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Community convergence in bird song

Gonçalo C. Cardoso · Trevor D. Price

Abstract Species in similar habitats are often similar in morphology or behaviour, attributed to adaptation to similar environmental selection pressures, sometimes mediated by competitive interactions. For passerine songs, similarity of phenotype in identical habitats and character displacement have been documented, the former due to adaptation to the acoustics of the habitat, and the latter due to competition for acoustic space among species. If these phenomena are widespread, they should lead to community convergence of bird songs. Here, we test if passerine communities in similar habitats converge in song attributes or in acoustic differentiation among species. We compared the songs of European and North American Mediterranean climate passerine communities in open and closed habitats. Song frequency varied across different habitats but not continents. This was independent of both phylogeny and body size, indicating community convergence due to acoustic adaptation, rather than species sorting or similarity as a by-product of another type of ecological convergence. We found little evidence for regular spacing in song features among species, as would be expected if acoustic competition shapes within-community structure. However, for one of five song components, the open habitat communities showed a similar distribution of phenotypes on each continent. The proportion of interspecific variation in song explained by these effects was small. The fact that songs are complex signals that vary in many dimensions may explain why competition for acoustic space seems to be of small importance in structuring songs in these passerine communities.

Keywords Birdsong · Community convergence · Community structure · Acoustic competition

G. C. Cardoso (✉)
Department of Zoology, University of Melbourne, Melbourne, VIC 3010, Australia
e-mail: gcardoso@unimelb.edu.au

T. D. Price
Department of Ecology and Evolution, University of Chicago, Chicago, IL, USA

Introduction

Similar habitats often promote convergence, defined as evolution towards similar pheno-
types from distinct ancestral forms. Spectacular examples of morphological convergence
among species abound (for example the New World and Old World vultures: Wink 1994;
Seibold and Helbig 1995). Convergence may also happen at the level of the ecological
community and, although ancestral states of communities are hard to infer, it is possible to
test for convergence by comparing communities of two or more habitat types in different
regions of the world (e.g. Schluter 1986; Pavoine et al. 2004). On the assumption that each
region's communities established independently, any parallel differences across habitats
within regions is strong evidence for convergence. An extreme result of community
convergence is the production of communities that are significantly similar in the distri-
bution of phenotypes. For example, finch communities in similar habitats of different
continents have distributions of body size and beak shape that are more similar than
expected by chance (Schluter 1986). Such similarity of distributions implicates competi-
tion among species (Schluter 1986, 1990).

Community convergence and community structure have been studied especially
regarding ecomorphological traits (Emerson and Gillespie 2008), but both phenomena may
apply to communication signals (Gröning and Hochkirch 2008). Physical characteristics,
such as light filtering or acoustic properties, vary among habitats and influence how
effectively different signals are broadcast and perceived (Bradbury and Vehrencamp
1998). While the role of the environment generally favours the same kind of signal for all
species in the community, competition between species may result in dispersion of signals.
This may happen either indirectly because morphological changes driven by ecological
competition impact the signal (e.g. body size affects the frequency of acoustic signals;
Wallschläger 1980; Ryan and Brenowitz 1985), or because of direct signal interference or
similarity (reviewed in Gröning and Hochkirch 2008). In the latter case, species may
compete for "signal space" to avoid signal masking or species misidentification, which is
especially relevant for long-range mating and territorial signals (Miller 1982; Nelson and
Marler 1990; Chek et al. 2003). For example, in some South-American frog communities
the vocalizations of the different species may be more widely and regularly spaced in
acoustic space than random, suggesting community structure due to interspecific acoustic
competition (Chek et al. 2003). Here, we test for community convergence and similarity of
spacing among species in an important class of communication signals, birdsongs.

Passerine songs are acoustic signals used mostly in long-range communication for mate
attraction and territoriality (Catchpole and Slater 2008) and can potentially be shaped by
interspecific interactions. Some birds avoid singing when other species that use the same
frequency range are singing (Planqué and Slabbekoorn 2008), suggesting acoustic masking
by heterospecific song. Species singing similar songs may also suffer fitness costs due to
ambiguity in species recognition. For example, blue tits (*Cyanistes caeruleus*) suffer from
territorial aggressiveness by the larger bodied great tits (*Parus major*), and in sympatry
have character displacement of song (Doutrelant and Lambrechts 2001), which reduces
interspecific aggression (Doutrelant et al. 2000). Collared flycatchers (*Ficedula albicollis*)
in sympatry with pied flycatchers (*F. hypoleuca*) also show character displacement of song,
which in these species is primarily an epigamic signal, putatively to avoid hybridisation
(Wallin 1986), but many male pied flycatchers learn mixed song types in sympatry (i.e.
song containing both pied and collared syllables), which leads to hybridisation (Qvarn-
ström et al. 2006). Sympatric antbird species have also diverged in song more than allo-
patric species (Seddon 2005). More general acoustic competition from the community may

