Title: Individual identity information persists in learned parrot calls after invasion

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Abstract

Animals can actively encode different types of identity information in communication signals, such as group membership, individual identity, or social status. The social environments in which animals interact may favor different types of information, but whether identity information conveyed in learned signals is resilient or responsive to short-term changes in the social environment is not well understood. We inferred the type of identity information that was most salient in vocal signals by combining computational tools, including supervised machine learning, with a conceptual framework of “hierarchical mapping”, or patterns of relative acoustic convergence across social scales. We used populations of an invasive vocal learning species as a natural experiment to test whether social environments altered over ecological timescales changed the type of identity information that different populations emphasized in learned vocalizations. We compared the social scales with the most salient identity information among native and invasive range monk parakeet (*Myiopsitta monachus*) calls recorded in Uruguay and the United States, respectively. We also evaluated whether the identity information emphasized in invasive range calls changed over time. To place our findings in an evolutionary context, we benchmarked our results with another parrot species that exhibits well-established and distinctive regional vocal dialects that are consistent with signaling group identity. We found that native and invasive range monk parakeet calls both displayed the strongest convergence at the individual scale and minimal convergence within sites. We did not identify changes in the strength of acoustic convergence within sites over time in the invasive range calls. These results indicate that the individual identity information in learned vocalizations was resilient to social environments perturbed over ecological timescales. Our findings point to exciting directions for further research on the responsiveness of communication systems to changes in the social environment over different evolutionary timescales.

1. Introduction

Animals can use communication signals to transmit identity information, including group membership, individual identity, social status, sex, or other social characteristics (Bradbury & Vehrencamp, 1998; Seyfarth, Cheney, Bergman, Fischer, Zuberbühler, et al., 2010). The types of identity information that animals encode in signals may be an outcome of differences in the social environment within or among species. Different types of information may be more or less important for animals to communicate in social environments that can change over ecological or evolutionary timescales (Bergman, 2010; Hobson, 2020; Hobson, Mønster, & DeDeo, 2021; Ramos-Fernandez, King, Beehner, Bergman, Crofoot, et al., 2018).

Vocalizations are well-studied communication signals that can contain identity information. For example, voice cues arising from vocal tract filtering can provide receivers with information about individual identity (Furuyama, Kobayasi, & Riquimaroux, 2016; Prior, Smith, Lawson, Ball, & Dooling, 2018; Rendall, Owren, & Rodman, 1998). However, individuals can also use social learning to modify identity information, such as vocal learning species that can encode both group-level and individual identity information in learned vocalizations. When individuals imitate vocalizations of their social companions, the resulting group-level acoustic convergence can be used to recognize group members (Aplin, 2019; Boughman & Wilkinson, 1998; Nowicki & Searcy, 2014; Sewall, Young, & Wright, 2016). Learned vocalizations with group identity information, such as vocal dialects, have been reported in several vocal learning taxa, including cetaceans (Janik & Slater, 1998; Jones, Daniels, Tufano, & Ridgway, 2020; Nousek, Slater, Wang, & Miller, 2006; Rendell & Whitehead, 2003; Watwood, Tyack, & Wells, 2004), bats (Boughman, 1998), songbirds (Mammen & Nowicki, 1981; Sewall, 2009;2011), and parrots (Martinez & Logue, 2020; Wright, 1996). Individuals can also communicate individual identity information by developing distinctive vocalizations that differentiate them from other individuals. For instance, bottlenose dolphins (*Tursiops truncatus*) and green-rumped parrotlets (*Forpus passerinus*) can use vocal learning to produce distinctive individual signatures used for individual vocal recognition (Berg, Delgado, Okawa, Beissinger, & Bradbury, 2011; Berg, Delgado, Cortopassi, Beissinger, & Bradbury, 2012; Janik, Sayigh, & Wells, 2006; Kershenbaum, Sayigh, & Janik, 2013).

These findings from closely related taxa suggest that changes in the social environment can influence the identity information that animals encode in learned vocalizations. For instance, living in large social groups or interacting repeatedly with many different individuals may favor signaling individual identity information (Pollard & Blumstein, 2011; Seyfarth et al., 2010; Tibbetts & Dale, 2007). However, the degree to which identity information encoded in learned communication signals dynamically responds to changes in the social environment is not well understood. To test whether identity information in vocalizations is resilient or responsive to short-term changes in the social environment, we need two analytical approaches: a way to quantify the relative salience of different types of identity information in learned signals, and comparisons of identity information across groups with different social characteristics.

First, new tools are needed to better quantify the salient types of information in vocalizations. Computational approaches like machine learning can be applied within a conceptual framework that links patterns of vocal convergence to identity signaling. Individuals should use vocal learning to converge on vocalizations across different scales of social organization (Smith-Vidaurre, Araya-Salas, & Wright, 2020), and such vocal convergence should yield “hierarchical mapping” patterns, which are patterns of relative acoustic convergence that vary across social scales (Bradbury et al., 1998). To evaluate hierarchical mapping patterns, we can use machine learning tools to quantify relative acoustic convergence over different social scales, for example, from individuals to flocks or regional populations. From hierarchical mapping patterns, we can use the social scale with the strongest relative acoustic convergence to infer the most salient type of identity information encoded in vocalizations.

Second, we need to compare hierarchical mapping patterns among groups with distinct social environments to test whether identity information in learned vocalizations is resilient or responsive to changes in the social environment. We can leverage different types of natural experiments for this comparison, including species invasions, which can cause founder effects that influence traits transmitted by genetic inheritance and by social learning in invasive populations (Aplin, 2019; Dlugosch & Parker, 2008). Biological invasions should also perturb the social environment, particularly at early stages, due to changes in population size and the disruption of population contiguity with respect to original native range populations. Social perturbation could be reduced by the gradual re-establishment of social environments similar to those in undisturbed populations, or could persist after the early stages of population establishment. For example, invasive range populations should be small when newly founded and then can either remain small, grow to sizes comparable to source populations in the native range, or outstrip source populations (Blackburn, Pysek, Bacher, Carlton, Duncan, et al., 2011). Reduced population sizes may change the social environment, such as limiting the overall number of individuals available for social interactions, which could alter the cognitive costs of social recognition for receivers (Sewall et al., 2016; Tibbetts et al., 2007), and in turn, alter the type of identity information that signalers convey in learned vocalizations compared to the native range.

In this study, we focused on native and invasive range populations of monk parakeets (*Myiopsitta monachus*) to test how changes in the social environment due to invasion could cause changes in the type of identity information encoded in contact calls. Parrots are suitable for this research because they can use social learning to both acquire and modify contact calls (Bradbury & Balsby, 2016). Monk parakeets in particular are also suitable because they have established new populations worldwide through the pet trade since the late 1960s, enabling comparisons between native and invasive range populations. The independently established invasive range populations share a common origin, with the majority of these populations stemming from native range populations in Uruguay and the surrounding region of northern Argentina (Edelaar, Roques, Hobson, Goncalves Da Silva, Avery, et al., 2015; Hobson, Smith-Vidaurre, & Salinas-Melgoza, 2017; Russello, Avery, & Wright, 2008; Smith-Vidaurre, 2020). We used invasive range populations in the United States (U.S.) as independent experimental replicates of social environments perturbed over ecological timescales compared to native range populations in Uruguay.

