Birdsong characteristics are related to fragment size in a neotropical forest

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The oscine passerines, an avian suborder that comprises almost half of all bird species worldwide, learn their song primarily through cultural transmission. As the world’s forests become increasingly fragmented and the population sizes of many forest-dwelling species decline, there may be increasingly restricted opportunities for the transmission of cultural information. However, the effects of forest fragmentation on birdsong have not been well documented. In this paper, we examine the relationship between forest fragment size and song characteristics for two forest bird species, an oscine passerine (orange-billed sparrow, Arremon aurantiacus) that learns its song culturally, and a suboscine passerine (scale-crested pygmy tyrant, Lophotrichus pileatus) that does not. Recordings were taken from individuals in 12 premontane wet forest fragments ranging in size from approximately 1.4 ha–360 ha in southern Costa Rica. As predicted under the ‘cultural erosion’ hypothesis, we found that acoustic characteristics associated with song complexity such as the number of syllables per song and song duration decreased with decreasing fragment size for the oscine but not for the suboscine species. This study supports the idea that learned cultural elements are sensitive to fragment size and that cultural diversity should be considered along with other forms of biodiversity in the conservation of social learning species.

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that repertoire size or complexity may be associated with increased fitness and longevity (Nowicki, Hasselquist, Bensch, & Peters, 2000; Reid et al., 2005; Searcy & Yasukawa, 1996; Yasukawa, Blank, & Patterson, 1980). Large differences in vocal behaviour among fragmented populations could result in cultural divergence and dialect formation among populations over time (Laiolo & Tella, 2007). Reproductive isolation through the formation of local mating preferences for particular dialects may even lead to speciation (Irwin, Bensch, & Price, 2001).

Alternatively, under the ‘acoustic competition’ hypothesis (Naugler & Ratcliffe, 1994), song meme richness or complexity will increase with decreasing fragment size. In diverse animal communities, acoustic niche space may be heavily partitioned due to competition, particularly during key periods such as sunrise. The decline in species diversity with forest fragmentation opens up acoustic niche space within bandwidths commonly used by calling animals. This could lead to increased acoustic richness or complexity (acoustic character release) in those species remaining in the smaller fragments that previously were more constrained spectrally or temporally in their production of acoustic signals. This latter idea may be controversial, as recent studies (e.g. Tobias, Planqué, Cram, & Seddon, 2014) have demonstrated clustering and synchrony in signals (and thus decreased acoustic richness) with increasing species richness.

Because meme richness may change more quickly than gene richness, cultural divergence, either through erosion or release, would be expected to occur more quickly in birds that learn their song based on individuals heard in the same area. In this paper, we examine the effects of forest fragmentation on vocal behaviour for two passerine species, an oscine passerine (orange-billed sparrow, Arremon aurantirostri) that learns its song culturally, and a suboscine passerine (scale-crested pygmy tyrant, Lophotriccus pileatus) that does not. We address the general hypothesis that acoustic characteristics such as the number of syllables per song, the frequency bandwidth of each song and song duration vary with fragment size for the oscine but not for the suboscine species. Specifically, under the cultural erosion hypothesis, we predicted that these characters, closely associated with vocal performance or ‘song complexity’ (Morinay, Cardoso, Doutrelant, & Covas, 2013), would decrease with decreasing fragment size, but only for the orange-billed sparrow. Alternately, under the acoustic character release hypothesis, we predicted that these same characters would increase with decreasing fragment size.