also influence the optimal song phenotype of a species. For example, Bewick's wrens (*Thryomanes bewickii*) and American tree sparrows (*Spizella arborea*) have increased song variability where fewer sympatric passerine species exist (Kroodsma 1985; Naugler and Ratcliffe 1994), although this may be a consequence of other environmental factors associated with the decrease in species richness (e.g. higher local densities, Price 2008, chapter 12). While interspecific competition for acoustic space may affect birdsong, some studies did not find effects of sympatric species on song (Hunter and Krebs 1979; Espmark 1999), no character displacement when closely related species coexist in sympatry (Lohr 2008), and no consistent within-species reduction of variation in the song traits that are potentially more informative for species recognition (Nelson 1989). Also, interspecific territoriality sometimes leads to convergent, rather than divergent, character displacement of song (Cody 1969; Qvarnström et al. 2006; Price 2008, chapter 14). Thus, the importance of interspecific acoustic competition in structuring song phenotypes within communities remains unknown.

We use passerine communities of open and closed habitats in two Mediterranean climate regions—southern Europe and California—to ask if songs have converged between communities in identical habitats. Testing for convergence of phenotypes is straightforward: in a two-way ANOVA (habitat × continent) songs should differ among habitat types, but not among continents (Schluter 1986). We test this controlling for phylogeny, so that similarity between identical-habitat communities reflects evolution rather than related species colonizing similar habitats (Ryan and Brenowitz 1985). To test for similarity in community structure we compare the distribution of phenotypes between communities that inhabit matched habitats (Schluter 1990). We also ask if song phenotypes are uniformly distributed within each community, as could result if song evolves due to acoustic competition among sympatric species.

Methods

Passerine communities

We studied the passerine communities of open and closed Mediterranean climate habitats in California and Provence described by Cody (1975) and Blondel (1979, 1981), respectively, and compiled in Blondel et al. (1984). These communities are representative of mainland Californian and European Mediterranean habitats. We chose to study these communities because they were previously used in several studies of ecomorphology and community convergence (e.g. Cody and Mooney 1978; Blondel et al. 1984; Pavoine et al. 2004), and because song recordings are available for all species.

We used the species lists for the open (sagebrush, matorral) and closed (woodland) habitats (codes 2 and 5 in Blondel et al. 1984). Lists for two habitat types of intermediate vegetation density are also available, but we did not use them because most species in these intermediate habitats also occur in either the open or closed habitats. We excluded the Corvidae because corvids in these areas do not have long-range songs, and because they are much larger than the other passerines so that their calls sound distinctively different and should not be important for acoustic competition with the smaller passerines. The dataset comprises 7 and 23 species for open and closed habitats in California, two of which are common to both habitat types, and 8 and 17 species for these habitats in Europe, one of which is common to both habitat types (Fig. 1). There are no species in common between the European and Californian communities.
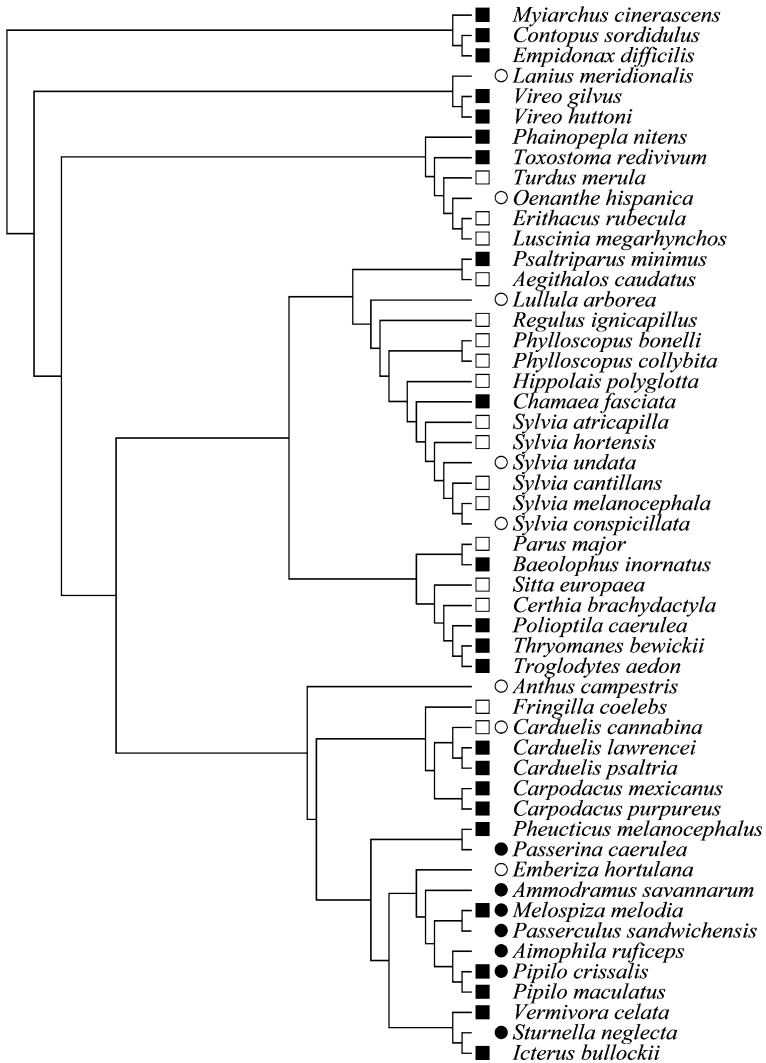
Fig. 1 Phylogeny of the passerine species studied, obtained collating information from different molecular phylogenies (see text for sources). *Symbols* indicate *open* (●○) or *closed* (■□) habitat, and *shading* indicates Europe (□○) or California (■●). Lengths from each node to tips are drawn as number of daughter species minus one