We used call recordings to infer which type of identity information was most salient in learned monk parakeet vocal signals. We used this approach on both native and invasive range calls to test whether the type of identity information was the same or differed between the native and invasive ranges. We expected that if populations had recovered from the invasion process, then the type of identity information in invasive range calls would not change. However, if the invasion process was sufficiently disruptive, then we expected that invasive range parakeets would diverge from the type of identity information used in the native range. We placed our results in context by benchmarking against another parrot species with strong call convergence at higher social scales and distinctive vocal dialects. Our integration of quantitative approaches with a conceptual framework of identity information encoding can be used to evaluate learned identity signaling more broadly across taxa. Together, our rigorous computational approach and comparisons provide new insight into how identity information in learned vocal signals is resilient or responsive to the social environment over ecological and evolutionary timescales.

2. Methods

2.1 Recording contact calls

We recorded contact calls from native range monk parakeets in 2017 at 37 sites across 7 departments in Uruguay in our previous work (Smith-Vidaurre et al., 2020). Our invasive range dataset included contact calls recorded at 26 sites across 5 states in the U.S. in 4 different sampling years: 2004, 2011, 2018, and 2019. In 2004, invasive range contact calls were recorded in Connecticut, Florida, Louisiana, and Texas (calls were provided by Buhrman-Deever, Rappaport, & Bradbury, 2007). We recorded parakeets in Texas and Louisiana in 2011, Arizona in 2018, and Texas again in 2019. For our temporal analyses below, we relied on calls that we recorded in Texas in 2004, 2011, and 2019 (3 sampling years), and calls recorded in Louisiana in 2004 and 2011 (2 sampling years, see supplementary section 1).

Recording sessions in 2004 used Marantz PMD670 or PMD690 recorders with Sennheiser ME67K6 shotgun microphones, and these recordings were digitized at 48000 Hz and 16 bit depth (Buhrman-Deever et al., 2007). In all other recording sessions we used Marantz PMD661 MKII and PMD660 solid state recorders, Sennheiser ME67 long shotgun microphones and foam windscreens, and we digitized our recordings at 44100 Hz sampling rate and 16 bit depth (Smith-Vidaurre et al., 2020; Smith-Vidaurre, Perez-Marrufo, & Wright, 2021). All recorded individuals were unmarked, with the exception of a few marked individuals in the native range (Smith-Vidaurre et al., 2020).

Figure 1:

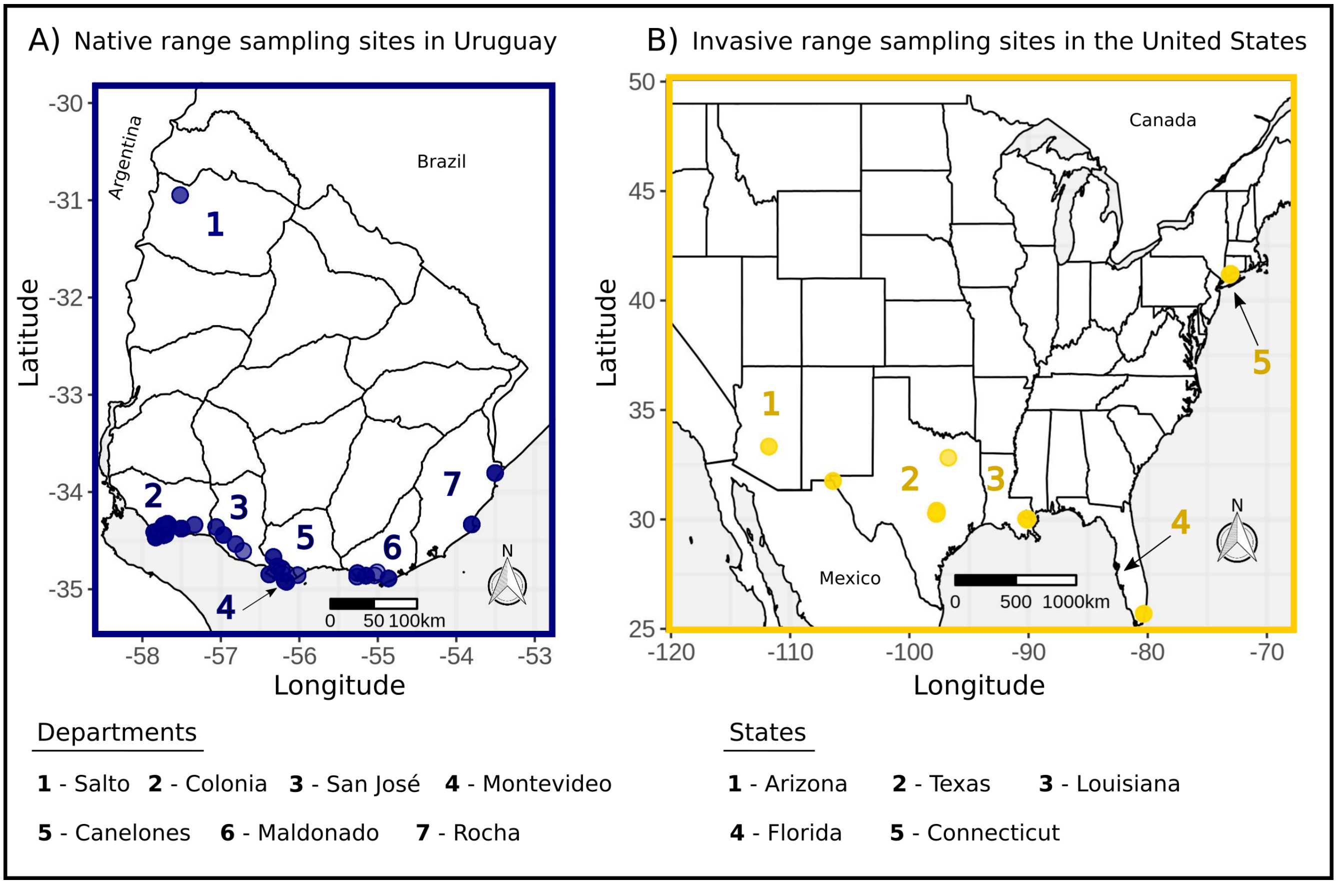

Figure 1: Map of call recording sites for (a) native range populations in Uruguay and (b) invasive range populations in the United States (U.S.). We recorded parakeets across 7 departments in Uruguay and 5 states in the U.S. Our geographic sampling was more contiguous in the native range, which reflected the natural contiguity of populations across the southeastern coast of Uruguay, compared to the more geographically isolated populations in the U.S. invasive range.

2.2 Pre-processing contact calls

We manually selected contact calls from our field recordings. For our invasive range recording sessions in later years, we selected contact calls using Raven version 1.4 (The Cornell Lab of Ornithology Bioacoustics Research Program, 2014), consistent with native range call selection in Smith-Vidaurre et al. (2020). The previously published invasive range calls from 2004 were provided as clips of original recordings (Buhrman-Deever et al., 2007). We performed pre-processing for all invasive range calls, including the 2004 clips, with the warbleR package in R (Araya-Salas & Smith-Vidaurre, 2017) to implement the same quality control pipeline we had previously used for native range calls (supplementary section 1, Smith-Vidaurre et al., 2020;2021). Our quality control criteria included calls with signal to noise ratios of 7 or higher (e.g. calls that were at least 7 times louder than background noise) that also did not display loud signals or other background noise that overlapped with call structure.

