be spreading beyond urban centres. Their apparent confinement to the city fits with the conclusion from a large comparative study of introduced species (Abellán et al., 2017), which suggested that climatic mismatch constrains geographic spread from the point of initial colonization, whereas species-specific life-history factors are more important to their initial establishment (Luna et al., 2017; Sol et al., 2017).

4.2 | Idiosyncratic niche shifts across introduced US parrot populations

We did not attempt a full exploration of the niche dynamics of the Florida and Texas populations, but our comparative results help place the southern California niche shifts into context and suggest two conclusions. One, each introduction to a new area seems to result in a unique kind of niche shift, similar to findings from other species with multiple geographic introductions (Pili et al., 2020; Tingley et al., 2016). For instance, the Texas population of Red-crowned Parrots is so geographically close to the native range that some have considered whether it might be a natural range expansion (summarized in Kiacz et al., 2021). Still, our results suggest that the Texas population inhabits a divergent environmental niche from the native population, one with higher temperatures and less seasonal rainfall, combined with much less vegetation greenness and tree cover, as expected for an urban area. At least in comparing environmental niche characteristics between the introduced ranges, the Texas population appears more like the introduced southern California population, although the California niche shifts are more extreme across individual variables. Meanwhile, the introduced Florida population occupies an environmental niche with much higher, year-round precipitation compared with both native and introduced populations, although tree cover and greenness are still comparatively low. Together, these results indicate that *Amazona* parrots are capable of thriving under a wide range of environmental conditions that extend far beyond those inhabited in their native ranges. Furthermore, our results do not suggest a single unifying environmental factor explaining their establishment across multiple urban areas, although we did not examine every aspect of the environmental factors affecting parrots.

A second conclusion is that independent mainland U.S. introductions differ in their support for niche divergence and conservatism. While niche shifts are evident in all populations, in this context, niche conservatism implies that the introduced population is found in areas where environmental conditions *more closely match the native range given what is available to them* (McCormack et al., 2010). Niche divergence, in contrast, is supported if portions of the native niche are actually available in the introduced range, but these areas are left unoccupied (i.e. niche unfilling). Occurrence data from the introduced populations we investigated supports a degree of niche conservatism in introduced parrots in southern California and Texas, but niche divergence in the introduced parrots in Florida. The fact that the Florida population shows significant niche divergence drives home the notion that factors other than niche-matching are determining the success of parrot populations in urban areas.

4.3 | Why are parrots doing so well in cities?

The ability of introduced *Amazona* parrots to thrive under novel environmental conditions, though striking, still does not fully explain why they have been so successful in establishing outside their native range, especially in cities. In addition to the populations discussed here, Red-crowned Parrots have also become established in Hawaii and Puerto Rico (Kiacz et al., 2021). It is hard not to notice that these introductions have all occurred in densely populated areas with relatively benign climates. Although our study did not seek to test for the underlying causes of introduction success, we discuss some hypotheses below.

One possible explanation is classic ecological release, where parrots in their introduced ranges suddenly find themselves free of competitors, predators, and diseases that kept their numbers in check in their native ranges, allowing the realized niche to more closely match the fundamental niche (Shwartz et al., 2009). For example, Lilac-crowned Parrots in their native range are apparently limited by both nest predation and food availability (Renton & Salinas-Melgoza, 2004). Though ecological release has mostly been used to explain natural colonizations like those occurring on islands, it has recently been extended to explain both the establishment of invasive species (Herrmann et al., 2021) and recent range expansions of native species (Battey, 2019). However, if ecological release is the key driver of parrots' success in their introduced ranges, and they can clearly adapt to a wide range of environmental conditions, then why are successful introductions only happening in modern times?