Song measurements

We created spectrograms (FFT length of 512 and overlap of 87.5% on sound files with a sampling frequency of 22,050 Hz, corresponding to a resolution of 43 Hz and 2.9 ms) for all songs (not other vocalizations) in the recordings of Perrins (1998) and the Cornell Laboratory of Ornithology (1992) with the software Avisoft-SASLab Pro v.4.40 (Avisoft Bioacoustics, Berlin). Songs were identified as groups of syllables separated from other

songs by more than 0.5 s and, within-songs, syllables were identified as isolated sound elements or groups of elements closely spaced comparatively to other syllables. On average we measured four songs and 47 syllables per species (Appendix Table 4).

We measured 11 song traits that together quantify variation in song phonology among species. *Syntax* was quantified as the proportion of syllables that are repeated (i.e. trilled) and *song length* measured as the average duration of songs. The remaining measurements were made for every syllable and then averaged for each species. *Peak frequency* was measured as the frequency with maximum amplitude in the power spectrum of the syllable. *Frequency bandwidth* was computed as the maximum minus minimum frequencies, where maximum and minimum frequencies are the frequencies at which sound amplitude drops below minus 24 dB relatively to maximum amplitude in the power spectra (e.g. Podos 1997). The other measurements were made on spectrograms following the methods in Cardoso and Mota (2007). Briefly, *length of syllables* and *length of intervals* are the durations of syllables and of intervals separating syllables within songs, *elements per syllable* is the number of temporally separated sounds within each syllable, *number of frequency inflections* is the number of times a rising frequency modulation is followed by a descending one or vice versa, and *two voiced sounds*, *harmonics*, and *rattles* are the proportion of each syllable's length that contains, respectively, two voices (two simultaneous sounds produced by the two sides of the syrinx and modulated in frequency independently of each other), harmonics (octaves of the fundamental frequency), or rattles (sometimes referred to as 'buzzes': broadband and harsh sounding fast modulations or repetitions within syllables, e.g. last syllable in Fig. 4D of Cardoso and Mota 2007). In two species (*Anthus campestris* and *Lanius meridionalis*) all songs were monosyllabic, and therefore no intervals between syllables could be measured. In these two species the length of intervals was set to the threshold to identify different songs (0.5 s) because intervals between syllables (in this case equivalent to intervals between songs) are comparatively very long. Average values of all measurements for each species and sample sizes are given in the Appendix Table 4.

Most song measurements were approximately normally distributed, but *song length*, *syllable duration*, *interval duration* and *number of elements* were not (Kolmogorov–Smirnov tests against a normal distribution: all $Z > 1.47$, all $N = 52$, all $P < 0.03$). These four measurements were log transformed (after transformation, all $Z < 1.26$, all $P > 0.08$), and the transformed values used instead of the original ones. We reduced the 11 measurements into a set of orthogonal axes by principal component analysis (PCA) on the correlation matrix of the 11 measurements across all species.

Relations with body size

We obtained body masses from Dunning (2008) (male values were used when body mass is given separately for males and females, Appendix Table 4). The distribution of body masses was right-skewed (Kolmogorov–Smirnov $Z = 2.09$, $N = 52$, $P < 0.01$), and therefore we log transformed it (after transformation, $Z = 0.95$, $P = 0.33$). We tested for a relation between body mass and each of the song principal components (PCs) using general least squares (GLS) regressions controlling for phylogeny (Pagel 1999). GLS regressions were run with the software BayesTraits (M. Pagel and A. Meade, available from www.evolution.rdg.ac.uk), each time estimating λ to adjust the phylogenetic correction to the degree of phylogenetic signal in the data (Pagel 1999; Freckleton et al. 2002).

To run the GLS regressions we assembled a phylogeny (Fig. 1) based primarily on Barker et al. (2004) and expanded using several other molecular phylogenies (Alström et al. 2006; Barhoum and Burns 2002; Bleiweiss 2007; Blondel et al. 1996; Carson and Spicer 2003; Groth 1998; Johnson and Lanyon 1999; Lovette and Bermingham 2002; Sibley and Ahlquist 1990; Voelker and Spellman 2004; Yuri and Mindell 2002). Because this phylogeny collates information from multiple sources, the original branch lengths cannot be used. As an approximation, as a first step we set branch lengths at each node proportionally to the number of daughter species of that node (e.g. Grafen 1989; Garland et al. 1992), as drawn in the Fig. 1, and then estimated δ (a parameter that scales relative lengths from root to tips to fit the phenotypic data, Pagel 1999) for each regression.