2.3 Social scales represented in our contact call datasets

We obtained calls at two different social scales for the purposes of this study: the individual scale, and a group scale that represented a higher level of social organization. To determine call convergence at the individual scale, we repeatedly sampled known individuals to obtain multiple exemplar calls produced by the same individual. This individual-level dataset included 229 total calls from 8 native range birds (3 marked, 5 unmarked) recorded at 3 different sites in 2017, and 9 invasive range birds (all unmarked) recorded at 7 different sites in either 2004, 2011, or 2019 (see Table A5 in Smith-Vidaurre et al. (2021)). Each individual was recorded at one site only, and because the birds we recorded were generally unmarked, we recorded repeat calls from particular individuals while the calling bird was producing multiple calls within a short period of time (e.g. a few minutes (Smith-Vidaurre et al., 2020)).

After pre-processing calls, our individual scale dataset included a median of 10 (range: 4 - 25) calls for the native range individuals and a median of 12 (range: 5 - 28) calls for the invasive range individuals. Our individual scale dataset provided us with sufficient sampling depth per individual to assess acoustic convergence at the individual scale, or individual vocal signatures.

To address call convergence at a group scale, we recorded and compared calls across nesting sites. We used sites as groups because parakeets likely interact frequently with other individuals at the same site. Monk parakeet nesting sites include clusters of single or multi-chambered stick nests that are often built in close proximity (Eberhard, 1998), and parakeets from nearby clusters of nests engage in social interactions (Hobson, Avery, & Wright, 2014), making it difficult to determine the boundaries of a nesting colony. In this study, we characterized recording sites as groups of nests that were geographically separate (the shortest distance among sites was 0.15 km). For our site scale dataset, we obtained a single contact call per bird at each site. Because the parakeets usually produced a single contact call when leaving or returning to their nests, we sampled a single call per unmarked individual at this higher social scale.

After pre-processing, our site scale dataset included 1353 total calls recorded at 63 sites across 37 native and 26 invasive range sites (some invasive range sites were repeatedly sampled in different sampling years, see Tables A3 and A4 in Smith-Vidaurre et al. (2021)). This dataset contained a median of 15 (range: 5 - 53) and 15.5 (range: 5 - 91) calls across the native and invasive range sites, respectively. Since we recorded a single call per unique individual at each site, our site scale dataset did not provide sufficient resolution of individual vocal signatures. However, this dataset allowed us to compare patterns of acoustic variation at a higher scale of social organization over broader geographic areas in each range (Figure 1).

To compare hierarchical mapping patterns between the native and invasive ranges, we used 37 native range sites separated by 0.15 – 513.59 km across 7 departments in Uruguay, and 18 invasive range sites across 5 U.S. states that were separated by 0.74 – 3502.98 km (Smith-Vidaurre et al., 2020;2021). To compare hierarchical mapping patterns over time in the invasive range, we used a subsample of sites in Texas and Louisiana that were recorded in more than one sampling year (see the respective number of sites and geographic distances in supplementary section 1). For our analyses at the site scale, we also generated 3 versions of the site scale dataset to account for the possibility that some calls could represent repeated sampling of the same unmarked individual(s) (supplementary section 2). These 3 datasets included the full dataset of calls, as well as the full dataset filtered by either clustering or visual classification methods to remove calls were likely to represent such repeated individual sampling (supplementary sections 3 - 7). Following call similarity measurements, we performed all subsequent analyses with these 3 site scale datasets to compare the degree of repeated individual sampling in each of the native and invasive ranges, as well as to assess the robustness of our results at this higher social scale.

2.4 Measuring contact call similarity with spectrographic cross-correlation

We used contact call similarity measurements to quantify hierarchical mapping patterns. Call similarity measurements formed the basis for our comparisons of calls within and among social groups to assess hierarchical mapping patterns, or the relative strength of acoustic convergence across different social scales. For instance, if individuals were converging on shared calls within sites, then we expected that contact calls compared within the same site would exhibit high similarity measurements, and lower similarity measurements when compared to calls from different sites. We measured call similarity with spectrographic cross-correlation (SPCC) (Clark, Marler, & Beeman, 1987), which has traditionally been used in studies reporting patterns of acoustic variation consistent with social learning of vocalizations in parrots (Balsby & Bradbury, 2009; Berg et al., 2011; Bradbury, Cortopassi, & Clemmons, 2001; Buhrman-Deever et al., 2007; Eberhard, Zager, Ferrer-Paris, & Rodríguez-Clark, 2022; Guerra, Cruz-Nieto, Ortiz-Maciel, & Wright, 2008; Salinas-Melgoza & Wright, 2012; Salinas-Melgoza & Renton, 2021; Scarl & Bradbury, 2009; Smith-Vidaurre et al., 2020; Wright, 1996; Wright, Dahlin, & Salinas-Melgoza, 2008). We performed SPCC with a Hanning window, a window length of 378 samples, and a window overlap of 90 samples for Fourier transformations, as well as Pearson's correlation method and a bandpass filter of 0.5 to 9kHz (Araya-Salas et al., 2017). Unless otherwise specified, we used these same parameters for subsequent spectrum-based analyses. We conducted SPCC with all calls across the native and invasive ranges, which allowed us to use this similarity measurement in subsequent quantitative assessments of hierarchical mapping patterns.

2.5 Measuring contact call similarity with supervised machine learning

We also measured similarity among monk parakeet contact calls using a supervised machine learning approach that identifies biologically relevant patterns of variation in avian acoustic signals (Humphries, Buxton, & Jones, 2018; Keen, Ross, Griffiths, Lanzone, & Farnsworth, 2014; Smith-Vidaurre et al., 2020). As in our previous work (Smith-Vidaurre et al., 2020), measuring similarity with a traditional method (SPCC) and a newer method (supervised random forests), allowed us to verify that the hierarchical mapping patterns we identified were not an artifact of using a single similarity method. We built supervised random forests models with 1844 acoustic and image features, including features derived from spectrographic cross-correlation (SPCC) and dynamic time warping similarity measurements, standard spectral acoustic measurements, descriptive statistics of Mel-frequency cepstral coefficients, and spectrogram image measurements (see supplementary sections 8 - 9). We trained random forests models to classify calls back to 4 repeatedly sampled individuals in each of the native and invasive ranges (156 calls and 8 individuals total, see supplementary section 10) (Breiman, 2001).

We built our first model with the full set of 1844 acoustic and image features. We built a second model by performing automated feature selection and using the most important features (114 total) from that analysis (supplementary section 11). We used our second model with 114 features for final analyses, as this model outperformed the first. To predict the similarity of the individual scale calls that we used for validation, as well as the site scale calls, we ran the remaining individual scale calls (73 total calls, 4 and 5 repeatedly sampled native and invasive range individuals, respectively) and the 1353 site scale calls down the final model. We extracted the resulting proximity matrix as the random forests similarity measurements (Humphries et al., 2018; Keen et al., 2014; Keen, Odom, Webster, Kohn, Wright, et al., 2021; Odom, Araya-Salas, Morano, Ligon, Leighton, et al., 2021; Smith-Vidaurre et al., 2020). To validate model performance, we used these similarity measurements to cluster the validation calls with Gaussian mixture modeling, which allowed us to determine whether the random forests model identified biologically relevant patterns of acoustic variation within and among calls of new individuals (e.g. individuals that were not present in the training dataset).