METHODS

Study Sites

Recordings were taken from individuals in a total of 12 forest fragments ranging in size from approximately 1.4 ha to 360 ha and located in or near the Organization for Tropical Studies Las Cruces Field Station in Coto Brus county, southern Costa Rica (Fig. 1, Table 1). The entire area was primarily tropical premontane wet forest (Holdridge, Grienke, Hatheway, Liang, & Tosi, 1971) until the late 1940s when a government programme was established to encourage settlement and agriculture in the county (Zahawi, Duran, & Kormann, 2015). All fragments were at elevations between 1025 and 1200 m and were dominated by secondary wet forest with a canopy up to 25 m tall and a midcanyon layer composed of broadleaf trees, palms and tree-ferns. We did not conduct detailed analyses of understory density, but it appeared broadly similar among all fragments. All study sites were separated by a matrix of mixed-use pasture lands, agricultural (primarily coffee) fields and other forest fragments not included in this study. Annual precipitation ranges from 3.5 m to 4.0 m and mean annual temperature at Las Cruces Biological Station is ~21 °C (Zahawi et al., 2015).

Study Species

The orange-billed sparrow and the scale-crested pygmy tyrant were chosen because both are commonly found in fragments of various sizes and have demonstrated extremely low movement rates among fragments (Borgella, 1995). The latter is important because regular movement among fragments could result in confounding the effects of fragment size on vocal meme richness. Both species appear to maintain year-round territories, however, territory size estimates have not yet been conducted. The orange-billed sparrow is omnivorous and forages for insects and fruits on or near the ground. It can commonly be found in dark understory of humid forests and tall second-growth woods from southern Mexico to Ecuador (Hart et al., 2013). The scale-crested pygmy tyrant can be found in the middle and upper understory of wet, mossy mountain forest foraging for insects on foliage or on branches (Stiles & Skutch, 1989). Understory insectivores such as these comprise one of the most sedentary groups of birds in the Neotropics (Levey & Stiles, 1992).

The primary male song of the orange-billed sparrow can be best described as a tinkling series of high-pitched, thin metallic or squeaky notes that alternately rise and fall (Stiles & Skutch, 1989; Fig. 2a). The male song of the scale-crested pygmy tyrant may be characterized as a series of sharp, loud and emphatic notes that may be all on the same pitch or rise and accelerate (Stiles & Skutch, 1989; Fig. 2b). The broad similarity in the structure of song between orange-billed sparrows and scale-crested pygmy tyrants (both are composed of a series of individual notes or syllables) facilitates comparison of song characteristics.

Sound Recording and Analysis

Recording was conducted between 0600 and 0930 hours for a single day per year per fragment. The primary songs of orange-billed sparrow males were recorded in 2008, 2009 and 2016, but the songs of male scale-crested pygmy tyrants were only recorded in 2008 and within seven of the 12 fragments. We focused on the primary male song for both species, and did not analyse less common song types or calls. Individuals were identified either visually or aurally, and recorded for 1–5 min from a distance of 10–20 m. After an individual was recorded, we moved at least 50 m to a new territory within the fragment to minimize the chance of recording the same singing individual. For orange-billed sparrows, the total number of individuals recorded ranged from four in the smallest fragments, to 35 in the largest (Table 1). For the rarer scale-crested pygmy tyrant, this number ranged from two to three individuals. For each recorded individual, we analysed a minimum of eight songs, with the exception of scale-crested pygmy tyrant songs at one site (Cedeno) where the minimum was three. Only those songs that had the highest signal/noise ratio and did not overlap with other bird calls were chosen for analysis. Because this research was purely observational, it was exempted from institutional (University of Hawaii Office of Research Compliance, Animal Welfare and Biosafety Programs, EX 17-007) and governmental (United States Department of Agriculture, Animal Plant Health Inspection Service, Public Health Service) policy regulations.

All vocalizations were recorded using a Marantz PMD 660 or 661 professional field recorder connected to a directional Sennheiser ME 67 shotgun microphone with a Rycote Softie windshield mounted in a Rycote Pistol-grip (Rycote Microphone Windscreens Ltd, Gloucestershire, U.K.). The Sennheiser ME 67 microphone had a...
frequency response of 40 Hz–20 kHz (±2.5 dB) and a maximum input sound level of 125 dB at 1 kHz (total harmonic distortion, THD = 1%). All tracks were recorded in 24-bit WAV format at a 44.1 kHz sampling rate. Digital sound files were downloaded directly to Raven 1.5 software (Bioacoustics Research Program, 2014) and converted into spectrograms, which were measured using a Hann window with a window size of 23.2 ms, window overlap of 50% and discrete Fourier transform (DFT) size of 1024 samples.