Differences among habitat types and continents

We tested for differences in song among habitat types and among continents using multiple GLS regressions controlling for phylogeny. In these multiple GLS regressions the dependent variable was a song PC or body mass, and the independent variables were habitat type, continent, and their interaction term. The three species that occur both in open and closed habitats were not used in this analysis, and the phylogeny in the Fig. 1 was modified accordingly. We also repeated the song regressions adding body mass as an independent variable, to check if song convergence is mediated by body size.

Distribution of phenotypes

We compared the distribution of phenotypes between communities in the same habitat type using 2-sample Kolmogorov–Smirnov tests and testing for significance at the lower tail (Schluter 1990). Unlike its most common usage, which looks at the upper tail to test for differences between samples, we look at the lower tail to test for "significant similarity". A Kolmogorov–Smirnov Z lower than the 5th percentile of its distribution indicates that the two samples have distributions more similar than random (at $\alpha = 0.05$).

We also tested if the distribution of phenotypes in each community is significantly similar to a uniform distribution using 1-sample Kolmogorov–Smirnov tests. As above, we evaluated significance at the lower tail, which tests if distribution is significantly similar to uniformity. This would indicate that the spacing of phenotypes within a community is significantly more even than random draws from a uniform distribution, as could happen if song evolves due to acoustic competition among sympatric species. Apart from the GLS regressions, all statistical tests were done in SPSS v13.0.

Results

Song PCA

A PCA on the correlation matrix of the 11 song measurements returned five PCs with eigenvalues larger than one, which together explained 76% of the variation in measurements among species (Table 1). PC1 reflects mostly songs with long and complex

Table 1 Trait loadings of song measurements on each of the 5 principal components (PC) with eigenvalues larger than 1

Trait	PC1	PC2	PC3	PC4	PC5
Syntax	−0.14	0.39	**−0.61**	0.09	0.33
Song length	−0.45	0.20	0.31	−0.29	**0.61**
Length of syllables	**0.67**	**−0.56**	0.10	0.08	0.10
Length of intervals	**0.65**	−0.03	−0.16	−0.13	**0.58**
Peak frequency	−0.45	0.17	−0.27	**0.63**	0.06
Frequency bandwidth	0.29	**0.82**	0.27	0.02	−0.17
Elements per syllable	**0.70**	0.07	−0.03	0.27	−0.22
Frequency inflections	**0.70**	0.00	**−0.55**	−0.16	0.04
Two voiced sounds	0.33	0.42	0.15	**0.58**	0.24
Harmonics	0.37	**0.66**	0.32	−0.34	−0.10
Rattles	0.17	−0.31	**0.68**	0.33	0.24
Eigenvalue (variation explained)	2.64 (24%)	1.92 (17%)	1.54 (14%)	1.17 (11%)	1.03 (9%)

Trait loadings larger than 0.5 are in bold typeface

syllables. PC2 quantifies songs with harmonics, large bandwidths, and short syllables. PC3 quantifies songs with few syllable repetitions and frequency inflections, but many rattles. PC4 is related mostly to high song frequency, and also to two voiced sounds (two simultaneous and independently modulated sounds). PC5 is characterized by long songs and long intervals between syllables. We use these five PCs in the following analyses. Figure 2 shows the distribution of these five PCs in each of the four communities.

Relations with body size

Body mass was negatively related to PC4 (GLS regression: standardized $\beta = -0.44$, $N = 52$, $P = 0.004$); i.e. larger species sing lower frequency songs. Body mass also tended to vary with PC1 (standardized $\beta = 0.33$, $P = 0.02$) and PC2 (standardized $\beta = -0.28$, $P = 0.03$), but these trends are not significant after correcting for multiple comparisons (5 PCs, Bonferroni adjusted $\alpha = 0.01$). Body mass was not related with PC3 and PC5 (both $|\beta| < 0.15$, $P > 0.30$).

Differences among habitat types and continents

Table 2 shows the results of multiple GLS regressions of each song PC or body mass on habitat type and continent. For song PC4 the full regression model was significant ($F_{3,45} = 11.79$, $P = 0.001$), and explained 21% of the variation. This was due to an effect of habitat type on song PC4 (standardized partial $\beta = -0.45$, $P = 0.002$). Song PC 4 did not differ among continents and the interaction term was not significant either (Table 2). The regression of song PC1 was also significant ($R^2 = 0.18$, $F_{3,45} = 10.04$, $P = 0.003$) due to the interaction term only ($P = 0.01$), not to any of the main effects (both $|\beta| < 0.13$, both $P > 0.40$). For the remaining song PCs and also for body mass there were no differences between habitat types or continents (all $|\beta| < 0.17$, all $P > 0.26$, Table 2).