After confirming that the final model captured relevant patterns of variation among the individuals we used to validate model performance, we used random forests similarity measurements to generate low-dimensional acoustic space for the individual scale validation calls and the site scale calls. Since we had used the individual scale calls to train and validate the random forests model that we used to predict call similarity, we did not use random forests similarity measurements to perform quantitative analyses of acoustic convergence at the individual scale. Instead, we used the training classification performance of our final random forests model, and the clustering performance during validation with random forests similarity, to support our individual scale analyses with SPCC similarity.

2.6 Comparing native and invasive range hierarchical mapping patterns in acoustic space

To assess hierarchical mapping patterns in each of the native and invasive ranges, we compared patterns of acoustic convergence in low-dimensional acoustic space at the individual and site social scales. To generate acoustic space we optimized non-metric multidimensional scaling (MDS) to reduce the dimensionality of the SPCC and random forests similarity matrices, respectively (supplementary section 12). For acoustic space at the individual scale, we used 4 native range parakeets recorded at 3 sites in the department of Colonia, Uruguay in 2017, and 4 invasive range birds recorded at 3 sites in Austin, United States in 2019. We used random forests similarity obtained during model validation. For the site scale, we used 5 native range sites in the department of Colonia, Uruguay in 2017, and 5 invasive range sites in Austin, United States in 2019. We also filtered MDS coordinates by calls in each of the 3 site scale datasets that we used to address repeated sampling of individuals (see section 2.3). Acoustic space can be interpreted on the same axes for each similarity method. We interpreted calls that grouped together in acoustic space by individual or site as structurally similar calls (e.g. high convergence), while calls dispersed in acoustic space were structurally different (e.g. low convergence). We compared hierarchical mapping patterns between the native and invasive ranges by comparing the relative patterns of overlap in acoustic space among individuals or sites.

2.7 Using Mantel tests to compare hierarchical mapping patterns between the native and invasive ranges

After assessing hierarchical mapping patterns in acoustic space, we used Mantel tests to quantify the strength and statistical significance of acoustic convergence at each social scale for both the invasive and native ranges. We performed Mantel tests with matrices of call similarity (SPCC for the individual scale; random forests and SPCC for the site scale) and matrices of binary social identity per social scale over 9999 permutations. These tests allowed us to ask whether calls were more similar within an individual or site compared to among individuals or sites for both the native and invasive ranges. We used the magnitude and sign of Mantel test statistics as indicators of the strength and directionality of the correlation between matrices of call similarity and binary identity. For example, positive test statistics of greater relative magnitude pointed to stronger convergence for a given social scale or range.

Matrix values were converted to distances by subtracting each matrix value from 1. We used a partial Mantel test to control for site identity in the individual scale test for the invasive range, as we had recorded these calls from 3 different sites. For the site scale, we used calls from the most recent sampling year per site when sites were sampled over time. For this higher social scale, we also ran Mantel tests for each of the native and invasive ranges with each of the 3 datasets that we used to address the effect of inadvertent repeated sampling of individuals. We performed a total of 2 Mantel tests for the individual scale and 12 Mantel tests for the site scale in this comparison of hierarchical mapping patterns between ranges. We adjusted alpha of 0.05 to 0.0036 by a Bonferroni correction to account for 14 tests total (supplementary sections 13 - 14). We compared hierarchical mapping patterns by comparing Mantel test statistics at each social scale between the native and invasive ranges.

2.8 Evaluating hierarchical mapping patterns over time in the invasive range

We also used Mantel tests to determine whether the degree of acoustic convergence at the site scale changed over time in the invasive range. For these analyses, we used invasive range populations that we had repeatedly recorded in Austin, Texas and New Orleans, Louisiana. For each year that we had sampled calls in each city, we performed a Mantel test to correlate matrices of call similarity against matrices of binary site identity. We performed Mantel tests per city because we did not always sample the same sites in each year. For Austin, we performed Mantel tests using different sites recorded in each of 3 sampling years: 3 sites in 2004, 5 sites in 2011, and 6 sites in 2019. For New Orleans, we conducted Mantel tests using different sites sampled in 2 years: 3 sites in 2004 and 2 sites in 2011. We conducted Mantel tests with SPCC and random forests similarity measurements, as well as each of the 3 site scale datasets, and adjusted alpha of 0.05 to 0.0017 account for 30 tests total (supplementary sections 13 - 14). We assessed whether the strength of site scale convergence had changed over time in each city by comparing the relative magnitudes of Mantel test statistics. We also addressed the possibility of population recovery since invasion by evaluating population trends from eBird checklists in each city over our sampling years (supplementary section 15).

2.9 Benchmarking hierarchical mapping patterns with another parrot species

We placed our results in context by quantifying and directly comparing hierarchical mapping patterns among populations of monk parakeets with a species well-known for having regional information in their calls, the yellow-naped amazon. These amazon parrots imitate the contact calls of conspecifics and exhibit distinctive regional vocal dialects that are audibly perceptible to humans (Wright, 1996). Such vocal sharing may facilitate recognizing familiar group members (Sewall et al., 2016; Wright, 1996). Regional dialects in yellow-naped amazon calls have provided a baseline for identifying strong acoustic convergence within social groups for other vocal learning taxa (Bradbury et al., 2001; Buhrman-Deever et al., 2007; Guerra et al., 2008), including monk parakeets (Smith-Vidaurre et al., 2020). Here we used yellow-naped amazon calls as a point of reference for strong site-scale acoustic convergence which could occur in invasive range monk parakeet calls if group membership information became more important to signal after invasion than individual identity.

For our benchmarking analyses, we quantified hierarchical mapping patterns over the individual and site social scales for native and invasive range monk parakeets (separately), and over the individual, site, and regional dialect social scales for yellow-naped amazons. We performed SPCC for each species after matching sampling rates of audio files per species (supplementary section 17). For yellow-naped amazons, we used previously published contact calls recorded in Costa Rica in 1994 (Wright, 1996). We selected SPCC values for a subsample of individuals or groups at each social scale that represented similar sampling depth and geographic breadth for each range and species (supplementary section 18).

We compared hierarchical mapping patterns among native range monk parakeets, invasive range monk parakeets, and yellow-naped amazons by assessing patterns of relative overlap among distributions of the subsampled SPCC similarity values within and among categories (e.g. individuals or social groups). We also used the selected SPCC values in a bootstrapping analysis in which we randomly selected 5 similarity values within the given category and 5 similarity values among the given category in each bootstrapping iteration (supplementary section 19). This random sampling was performed with replacement, such that SPCC values within or among categories could be randomly selected more than once in the same iteration. We calculated bootstrapped similarity ratios by dividing similarity values within the given category by similarity values among the given category. We performed bootstrapping over 200 iterations and calculated 1000 similarity ratios for exemplars of each category (individual or group) at each social scale for native range parakeets, invasive range parakeets, and yellow-naped amazons. Similarity ratios close to 1 pointed to weaker convergence, while we used similarity ratios increasingly greater than 1 as evidence of stronger convergence (e.g. calls were more similar within categories than among categories).