We measured the number of syllables (generally a continuous trace within a song spectrogram) per song, song duration (total length of song from beginning to end, in seconds) and peak frequency (the frequency at which the most energy is expelled within the song, in Hz) using cursor placement in Raven. Frequency bandwidth was measured with the ‘threshold’ method (Podos, 1997; Ríos-Chelén et al., 2017) using the power spectrum view in Raven. A threshold of 24 dB was subtracted from the maximum amplitude at peak frequency for each vocalization measured. The minimum frequency was calculated as the intersection of this value with the power spectrum line to the left of the peak frequency, and the maximum frequency was calculated as the intersection of this value with the power spectrum line to the right of the peak frequency.
Table 1
Number of orange-billed sparrows and scale-crested pygmy tyrants recorded in 12 wet forest fragments in southern Costa Rica, the total number of songs analysed, song duration, peak frequency, number of syllables and bandwidth, ordered by forest fragment area

| Forest fragment | No. of individuals | No. of songs | Forest fragment area (ha) | Song duration (s) | Peak frequency (Hz) | No. of syllables | Bandwidth (Hz) |
|-----------------|-------------------|--------------|--------------------------|-------------------|---------------------|-----------------|----------------|
| **Orange-billed sparrow** | | | | | | | |
| Muñeco          | 6                 | 312          | 1.4                      | 1.4 ± 0.4         | 7393.5 ± 413.9      | 6.69 ± 2.3      | 4000.7 ± 774.1   |
| Copal           | 5                 | 326          | 3.0                      | 1.65 ± 0.4        | 7545.1 ± 646.0      | 8.49 ± 2.7      | 3648.1 ± 902.0   |
| Sabalito 2      | 9                 | 211          | 4.64                     | 1.61 ± 0.4        | 7767.5 ± 478.0      | 8.04 ± 2.5      | 4601.7 ± 946.2   |
| Los Ángeles     | 9                 | 214          | 6.2                      | 1.56 ± 0.4        | 7793.6 ± 584.4      | 7.24 ± 2.2      | 4117.5 ± 568.2   |
| Finca Soña      | 6                 | 117          | 7.24                     | 2.44 ± 0.8        | 7778.8 ± 450.7      | 13.35 ± 4.0     | 4706.0 ± 639.5   |
| Cantaros        | 4                 | 50           | 9.4                      | 1.57 ± 0.3        | 8103.4 ± 700.9      | 8.38 ± 2.0      | 4347.1 ± 508.5   |
| Brasilia        | 10                | 171          | 12.5                     | 1.71 ± 0.6        | 7685.4 ± 619.9      | 6.85 ± 2.9      | 3316.5 ± 811.2   |
| Finca China     | 8                 | 362          | 59.1                     | 1.90 ± 0.6        | 8304.5 ± 677.8      | 8.81 ± 2.9      | 4362.9 ± 828.0   |
| Loma Linda      | 14                | 207          | 75.7                     | 1.78 ± 0.4        | 7671.9 ± 563.5      | 10.12 ± 2.6     | 3866.9 ± 687.4   |
| Cedeño          | 19                | 348          | 86.4                     | 1.81 ± 0.6        | 7392.3 ± 565.9      | 9.03 ± 3.4      | 4482.0 ± 800.7   |
| Sabalito        | 11                | 222          | 127.2                    | 1.68 ± 0.5        | 7784.6 ± 706.0      | 7.66 ± 3.0      | 4745.2 ± 740.2   |
| Las Cruces      | 35                | 1163         | 360                      | 1.80 ± 0.5        | 7829.9 ± 607.5      | 10.63 ± 1.1     | 4713.7 ± 630.6   |
| **Scale-crested pygmy tyrant** | | | | | | | |
| Copal           | 3                 | 30           | 3.0                      | 1.11 ± 0.4        | 5325.1 ± 1038.5     | 3.40 ± 1.1      | 3848.2 ± 373.8   |
| Los Ángeles     | 2                 | 17           | 6.2                      | 0.62 ± 0.3        | 3108.4 ± 217.1      | 2.12 ± 1.1      | 4140.1 ± 682.9   |
| Brasilia        | 3                 | 56           | 12.5                     | 1.30 ± 0.6        | 4511.2 ± 1256.2     | 4.43 ± 2.5      | 4239.1 ± 397.8   |
| Loma Linda      | 3                 | 26           | 75.7                     | 1.06 ± 0.5        | 4003.8 ± 1703.1     | 4.29 ± 2.4      | 4177.0 ± 880.5   |
| Cedeño          | 2                 | 7            | 86.4                     | 1.21 ± 0.6        | 5819.6 ± 1668.7     | 4.57 ± 1.5      | 4481.0 ± 783.7   |
| Sabalito        | 3                 | 33           | 127.2                    | 1.18 ± 0.8        | 5632.6 ± 995.1      | 4.72 ± 3.0      | 4431.5 ± 463.2   |
| Las Cruces      | 2                 | 19           | 360                      | 0.94 ± 0.5        | 6108.6 ± 133.3      | 3.21 ± 1.5      | 4115.6 ± 211.2   |