Table 2 Standardized partial regression coefficients (β), proportion of variation explained (R^2), and significance values (P) of multiple GLS regressions of a song PC or body mass on habitat type and continent

Trait	R^2 (P), full model	β (P), habitat[a]	β (P), continent[b]	P, interaction
Song PC1	**0.18 (0.003)**	−0.11 (0.41)	0.12 (0.41)	**0.01**
Song PC2	0.03 (0.23)	0.16 (0.26)	0.09 (0.53)	0.87
Song PC3	0.01 (0.53)	0.02 (0.90)	0.01 (0.96)	0.53
Song PC4	**0.21 (0.001)**	**−0.45 (0.002)**	0.06 (0.68)	0.85
Song PC5	0.02 (0.35)	<0.01 (0.99)	0.11 (0.46)	0.57
Body mass	0.04 (0.17)	−0.18 (0.22)	0.03 (0.83)	0.59

In all cases, degrees of freedom are 3 and 45. Significant effects are in bold typeface

[a] A positive regression coefficient means that the trait is larger in closed than in open habitats, and vice versa for negative coefficients

[b] A positive regression coefficient means that the trait is larger in Europe than California, and vice versa for negative coefficients

These results were not due to differences in body mass among communities. When including body mass as a covariate the above results are stronger (song PC4: $F_{4,44} = 28.08$, $P < 0.001$, β of habitat = −0.57, $P < 0.001$; song PC1: $F_{4,44} = 19.52$, $P < 0.001$, interaction of continent and habitat, $P = 0.006$). Including body mass in the regression there was also a tendency for the model of song PC2 to be significant ($F_{4,44} = 6.58$, $P = 0.014$) due to the effect of mass (β of mass = −0.28, $P = 0.051$, all other $|\beta| < 0.11$ and $P > 0.21$), but this was not significant after correcting for multiple comparisons (5 PCs, Bonferroni adjusted $\alpha = 0.01$).

Distributions of phenotypes

The distribution of song PC5 was significantly similar between the two open habitat communities (2-samples Kolmogorov–Smirnov test, $Z = 0.41$, lower-tail $P = 0.005$, Bonferroni adjusted α for six tests in this pair of communities = 0.008), and PC4 had a non-significant tendency to be identically distributed in these two communities ($Z = 0.55$,

Table 3 Results of 2-samples Kolmogorov–Smirnov tests for similarity of the distribution of phenotypes between communities in identical habitats

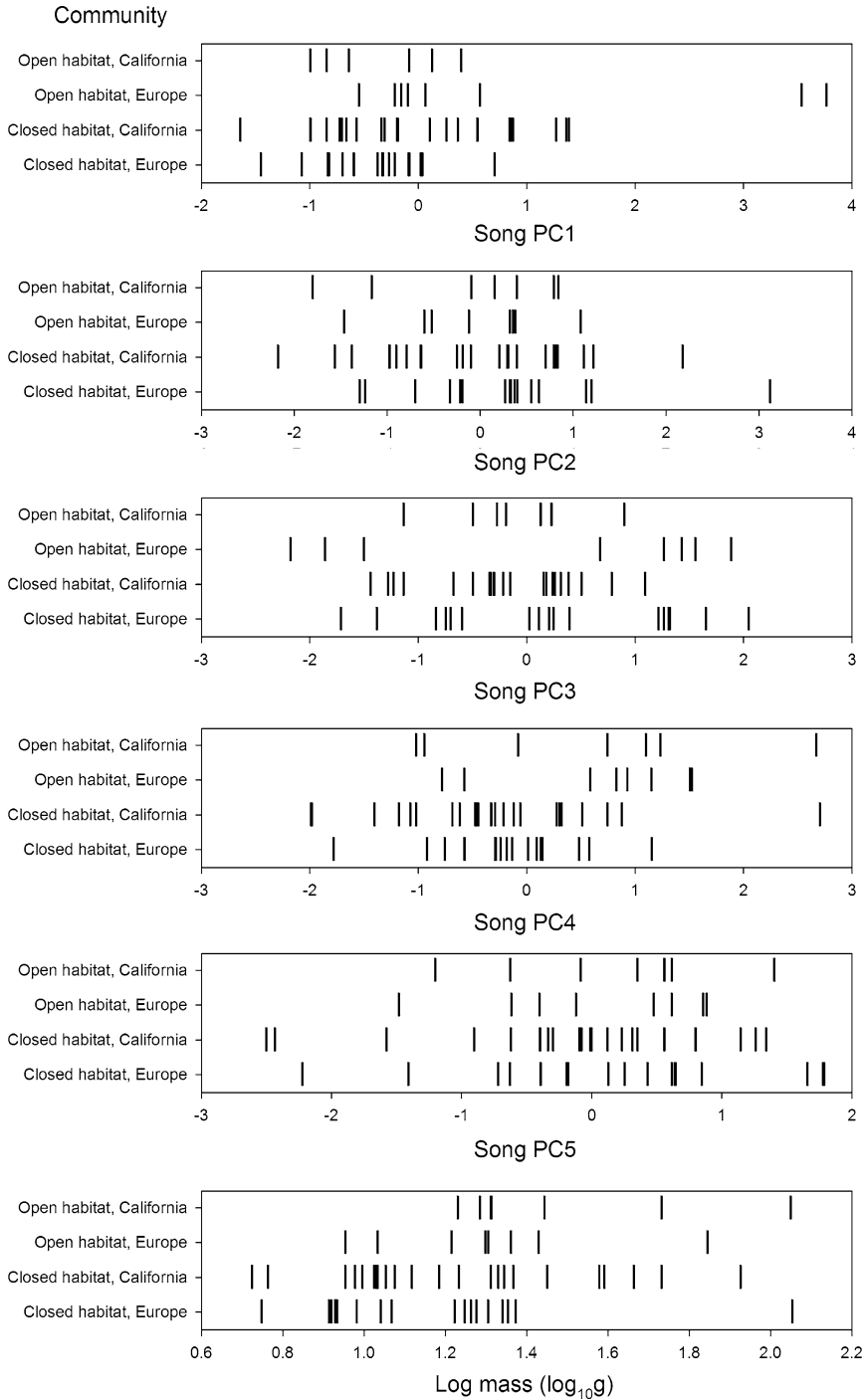|	Open habitat communities		Closed habitat communities	
	Z	Lower-tail P	Z	Lower-tail P
Song PC1	1.10	0.83	1.31	0.94
Song PC2	0.59	0.12	0.75	0.38
Song PC3	0.97	0.69	1.10	0.82
Song PC4	0.55	0.08	0.71	0.31
Song PC5	0.41	0.005	0.66	0.22
Body mass	0.72	0.33	0.65	0.20