3. Results

3.1 Strong individual signatures in native and invasive range contact calls

We identified strong acoustic convergence at the individual scale in contact calls recorded in both ranges. Call lexicons (or collections of spectrograms) for known repeatedly sampled individuals indicated that parakeets in each of the native and invasive ranges consistently produced calls that were distinctive from those of other birds (Figure 2A). This result was further supported by the general patterns of low overlap among individuals that we identified in random forests and SPCC acoustic space, although there was higher overlap among invasive range individuals (Figure 2B, Figure S1).

Our predictive modeling results also pointed to strong acoustic convergence at the individual scale. The final random forests model that we used to predict similarity of the site scale calls displayed high classification accuracy during training. The model classified calls back to the individuals that we used for training with 97.44% accuracy (95% CI: 93.57 - 99.30). The mean ± SE balanced accuracy of our model's classification performance per individual (representing the averaged sensitivity and specificity) was similarly high for the 4 native range (99.00% ± 0.010) and 4 invasive range training individuals (98.75% ± 0.008). Finally, Mantel tests also supported strong individual signatures in native and invasive range contact calls. The Mantel correlation statistics that we identified at the individual scale in each of the native and invasive ranges were of similar magnitude (Native range: $r = 0.48$; Invasive range: $r = 0.50$, Table 1) and were statistically significant under the Bonferroni-corrected alpha (Table 1).

Figure 2:

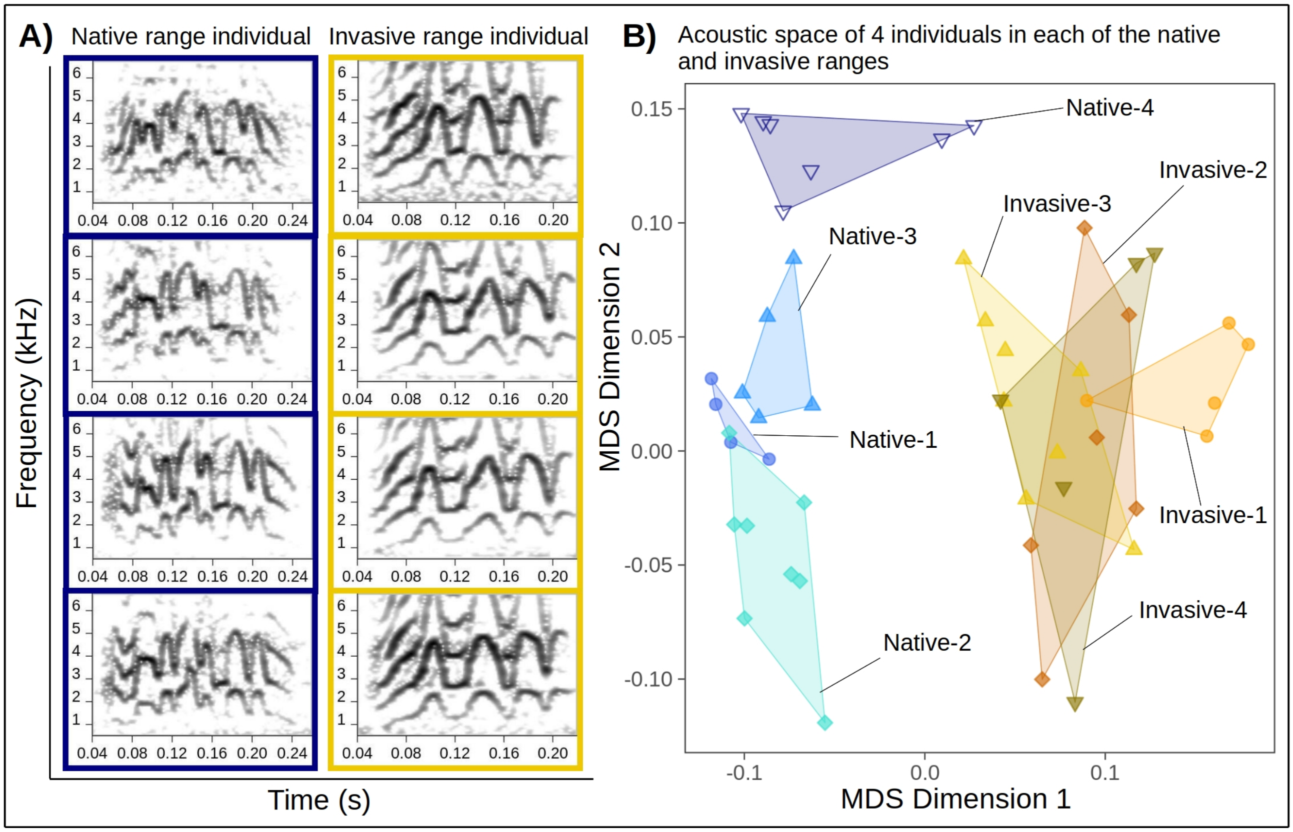

Figure 2 Legend: Native and invasive range monk parakeets displayed strong individual vocal signatures. Panel A shows a lexicon with 4 calls for one repeatedly sampled bird in each of the native and invasive ranges. In panel B, random forests acoustic space is shown for 4 native range and 4 invasive range individuals. Each point represents a different call per individual, and individual identities are encoded by shapes and hues. The convex hull polygons demonstrate the area per individual in acoustic space. The blue palette corresponds to the native range and gold-brown to the invasive range. See Table S1 for decoded individual identities. Individuals generally produced visibly consistent calls (Panel A) that were also distinctive from other individuals (Panel B).

Table 1. Assessing the strength and significance of acoustic convergence over two social scales with Mantel tests

Social scale	Similarity method	Range	Site scale dataset	Number of calls	Number of sites	Mantel r[a]	Permuted p-values
Individual	SPCC	Native	-	78	1	**0.48**	0.0001
		Invasive	-	52	3	**0.50**	0.0001
Site	SPCC	Native	Full	598	37	0.06	0.0001
			Clustering	410	37	0.04	0.0001
			Visual classification	336	37	0.04	0.0001
		Invasive	Full	579	18	**0.20**	0.0001
			Clustering	208	18	**0.11**	0.0001
			Visual classification	179	18	**0.11**	0.0001
	Random forests	Native	Full	598	37	**0.13**	0.0001
			Clustering	410	37	**0.10**	0.0001
			Visual classification	336	37	**0.10**	0.0001
		Invasive	Full	579	18	**0.29**	0.0001
			Clustering	208	18	**0.24**	0.0001
			Visual classification	179	18	**0.24**	0.0001

[a] Mantel r values an order of magnitude greater than the lowest values are shown in bold.

3.2 Call convergence within sites was low

We found that individuals at the same site did not produce similar calls (Figure 3A). When we assessed hierarchical mapping patterns in acoustic space, we found that contact calls did not group by site identity. Instead, calls from the same site were overdispersed, resulting in substantial overlap among different sites in acoustic space generated using random forests similarity (Figure 3B), as well as SPCC similarity (Figure S2). The low degree of acoustic convergence that we identified at the site scale was supported by Mantel test statistics that were of lower relative magnitude for the site scale compared to the individual scale (Table 1). This result held across the complementary SPCC and random forests similarity methods that we used for the site scale Mantel tests.