Figure 2. Typical orange-billed sparrow (a) 11-syllable song from a large forest fragment (Las Cruces) and (b) six-syllable song from a small forest fragment (Muñeco). Six-syllable song of a scale-crested pygmy tyrant from (c) a large forest fragment (Loma Linda) and (d) a small forest fragment (Copal).
frequency. Bandwidth (Hz) for a vocalization was then calculated as the difference between the maximum and minimum frequency.

Statistical Analyses

We tested our predictions that song characters vary with the fragment size using generalized linear mixed models (GLMMs) in R 3.0.2 (R Development Core Team, 2013). We used Poisson error distributions to model the number of syllables per song. A Poisson distribution was selected because ‘number of syllables’ is a discrete variable. The overdispersion coefficients of the models were small (5 for the orange-billed sparrow and 4.1 for the scale-crested pygmy tyrant) and the P value was corrected by this overdispersion value. Log-transformed fragment area was viewed as a fixed predictor variable, and recording year (for orange-billed sparrows) and bird identity were incorporated as random factors to account for data dependence. Significance of the GLMMs for song duration, bandwidth and peak frequency were assessed using a random permutation of the dependent variables (i.e. model parameters values) and rerunning model tests using the randomized variables (Sebastián-González, Pires, Donatti, Guimarães, & Dirzo, 2017). We repeated this procedure 1000 times and verified whether the GLMM coefficient estimates were within or outside the 95% confidence interval of the distribution of the same coefficients based on the randomizations. These models also included log-transformed fragment area as a fixed predictor variable, and recording year (for orange-billed sparrows) and bird identity as random factors.