Fig. 2 Distribution, in each of the 4 passerine communities, of the 5 song principal components (PCs) with eigenvalues above 1 (see text for details)

lower-tail $P = 0.08$, Table 3, Fig. 2). In all other cases, the distributions of song PCs and also body sizes were not significantly similar between communities in identical habitat type (all $Z > 0.58$, all lower-tail $P > 0.11$, Table 2).

The distribution of song PC3 and PC5 were similar to a perfectly spaced uniform distribution in the California open habitat community (1-sample Kolmogorov–Smirnov, $Z = 0.49$, lower-tail $P = 0.03$, and $Z = 0.44$, lower-tail $P = 0.01$, respectively), but these results do not withstand correction for multiple tests. For the other communities, PCs and body mass distributions were not significantly similar to a uniform distribution (all $Z > 0.54$, all $P > 0.07$).

Discussion

We asked if birdsongs converged between passerine communities in similar Mediterranean climate habitats, and if within communities song phenotypes are structured so as to reduce song similarity between sympatric species.

One axis of song variation, song PC4, related to song frequency, differed significantly between open and closed habitat communities (lower frequency songs in closed habitats), but not among the two continents. Song PC4 was also correlated with the species' body size (larger species singing lower frequency songs, e.g. Wallschläger 1980; Ryan and Brenowitz 1985), but the difference between habitats was independent of body size, which did not differ between habitat types. This result was also independent of phylogeny, implying that songs converged between communities in similar habitats in the two continents, rather than those habitats being colonized by related species. Compared to open habitats, closed habitats propagate low frequency sounds more efficiently than high frequency sounds, mostly because of vegetation scattering high frequencies (Morton 1975; Bradbury and Vehrencamp 1998), and noise profiles of forested environments usually contain more insect-made noise at high frequencies (Ryan and Brenowitz 1985). Both these factors are known to influence the optimal frequency for birdsong. For example, grey-breasted wood-wrens (*Henicorhina leucophrys*) in environments with high frequency cicada choruses sing lower-frequency songs than in otherwise acoustically identical habitats (Dingle et al. 2008). Accordingly, studies in different parts of the world have consistently found that species inhabiting closed habitats sing at lower frequencies (Chappuis 1971; Morton 1975; Ryan and Brenowitz 1985; reviewed in Boncaraglio and Saino 2007). Therefore, the similarities we found between communities (both closed habitat communities having lower frequencies, and the opposite for open-habitat communities) can be explained by acoustic adaptation of the individual species to their habitat.

We found only sparse evidence of structuring at the community level. We found that the distribution of phenotypes across one axis of song variation, characterized by the length of songs and of intervals between syllables, was significantly similar in the two open habitat communities. But in all other cases the distribution of songs among species was not more similar for communities in identical habitats than expected by chance. Acoustic competition between species could result in regularly spaced phenotypes within communities (e.g. Chek et al. 2003), even if that does not translate into strong similarity across communities. But we only found suggestive evidence of uniformly distributed song phenotypes for two of the axes of song variation in the smallest of the four passerine communities.