We also compared our Mantel test results across the 3 site scale datasets to determine how keeping or filtering out calls of potentially repeatedly sampled individuals affected our results at this social scale. While the Mantel test statistics for the 3 native range site scale datasets were consistently low, the test statistics for the invasive range varied across the site scale datasets. The invasive range test statistics for each dataset were uniformly greater than those we obtained for the native range datasets by each similarity method (Table 1). The highest Mantel test statistics that we observed at the site scale for the native and invasive ranges occurred with the full dataset of calls, in which we did not filter out calls attributed to repeatedly sampled unmarked individuals at this social scale.

Figure 3:

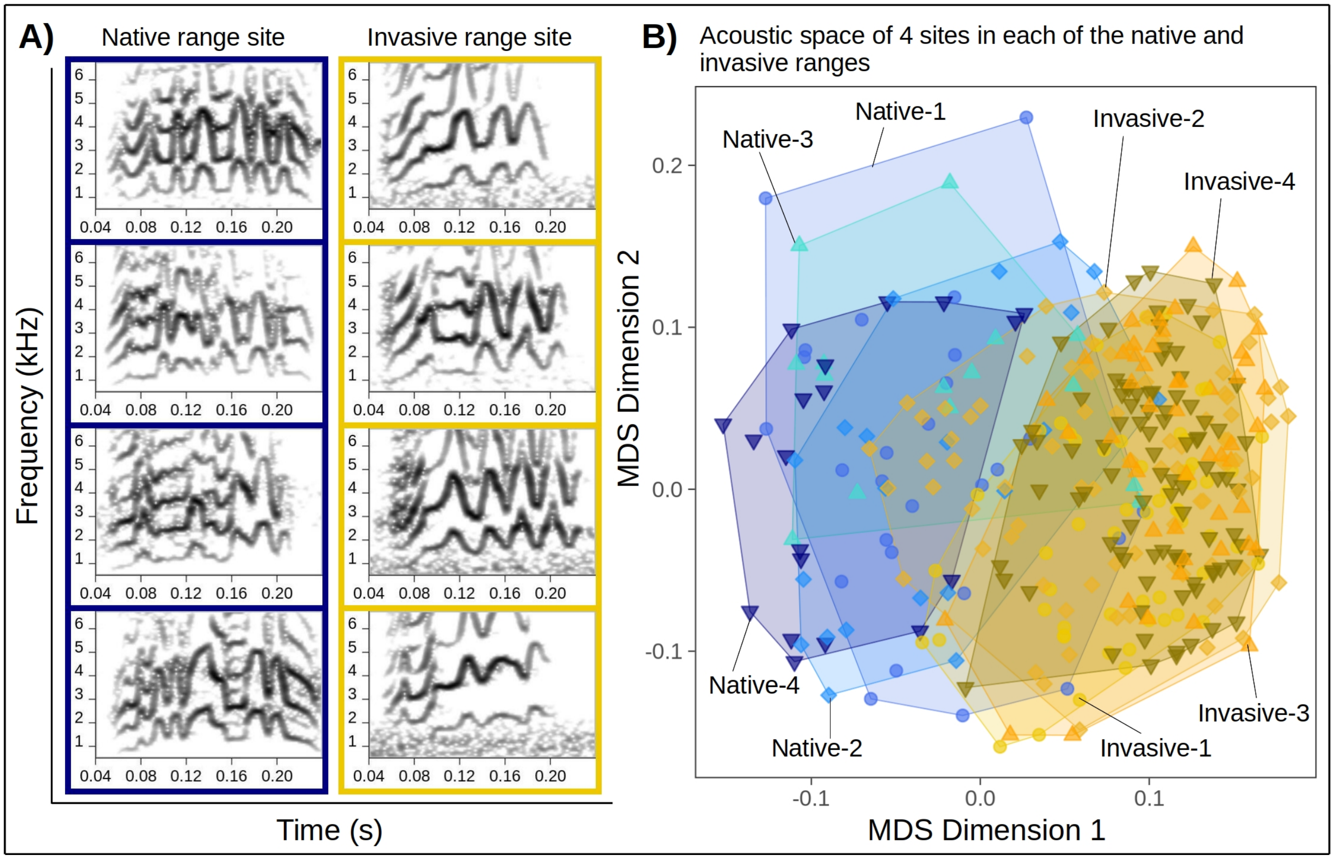

Figure 3 Legend: We identified minimal acoustic convergence at the site scale in the native and invasive ranges. Panel A shows a lexicon of 4 calls each for one native range site and one invasive range site, in which each call represents a unique individual. Panel B shows random forests acoustic space for 5 native range and 5 invasive range sites. The full dataset of calls was used per site (see Figure S2 for the other site scale datasets). Across panels, the color palettes, aesthetics, and polygons used are similar to Figure 3, but here encode site identities. See Table S1 for decoded site identities. Calls within sites were visibly different (Panel A), and there was low differentiation among sites in acoustic space (Panel B) compared to the individual scale (Figure 2B).

3.3 Patterns of site scale convergence in the invasive range were consistent over time

We did not identify clear evidence of temporal change in the strength of site scale acoustic convergence in the invasive range (Table 2). After adjusting alpha for multiple comparisons, we identified statistically significant acoustic convergence at the site scale in 2011 in the city of Austin using the full dataset of calls by both similarity methods, and the datasets filtered after clustering and visual classification, but only by random forests similarity (Table 2). We also found statistically significant convergence within sites in Austin in 2019 and New Orleans in 2004 using the full dataset of calls and both similarity methods (Table 2). Although these Mantel test statistics were statistically significant, the statistics were of lower magnitude relative to the Mantel test statistics that we identified at the individual scale for each range (Table 1). We used eBird checklists from these cities in a complementary analysis of population trends over time, to address the possibility that population size could have rebounded since establishment. However, we found that the mean annual frequency of monk parakeets reported in complete checklists in Austin and New Orleans remained low (less than 5% of all species sightings) and was also generally stable from 2004 to 2020 (supplementary section 15, Figure S3).

Table 2. Evaluating temporal change in site scale acoustic convergence in the invasive range

Similarity method	City	Year	Dataset	Number of calls	Number of sites	Mantel *r*[a]	Permuted p-values
SPCC	Austin	2004	Full	93	3	0.10	0.0796
			Clustering	37	3	0.09	0.1359
			Visual inspection	20	3	-0.03	0.5950
		2011	Full	65	5	**0.23**	0.0001
			Clustering	43	5	0.08	0.0067
			Visual inspection	54	5	0.07	0.0055
		2019	Full	295	6	**0.13**	0.0001
			Clustering	83	6	0.01	0.2513
			Visual inspection	56	6	-0.03	0.8498
	New Orleans	2004	Full	49	3	**0.18**	0.0005
			Clustering	18	3	0.03	0.3272
			Visual inspection	25	3	-0.02	0.6186
		2011	Full	29	2	0.27	0.0045
			Clustering	17	2	0.22	0.0196
			Visual inspection	17	2	0.21	0.0229
Random forests	Austin	2004	Full	93	3	0.03	0.2680
			Clustering	37	3	0.03	0.2912
			Visual inspection	20	3	0.04	0.3015
		2011	Full	65	5	**0.37**	0.0001
			Clustering	43	5	**0.13**	0.0004
			Visual inspection	54	5	**0.09**	0.0015
		2019	Full	295	6	**0.17**	0.0001
			Clustering	83	6	0.05	0.0099
			Visual inspection	56	6	0.01	0.4115
	New Orleans	2004	Full	49	3	**0.19**	0.0002
			Clustering	18	3	0.10	0.1161
			Visual inspection	25	3	-0.02	0.6051
		2011	Full	29	2	0.09	0.0826
			Clustering	17	2	0.08	0.1827
			Visual inspection	17	2	0.07	0.1963

[a]Mantel *r* values that were statistically significant under the corrected alpha are shown in bold.