A potential answer is that cities have only in the last 100 years provided a resource niche for parrots in the form of fruits and flowers of exotic trees (Garrett, 1998; Garrett et al., 1997; Pruett-Jones, 2021). Non-native trees are a resource that is largely untapped by native birds in Los Angeles (Smallwood & Wood, 2023; Wood & Esaian, 2020). Parrots might even be pre-adapted as 'resource super-generalists' (Blanco et al., 2015), making them more likely to find new food sources (Ducatez et al., 2015), including using bird feeders which are available year-round (Clergeau & Vergnes, 2011). Their intelligence and behavioural plasticity might further allow them to adapt to urban life (Caspi et al., 2022), allowing them to rapidly expand their fundamental niche through behavioural and cultural shifts (Salinas-Melgoza et al., 2013) and exploit urban resources (Klump et al., 2021; Le Louarn et al., 2018; Mori et al., 2013). One key resource being used by parrots are both natural and coincidental human-made cavity nests (Epps & Chatfield-Taylor, 2023), which can create complex biotic interactions between existing cavity-nesting species (Appelt et al., 2016; Hernández-Brito et al., 2021; Romero-Vidal et al., 2023) driven by breeding timing, nesting preferences, and access to nests (Orchan et al., 2013). Introduced parrots might in fact provide a useful model for examining how biodiversity can thrive in complex, urban environments.

If environmental conditions within these cities are within the fundamental niche, and existing untapped resources provide an available resource, then the limiting factor may have been dispersal or the timing of introduction. Humans have kept parrots as pets for hundreds of years, but the organized pet trade ramped up after World War II, especially in the 1960s and 1970s when the illegal importation of wild-caught parrots reached its peak (Guzmán et al., 2007). It was around this time that Bill Hardy began to note *Amazona* parrots in southern California and stories began to emerge of mass release events, which have formed the basis for urban legends about the parrots' origin. Scientifically, this phenomenon is called propagule pressure, quantified as the size and number of independent introductions (Da Silva et al., 2010; Lockwood et al., 2005). Propagule pressure for parrots in large cities has been increasing since the 1960s, which might explain why *Amazona* populations have become established in urban areas over the past 50 years. Meanwhile, despite evidence for broad niche tolerance of native *Amazona*, environmental factors like temperature might be acting as a filter dictating exactly where introduced populations can take hold. This conclusion is bolstered by the paucity of established *Amazona* populations in cities across the central and northern U.S. with severe winters, despite a strong likelihood of similar accidental introduction events in these areas.

4.4 | Conservation implications

Cities might provide critical refugia for parrot species that are threatened by habitat loss in their native ranges (Geary et al., 2021). However, one implication is that when multiple parrot species establish in the same city, they will potentially hybridize, which has implications for conservation. Although Red-crowned and Lilac-crowned Parrots often associate by species in Los Angeles, hybrids have also been noted in iNaturalist. The mechanisms of reproductive isolation between these two species, if any, are unstudied, as well as their potential hybridization with a third established *Amazona* species, the Yellow-crowned Parrot (*A. oratrix*). Given that both species are endangered in their native ranges, and could 1 day benefit from translocation or genetic rescue, it will be important to continue to monitor introduced and established flocks of parrots for conservation potential. The extent of hybridization could impact future decisions to reintroduce birds into their native habitats from introduced stocks. To that end, our continuing community science project on iNaturalist (Free-Flying Los Angeles Parrot Project) can help document observations of both species, as well as any hybrids, and interactions between species. These data, as well as future genetic investigations, will help us understand how niche shifts are affecting the ecology and evolution in this iconic and beloved group of birds.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.280gb5mvg. Note, the coordinates have been obscured in the shared online locality dataset following *Diversity and Distributions*' guidelines to protect the *Amazona* parrots from potential poaching.

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BIOSKETCHES

The Moore Laboratory of Zoology unites vintage museum collections with present day community science and cutting-edge DNA technology. Our mission is to understand how evolution has shaped biodiversity and how organisms cope with environmental change today. The Free-Flying Los Angeles Project is dedicated to understanding how the introduced parrots of southern California are being affected by the consistent anthropogenic influence associated with poaching and a changing environment.

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SUPPORTING INFORMATION

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