These results suggest that community-level effects are not of major importance in structuring song phenotypes within passerine communities. There are examples in the

literature of acoustic competition among species either causing character shift (Wallin 1986; Doutrelant and Lambrechts 2001; Seddon 2005; see also Kirschel et al. 2009, for an example with a non-passerine bird) or limiting song variation (Kroodsma 1985; Naugler and Ratcliffe 1994) that, if common, could shape community structure. There are also some studies that failed to find such interspecific effects (Hunter and Krebs 1979; Espmark 1999; Lohr 2008). A whole-community comparison had not been done to evaluate the importance of heterospecific acoustic competition in structuring song phenotypes within communities, and ours suggests it may play a minor role. We suggest that song evolution due to community composition, or species sorting based on song, may happen but generally be of a localised nature that does not shape the community overall. For example, acoustic competition could affect some closely related species (as in *Ficedula* flycatchers, Wallin 1986) and, since passerine songs are often complex signals that vary in many dimensions, most other species be sufficiently dissimilar that problems of species recognition are not important. Although similar songs can evolve in different lineages (e.g. Price et al. 2007), song evolution by sexual selection generally makes species diverge from each other rather than converge (e.g. Irwin 2000), and therefore the chances that unrelated species evolve songs to be very alike should be small. In addition, it was argued that, due to how vertebrates perceive and discriminate stimuli, song similarities are more likely to interfere with detection (when heterospecifics sing simultaneously using similar frequencies) than to cause species misidentification (Brumm and Slabbekoorn 2005), and temporal avoidance of heterospecifics may alleviate this problem (Planqué and Slabbekoorn 2008; Luther 2008).

We conclude that some song traits converge between communities in identical habitats, attributable to acoustic adaptation of the species individually. However, we did not find evidence for important effects of interspecific acoustic competition in these communities. Nevertheless, further research may be warranted in more diverse and densely populated passerine communities, such as tropical rainforests where many species sing simultaneously (Planqué and Slabbekoorn 2008; Luther 2009), and where interspecific acoustic competition or interference with detection may be more important selection pressures.

Appendix

See Table 4.

Table 4 Average values of all song measurements for each species, sample sizes, and body size

Species	Syntax	Song length (s)	Length of syllables (s)	Length of intervals (s)	Peak frequency (kHz)	Frequency bandwidth (kHz)	Elements per syllable	Frequency inflections per syllable	Two voiced sounds	Harmonics	Rattles	Body mass (g)	Songs measured	Syllables measured
Aegithalos caudatus	0.65	0.75	0.03	0.06	5.39	6.56	1.35	0.18	0.04	0.85	0.00	8.6	6	17
Aimophila ruficeps	0.10	2.49	0.08	0.04	5.24	4.53	1.64	2.08	0.21	0.09	0.03	19.3	3	39
Ammodramus savannarum	0.00	2.90	0.26	0.13	7.09	1.30	1.07	0.00	0.00	0.00	0.20	17.0	3	15
Anthus campestris	1.00	0.34	0.34	0.50	3.53	3.28	2.57	4.14	0.25	0.25	0.29	23.0	7	7
Baeolophus inornatus	0.98	3.03	0.07	0.03	4.45	2.73	1.00	1.46	0.02	0.14	0.03	17.1	10	83
Carduelis cannabina	0.42	10.2	0.13	0.07	4.19	3.42	1.18	0.44	0.04	0.51	0.31	20.2	2	78
Carduelis lawrencei	0.50	3.82	0.15	0.09	4.53	4.20	1.13	2.06	0.03	0.58	0.05	10.6	1	16
Carduelis psaltria	0.58	5.59	0.11	0.09	4.11	4.78	1.25	1.33	0.13	0.41	0.08	9.5	2	40
Carpodacus mexicanus	0.33	3.82	0.10	0.05	3.52	1.97	1.10	1.69	0.07	0.02	0.13	21.4	3	48
Carpodacus purpureus	0.21	4.20	0.15	0.07	3.20	2.50	1.28	2.72	0.18	0.26	0.07	23.3	4	43
Certhia brachydactyla	0.33	0.99	0.12	0.05	5.78	1.49	1.00	0.83	0.00	0.00	0.13	8.2	1	6
Chamaea fasciata	1.00	4.27	0.06	0.07	2.99	1.11	1.36	1.69	0.00	0.27	0.00	15.3	2	45
Contopus sordidulus	0.00	0.68	0.26	0.03	3.36	1.21	1.10	1.40	0.00	0.00	0.15	13.1	5	10
Emberiza hortulana	0.60	1.41	0.24	0.05	3.41	2.38	1.20	0.40	0.25	0.30	0.55	19.9	1	5
Empidonax difficilis	0.00	0.44	0.11	0.02	5.58	2.15	1.00	1.22	0.00	0.13	0.00	10.7	13	23
Erithacus rubecula	0.13	5.19	0.10	0.06	4.10	2.50	1.38	1.38	0.09	0.25	0.13	17.7	1	32
Fringilla coelebs	0.79	2.71	0.09	0.04	4.33	3.32	1.45	1.58	0.05	0.20	0.11	23.6	2	33
Hippolais polyglotta	0.36	22.9	0.11	0.06	4.16	3.86	1.35	0.92	0.09	0.68	0.17	11.0	1	133
Icterus bullockii	0.27	2.54	0.08	0.08	3.08	2.62	1.00	0.91	0.00	0.61	0.00	37.9	2	22
Lanius meridionalis	1.00	0.22	0.22	0.50	3.57	4.13	2.40	3.70	0.23	0.58	0.00	70.0	10	10
Lullula arborea	1.00	7.90	0.10	0.07	3.91	1.51	1.28	1.57	0.00	0.00	0.00	26.9	3	79
Luscinia megarhynchos	0.66	11.8	0.09	0.07	4.19	3.38	1.36	0.90	0.11	0.11	0.13	18.3	5	137
Melospiza melodia	0.78	5.45	0.09	0.05	5.65	2.66	1.08	0.56	0.13	0.14	0.07	20.5	4	78
Myiarchus cinerascens	0.45	2.70	0.13	0.12	2.68	1.37	1.21	1.24	0.00	0.08	0.45	28.2	10	29
Oenanthe hispanica	0.00	1.03	0.09	0.04	3.38	2.29	1.88	0.00	0.00	0.00	0.56	16.4	1	8
Parus major	0.74	5.78	0.12	0.13	4.67	1.18	1.00	0.38	0.00	0.00	0.43	18.9	7	47
Passerculus sandwichensis	0.75	3.88	0.10	0.08	7.18	1.74	1.17	0.00	0.27	0.11	0.22	20.6	3	36
Passerina caerulea	0.00	3.12	0.10	0.04	3.73	3.51	1.18	1.56	0.11	0.24	0.28	27.8	2	34