3.4 More repeated sampling of individuals in our invasive range site scale dataset

We attributed more calls in our invasive range site scale datasets to the inadvertent repeated sampling of unmarked individuals compared to our native range site scale datasets. The mean numbers of repeated individuals that we identified by our clustering and visual classification filtering approaches were only slightly higher for the invasive range than the native range (Table 3). However, we found that the mean number of calls attributed to repeated individuals was about twofold greater for invasive range sites by each of the clustering and visual classification approaches that we had used to identify repeated sampling of individuals in our site scale datasets (Table 3).

Table 3. Assessing the degree of repeated sampling of individuals for both the invasive and native ranges.

Filtering approach	Range	Repeated individuals (mean ± SE)	Calls per repeated individual (mean ± SE)
Clustering	Native	3.24 ± 0.38	10.4 ± 1.61
	Invasive	3.40 ± 0.47	23.6 ± 5.53
Visual classification	Native	3.48 ± 0.39	2.83 ± 0.15
	Invasive	3.57 ± 0.54	5.31 ± 0.64

3.5 Benchmarking hierarchical mapping patterns with another species

The hierarchical mapping patterns that we identified for both native and invasive range monk parakeet calls differed from the hierarchical mapping patterns that we recapitulated in yellow-naped amazon calls. Our benchmarking results showed that the individual scale was the social scale with the strongest acoustic convergence in native and invasive range monk parakeet calls, while the regional dialect scale displayed the strongest convergence in yellow-naped amazon calls. We found that the greatest separation between the median similarity values of the two categories of comparison per social scale (e.g. same or different individual or group) occurred at the individual scale for native and invasive range monk parakeets (Figure 4A, panels i and ii). For yellow-naped amazons, we detected the greatest separation between categories at the regional dialect scale (Figure 4A, panel vii). In addition, the bootstrapped similarity ratios that we used to assess the strength of acoustic convergence were greatest at the individual scale for monk parakeets in each of the native and invasive ranges (Figure 4B, panels i and ii). In contrast, the largest similarity ratio for yellow-naped amazons occurred at the regional dialect scale (Figure 4B, panel iii).

Figure 4:

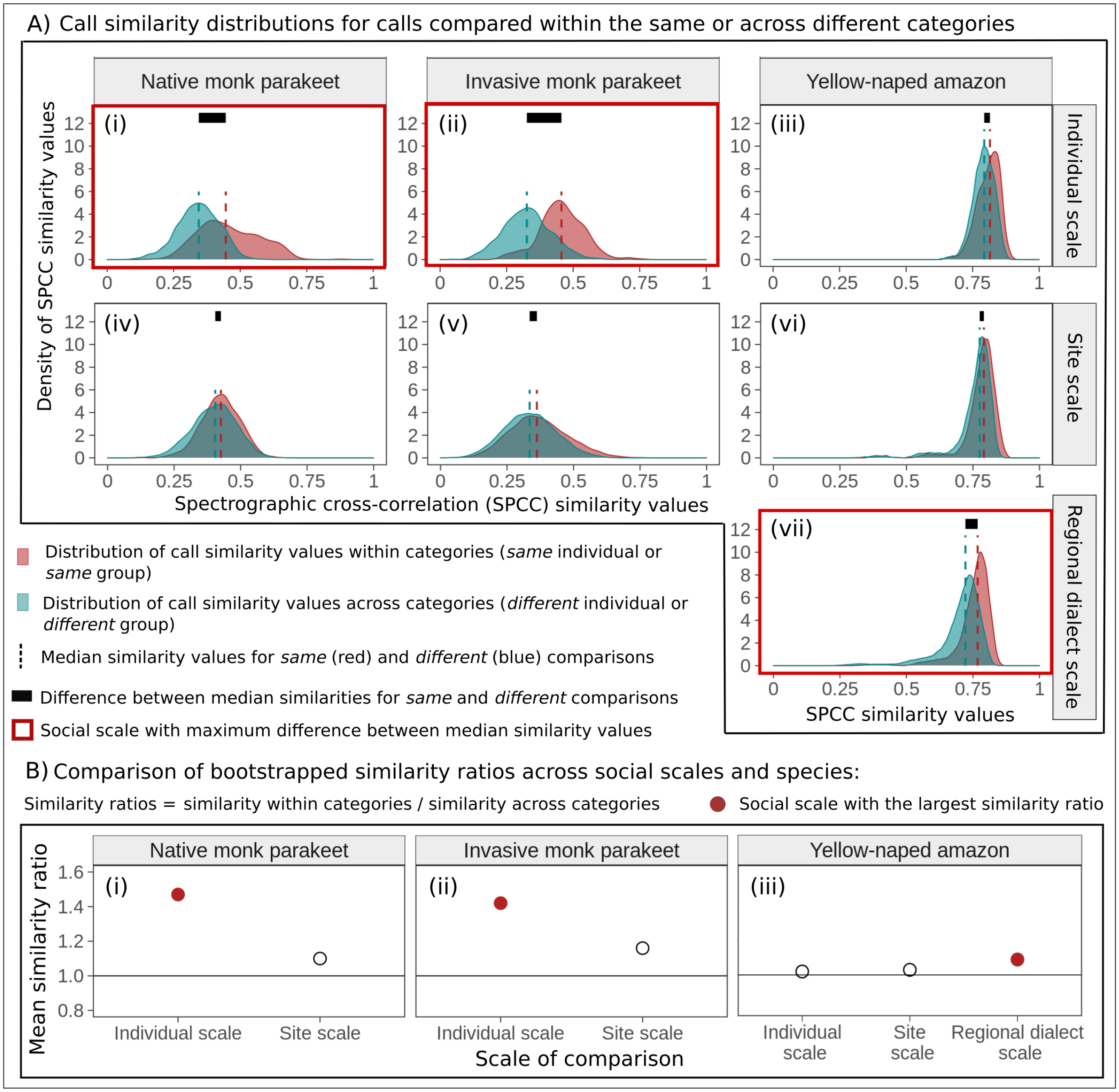

Figure 4 Legend: We benchmarked hierarchical mapping patterns in native and invasive range monk parakeet calls against yellow-naped amazon calls. Panel A shows density curves for the distributions of spectrographic cross-correlation (SPCC) similarity values that represent comparisons of calls within or among categories in red and blue shading, respectively. The dashed lines represent the median similarity values per distribution. In Panel B, we show the mean similarity ratios calculated from bootstrapped SPCC values. The solid line at 1 represents no convergence within a given category. For both native and invasive range monk parakeets, we show site scale results obtained from the full dataset of calls. Across both panels, the social scale at which the strongest convergence occurred is shown in red.

4. Discussion

We asked whether the type of identity information that is important to communicate in learned signals changes after the social environment is perturbed over the ecological timescale of a biological invasion. We found that individual identity remained the most important type of identity information to communicate in learned monk parakeet vocalizations. We discuss this new insight into the resilience of identity information encoded in learned communication signals, and point to possible directions for future work over ecological and evolutionary timescales.