RESULTS

The mean (±SD) number of syllables per song for orange-billed sparrows ranged from 6.6 ± 2.3 in the smallest fragment to 10.63 ± 3.1 in the largest (Table 1). However, the highest number of syllables per song were recorded from a medium fragment (Finca Sofía) with a mean of 13.35 ± 4.0 (Table 1). Similarly, song duration (s) was shortest in the smallest fragment (1.43 ± 0.4) and longest in the medium fragment, Finca Sofía (2.44 ± 0.8). There was a significant effect of fragment size on three of the four song parameters measured for the orange-billed sparrow. The number of syllables per song increased with fragment size ($\beta = 0.0295$, $P < 0.001$; Fig. 3), as did song duration ($\beta = 0.0238$, $P < 0.001$; Fig. 3) and the peak frequency of the song ($\beta = 51.17$, $P < 0.01$; Fig. 4), but not bandwidth ($\beta = 19.60$, $P = 0.447$; Fig. 4). For the scale-crested pygmy tyrant, the number of syllables per song ranged from 2.1 ± 1.1 to 4.72 ± 3.0 and song duration ranged from 0.62 ± 0.3 s to 1.3 ± 0.6 s. There was no effect of fragment size on either the number of syllables per song ($\beta = 0.057$, $P = 0.341$; Fig. 3), the length of song ($\beta = 0.035$,
Our results generally supported the predictions of the cultural erosion hypothesis. Song ‘complexity’ (measured here as the number of syllables per song) and song duration decreased with decreasing fragment size, but only for the song-learning orange-billed sparrows. The most likely explanation for this decrease is that birds in smaller fragments are exposed to fewer tutors during their song acquisition and learning period (Lynch, 1996), which may lead to a more limited variety of syllable combinations and shorter songs in general. However, the bandwidth of a song was not related to fragment size. This indicates that despite there being fewer syllables as fragment size decreases, the bandwidth occupied by those syllables stays relatively constant. Interestingly, peak frequency of songs also decreased with decreasing fragment size for orange-billed sparrows. There was no a priori expectation for the relationship between the frequency that receives the most power in a song and fragment size (or number of tutors). Under the acoustic adaptation hypothesis, birds structure their signals to maximize transmission in a given habitat (Morton, 1975). As signal frequency increases, the distance at which it travels in dense forest generally decreases (Ellinger & Hödl, 2003; Morton, 1975), so it might be expected that peak frequency would decrease in larger fragments so that the signal can travel further. One possibility for the decrease in peak frequency with decreasing fragment size is that the understory may have been more open in the larger fragments, allowing birds to effectively utilize a wider range of frequencies. We did not conduct detailed measurements of vegetation density within fragments so we cannot adequately address this idea. Anecdotally however, the understory was very similar among the different fragments. Another possibility is that higher species richness in larger fragments makes these fragments more acoustically diverse, so shifting to higher frequencies may reduce acoustic interference with other species.

Also, as expected under the cultural erosion hypothesis, three song variables (number of syllables, song duration and bandwidth) did not vary with fragment size for the non-song-learning scale-crested pygmy tyrant. This finding might have been strengthened with data from additional years, but this bird is not nearly as common within the fragments as the orange-billed
sparrow and is more difficult to locate, so we did not have an adequate sample size to use for any year other than 2008. Furthermore, the small sample size for scale-crested pygmy tyrants from 2008 (relative to orange-billed sparrows) raised the standard errors for these variables and increased the probability of incorrectly accepting a null hypothesis (no effect of fragment size on song) that was false. We did, however, detect a significant increase in peak frequency with fragment size for scale-crested pygmy tyrants, a species that presumably does not acquire song through learning, may justify further investigation.

The song traits measured here have not been studied in scale-crested pygmy tyrants or orange-billed sparrows before, and thus, we cannot assess their importance to sexual selection. Playback experiments broadcasting the primary male song of the orange-billed sparrows often resulted in strong response by conspecific male—female pairs in neighbouring territories (P. J. Hart, personal observation). Whether vocalizations that vary at the levels described in this study elicit different levels of response by either sex is unknown and perhaps worthy of future work. Also, this study would benefit by having better information on the process of song learning in juvenile orange-billed sparrows. We assume that the number of tutors to which young birds are exposed during their song-learning period has an effect on their song characteristics as adults, but other aspects of their social environment may play a greater role (Reecher, 2010).