Table 4 continued

Species	Syntax	Song length (s)	Length of syllables (s)	Length of intervals (s)	Peak frequency (kHz)	Frequency bandwidth (kHz)	Elements per syllable	Frequency inflections per syllable	Two voiced sounds	Harmonics	Rattles	Body mass (g)	Songs measured	Syllables measured
Phainopepla nitens	0.00	0.57	0.35	0.03	2.50	1.73	1.80	1.40	0.08	0.40	0.15	22.1	7	10
Pheucticus melanocephalus	0.00	7.27	0.18	0.19	2.86	3.09	1.06	2.68	0.02	0.18	0.01	46.1	3	31
Phylloscopus bonelli	1.00	1.16	0.06	0.02	4.16	3.56	1.00	1.31	0.00	0.00	0.00	8.5	3	29
Phylloscopus collybita	0.63	13.4	0.10	0.15	4.04	2.85	1.16	1.39	0.16	0.06	0.00	8.3	4	79
Pipilo crissalis	0.95	3.80	0.05	0.08	4.94	2.36	1.00	1.20	0.00	0.48	0.00	53.9	3	40
Pipilo maculatus	0.36	1.62	0.28	0.07	3.79	3.35	2.18	1.27	0.05	0.23	0.23	39.0	3	11
Polioptila caerulea	0.22	2.13	0.11	0.10	3.52	4.91	1.00	1.00	0.28	1.00	0.00	5.8	3	18
Psaltriparus minimus	0.62	7.34	0.08	0.05	7.43	3.18	1.10	1.23	0.35	0.10	0.15	5.3	2	79
Regulus ignicapillus	0.96	2.14	0.09	0.05	7.46	1.81	1.00	0.92	0.00	0.00	0.06	5.6	2	24
Sitta europaea	1.00	5.66	0.08	0.08	3.07	2.19	1.00	1.09	0.00	0.39	0.00	22.6	6	66
Sturnella neglecta	0.00	3.15	0.15	0.09	2.95	1.64	1.07	0.79	0.07	0.12	0.04	112	4	28
Sylvia atricapilla	0.04	7.08	0.09	0.06	3.59	2.12	1.22	0.34	0.04	0.06	0.03	16.7	2	67
Sylvia cantillans	0.25	7.69	0.08	0.05	4.31	4.69	1.42	0.86	0.10	0.53	0.25	9.6	4	119
Sylvia conspicillata	0.31	3.00	0.11	0.04	4.49	3.08	1.39	0.44	0.18	0.31	0.16	9.0	5	54
Sylvia hortensis	0.73	17.6	0.10	0.08	3.13	3.62	1.06	0.40	0.11	0.34	0.38	21.9	4	172
Sylvia melanocephala	0.34	7.77	0.07	0.05	3.50	3.78	1.25	0.17	0.18	0.36	0.49	11.7	2	99
Sylvia undata	0.31	2.71	0.07	0.04	4.20	4.36	1.39	0.31	0.12	0.26	0.58	10.8	5	51
Thryomanes bewickii	0.76	4.03	0.08	0.03	4.13	2.94	1.37	0.65	0.08	0.08	0.08	9.90	3	68
Toxostoma redivivum	0.37	7.51	0.12	0.14	2.92	2.65	1.22	1.48	0.05	0.42	0.34	84.4	4	46
Troglodytes aedon	0.71	3.25	0.06	0.03	4.18	3.29	1.15	1.15	0.16	0.25	0.10	10.8	4	72
Turdus merula	0.00	3.28	0.19	0.08	3.13	3.14	1.16	0.88	0.21	0.42	0.34	113	3	25
Vermivora celata	0.99	2.79	0.03	0.03	5.23	2.14	1.00	0.79	0.17	0.00	0.00	9.0	3	71
Vireo gilvus	0.00	3.32	0.11	0.05	3.69	1.86	1.02	1.60	0.13	0.03	0.20	11.9	4	43
Vireo huttoni	0.21	1.18	0.27	0.43	4.17	3.22	1.00	1.93	0.05	0.29	0.41	11.3	12	14

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