4.1 Hierarchical mapping patterns were similar between native and invasive range monk parakeet populations

Monk parakeets in native range populations in Uruguay and invasive range populations in the U.S. emphasized individual identity information in learned vocalizations. In each range, the hierarchical mapping patterns that we quantified in contact calls showed the strongest convergence at the individual scale and weaker convergence within sites. These results were robust to the greater degree of repeated individual sampling that we identified in our invasive range site scale dataset (supplementary section 16). In addition, the low convergence that we identified at the site scale in two cities sampled over time, which represented independent introduction events, suggested that these hierarchical mapping patterns were unlikely to have changed in the broader U.S. invasive range over the timespan of this study. We also recapitulated the structural differences between native and invasive range calls that reflected the simplification of individual vocal signatures associated with smaller local populations in the U.S. (see the separation in acoustic space among native and invasive range calls in Figure 2B and Figure 3B) (Smith-Vidaurre et al., 2021).

Our analyses indicate that despite invasion, individual identity remained the most important type of identity information to communicate to receivers. In other words, we inferred that the type of identity information emphasized in learned calls was resilient to the social disruption that is expected to occur during the early stages of a biological invasion. Our findings also indicate that although some features of the social environment changed after invasion, such as the smaller local population sizes that we identified in previous work (Smith-Vidaurre et al., 2021), monk parakeets' social environments may have been generally resilient to invasion or were re-established after initial perturbations. If the individually distinctive contact calls that we identified in the native and invasive ranges are used for individual vocal recognition, then parakeets in each range should be engaging in social interactions that favor signaling individual identity in learned communication signals. Our quantitative approaches with vocal signals allowed us to reach this inference about monk parakeets' social environments without depending on the time- and resource-intensive collection of social data. However, future work could directly address whether native and invasive range monk parakeets are engaging in similar types of social interactions that require individual vocal recognition, such as repeated interactions and differentiated relationships with many other individuals (Bergman & Beehner, 2015; Tibbetts et al., 2007).

4.2 Benchmarking our results against a parrot species that exhibits regional vocal dialects

We performed a comparative analysis with yellow-naped amazon contact calls to place our ecological comparison of native and invasive range monk parakeet calls in an evolutionary context. If invasive range monk parakeets switched to emphasizing group membership information in contact calls, then hierarchical mapping patterns in invasive range monk parakeet calls should have been more similar to yellow-naped amazons, which exhibit regional vocal dialects that are audibly and visibly distinctive to humans (Salinas-Melgoza et al., 2012; Sewall et al., 2016; Wright, 1996; Wright & Dahlin, 2018). Instead, we found that hierarchical mapping patterns were similar between native and invasive range monk parakeets, confirming that identity information in monk parakeet contact calls was resilient to the invasion process over ecological timescales.

Our benchmarking analysis also highlighted the importance of using quantitative tools to complement human perception of audible and visible variation in avian vocalizations. When relying on the human ear and eye, the variation among regional dialects in yellow-naped amazon calls is far more perceptible than individually distinctive monk parakeet calls. For example, the regional dialects that we recapitulated in the amazon calls are distinctive to the human ear (Wright, 1996), including North dialect calls that sound like “wah-wah”, and variants of the South dialect that sound like “weeup”. In contrast, patterns of individual variation in monk parakeet contact calls are difficult to distinguish by the human ear, and calls of different individuals sound no different than “chees”. However, when we used quantitative methods to compare hierarchical mapping patterns between species, we found that individual scale convergence in native and invasive range monk parakeet calls was stronger than regional dialect convergence for yellow-naped amazons (Figure 4A: panels i, ii, and vii).

Amazon vocal dialects may be more perceptible to humans than monk parakeet individual vocal signatures because of humans’ limited abilities to perceive fine-scale temporal variation at higher frequencies (Dooling, Leek, Gleich, & Dent, 2002; Lohr, Dooling, & Bartone, 2006). Parrots’ auditory perception abilities appear tuned for higher frequencies, such as orange-fronted conures (*Eupsittula canicularis*), which display the greatest auditory sensitivity in a frequency band that overlaps with the greatest spectral energies in contact calls (Wright, Cortopassi, Bradbury, & Dooling, 2003). In addition, yellow-naped amazon calls exhibit slower frequency modulation patterns that are more perceptible to humans, and can also be arranged into fewer categories (e.g. a few regional dialects), a task that should pose lower cognitive challenges compared to categorizing monk parakeet calls by many different individuals (Bradbury et al., 1998; Wiley, 2013). Overall, our benchmarking results point to the importance of using computational approaches to identify information in animal signals that is difficult for humans to perceive but may be critical in animal communication systems.

4.3 Future research considerations with hierarchical mapping patterns

We combined computational tools with a conceptual framework of how hierarchical mapping patterns are connected to identity signaling in animal vocal signals. This combined approach allowed us to quantify hierarchical mapping patterns and then infer the most salient social information encoded in vocal signals. Similar computational approaches could be applied to quantify hierarchical mapping patterns with existing datasets of animal signals to learn more about the social environments in which individuals communicate across a broader range of taxa, without depending on the time-intensive collection of social data from marked individuals. The hierarchical mapping patterns identified for a particular population or species can also be used as a foundation for designing biologically relevant playback experiments, which can be more time-consuming than recording communication signals, and are fundamental to understand how receivers use the social information that signalers communicate. Playback experiments are important because mismatches can occur between the social information encoded in signals and the information that receivers use for social recognition, especially when it is cognitively costly to track certain types of information (Bergman, 2010; Bergman et al., 2015).

Researchers using hierarchical mapping patterns to make inferences about identity signaling and the social environment should take additional considerations into account. For instance, recording unmarked individuals in natural populations provides only a snapshot of dynamic social interactions, as well as the social information conveyed in signals that is important in a given social environment. Some species may exhibit variation within a single signal type that should be considered carefully when quantifying hierarchical mapping patterns, such as parrots that use multiple contact call variants, including budgerigars and orange-fronted conures (*Eupsittula canicularis*) (Bradbury et al., 2001; Dahlin, Young, Cordier, Mundry, & Wright, 2014; Farabaugh, Linzenbold, & Dooling, 1994). Furthermore, sampling one or a few vocalizations per individual over a short time frame makes it difficult to assess how social information changes during dynamic social interactions, such as the rapid vocal matching exhibited by wild orange-fronted conures and rose-breasted cockatoos (*Eolophus roseicapillus*) (Balsby et al., 2009; Scarl et al., 2009). Finally, while the literature has focused on explaining how social signals arise in more complex social environments with frequent and repeated interactions among many individuals (Bergman et al., 2015; Pollard et al., 2011; Ramos-Fernandez et al., 2018; Sewall et al., 2016; Tibbetts et al., 2007), there is less of a conceptual foundation for how identity information in learned communication signals should change in social environments characterized by fewer individuals and differentiated relationships overall.

Data Accessibility: Annotated code and knitted RMarkdown files supporting this article will be made available on GitHub. Data that can be used to reproduce results will be deposited in figshare.

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Ethics: This research was conducted under an approved Institutional Animal Care and Use protocol (IACUC no. 2017-006, New Mexico State University, USA) and an animal care and use protocol approved by la Comisión de Ética en el Uso de Animales (CEUA no. 240011-002512-17, la Universidad de la República, Uruguay).

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