Past studies have demonstrated how a variety of factors, including distance, isolation and founder effects, may influence song variability in song-learning birds (e.g. Baker, 1996; Hamao & Ueda, 2000; Lachlan et al., 2013; Rivera-Gutierrez, Matthysen, Adriaensen, & Slabbekoorn, 2010). However, few have examined how singing behaviour and song meme richness may be affected as once continuous habitats become increasingly fragmented. Laioło and Tella (2007) demonstrated that, for populations of Dupont’s lark, Chersophilus duponti, inhabiting fragments of the Spanish shrub-steppe plant community, fragmentation has led to a linear decrease in song meme repertoires and thus ‘cultural erosion’. Similarly, Sebastián-González and Hart (2017) found a significant linear relationship between song meme richness and fragment size for four species of Hawaiian forest birds. Our study differs from the two above in that the bird species in both previous studies have relatively large song repertoires and fragmentation effects are at the level of reducing the size of these repertoires. Here we show similar patterns of cultural erosion (for song learners) but for birds with just a single song type. That fragmentation affects both the overall richness of song memes as well as within-song characteristics adds further support to the hypothesis that learned cultural elements are sensitive to fragment size. While the orange-billed sparrow is not currently threatened, these effects may be occurring in many other song-learning passerines that are. Thus, as populations of these species become reduced, there may be a loss of social behaviours that further impact survival and reproductive success.

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References

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos, 70, 355–366.
Baker, M. C. (1996). Depauperate meme pool of vocal signals in an island population of singing honeyeaters. Animal Behaviour, 51, 853–858.
Bebee, L., & Frye, M. (2010). Birdsong and vocal learning during development. Encyclopedia of Behavioral Neuroscience, 1, 164–168.
Bioacoustics Research Program. (2014). Raven Pro: Interactive sound analysis software (Version 1.5). Ithaca, NY: Cornell Lab of Ornithology.
Borgella, R., Jr. (1995). Population size, survivorship, and movement rates of resident birds in Costa Rican forest fragments (M.S. thesis). Ithaca, NY: Cornell University.
Briefer, E., Osiejk, T. S., Rybak, F., & Aubin, T. (2010). Are birdsong complexity and song sharing shaped by habitat structure? An information theory and statistical approach. Journal of Theoretical Biology, 262, 151–164.
Catchpole, C. K., & Slater, P. J. B. (1995). Bird song: Biological themes and variations. Cambridge, UK: Cambridge University Press.
Cavalli-Sforza, L. L., & Feldman, M. W. (1981). Cultural transmission and evolution: A quantitative approach. Princeton, NJ: Princeton University Press.
Ellinger, N., & Hôlldobler, W. (2003). Habitat acoustics of a Neotropical lowland rainforest. Bioacoustics, 13, 297–321.
Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics, 34, 487–515.
Frankham, R., Ballou, J., & Briscoe, D. (2002). Introduction to conservation genetics. New York, NY: Cambridge University Press.
Hamao, S., & Ueda, K. (2000). Simplified song in an island population of the bush warbler, Cettia diphone. Journal of Ethology, 18, 53–57.
Hart, P., Ramos-Ordóñez, M. F., Rodríguez-Flores, C., Soberanes-González, C., Behrstock, B., Arizmendi, M. C., et al. (2013). Orange-billed sparrow (Arremom aurirostris). In T. S. Schulenberg (Ed.), Neotropical birds online. Ithaca, NY: Cornell Lab of Ornithology. https://doi.org/10.2173/nb.orbspa1.01.
Holdridge, L. R., Grenke, W. C., Hathaway, W. H., Liang, T., & Tosi, J. A., Jr. (1971). Forest environments in tropical life zones: A pilot study. Oxford, UK: Pergamon Press.
Irwin, D. E., Benisch, S., & Price, T. D. (2001). Speciation in a ring. Nature, 409, 333–337.
Lachlan, R. F., Verzijden, M. N., Bernard, C. S., Jonker, P., Koebe, B., Jaarsma, S., et al. (2013). The progressive loss of syntactical structure in bird song along an island colonization chain. Current Biology, 23, 1896–1901.
Laioło, P., & Tella, J. L. (2007). Erosion of animal cultures in fragmented landscapes. Frontiers in Ecology and the Environment, 5, 68–72.
Levey, D., & Stiles, G. (1997). Vocalizers of long-distance migration: Resource availability and movement patterns in neotropical landbirds. American Naturalist, 140, 447–476.
Lynch, A. (1996). The population genetics of birdsong. In D. E. Kroodsma, & E. H. Miller (Eds.), Evolution and evolution of acoustic communication in birds (pp. 181–197). Ithaca, NY: Cornell University Press.
Marler, P. (1970). A comparative approach to vocal learning: Song development in white-crowned sparrows. Journal of Comparative and Physiological Psychology, 71, 1–25.
Morinay, J., Cardoso, G. C., Doutrelant, C., & Covas, R. (2013). The evolution of birdsong on islands. Ecology and Evolution, 3, 5127–5140.
Morton, E. S. (1975). Ecological sources of selection on avian sounds. American Naturalist, 109, 37–38.
Naugler, C. T., & Ratcliffe, L. (1994). Character release in bird song: A test of the acoustic competition hypothesis using American tree sparrows (Spizella arborea). Journal of Avian Biology, 25, 142–148.
Novicki, S., Hasselquist, D., Benich, S., & Peters, S. (2000). Nestling growth and repertoire size in great reed warblers: Evidence for song learning as an indicator mechanism in mate choice. Proceedings of the Royal Society B: Biological Sciences, 267, 2419–2423.
Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). Evolution, 51, 537–551.
R Development Core Team. (2013). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
Reid, J., Arcepe, P., Cassidy, A. I., E. V., Hebert, S. M., Smith, J. N. M., Stoddard, P. K., et al. (2005). Fitness correlates of song repertoire size in free-living song sparrows (Melospiza melodia). American Naturalist, 165, 299–310.
Rivera-Gutierrez, H. F., Matthysen, E., Adriaensen, F., & Slabbekoorn, H. (2010). Repertoire sharing and song similarity between great tit males decline with distance between forest fragments. Ethology, 116, 951–960.
Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecological fragmentation: A review. Conservation Biology, 5, 18–32.
Schmiegelow, F. K. A., & Mönkkönen, M. (2002). Habitat loss and fragmentation in dynamic landscapes: Avian perspectives from the boreal forest. *Ecological Applications, 12*, 375–389.

Searcy, W. A., & Yasukawa, K. (1996). Song and female choice. In D. E. Kroodsma, & E. H. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 454–473). Ithaca, NY: Cornell University Press.

Sebastián-González, E., & Hart, P. J. (2017). Birdsong meme diversity in a fragmented habitat depends on landscape and species characteristics. *Oikos, 126*, 1511–1521.

Sebastián-González, E., Pires, M., Donatti, C. L., Guimarães, P. R., & Dirzo, R. (2017). Species traits and interaction rules shape a species-rich seed-dispersal interaction network. *Ecology and Evolution, 7*(12), 4496–4506. https://doi.org/10.1002/ece3.2865.

Stiles, G., & Skutch, A. (1989). *A guide to the birds of Costa Rica*. Ithaca, NY: Cornell University Press.

Tobias, J. A., Planqué, R., Cram, D. L., & Seddon, N. (2014). Species interactions and the structure of complex communication networks. *Proceedings of the National Academy of Sciences of the United States of America, 111*, 1020–1025.

Yasukawa, K., Blank, J. L., & Patterson, C. R. (1980). Song repertoires and sexual selection in the red-winged blackbird. *Behavioral Ecology and Sociobiology, 7*, 233–238.

Zahawi, Z., Duran, G., & Kormann, U. (2015). Sixty-seven years of land-use change in southern Costa Rica. *PLoS One, 10*(11), e0143554. https://doi.org/10.1371/journal.pone.0143554.