

1 Golden-cheeked warbler habitat changes

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3 *RESEARCH ARTICLE*

4 **Spatiotemporal patterns in Golden-cheeked Warbler breeding habitat quality and quantity**

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15

16 Data Availability: Analyses reported in this article can be reproduced using publicly available
17 data listed in Table 1. Final outputs are available on OSF at [DOI 10.17605/OSF.IO/T4DJX](https://doi.org/10.17605/OSF.IO/T4DJX)

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32 **ABSTRACT**

33 The Golden-cheeked Warbler, *Setophaga chrysoparia*, is a migratory songbird listed as
34 endangered under the federal Endangered Species Act that breeds exclusively in central Texas
35 and is heavily impacted by habitat conversion. The species relies on mixed Ashe-juniper and oak
36 woodlands for nest-building and shelter during spring and early summer months. Using land
37 cover data spanning the last 25 years, we conducted a geospatial analysis to quantify changes and
38 identify shifts in breeding habitat quantity and quality. Since 1985, 13% of all forests within the
39 warbler's breeding range were disturbed, with greater incidences near San Antonio (32%) and
40 Austin (24%) metropolitan areas. Additionally, there was a 45% decrease in high-quality habitat
41 (i.e., intact mixed or evergreen core forests) and a decrease in patch size. Habitats within
42 protected areas saw a less sharp decline in habitat quality and large increases in warbler
43 sightings, but these only represent 10% of all highest-quality habitat in the breeding range.
44 Drastic declines in habitat quality suggest that generalized metrics of conversion may
45 underestimate true habitat loss as degradation may impact the ecological viability of remaining
46 forests for warbler nesting. Further evidence suggests that the few protected areas within the
47 Texas range continue to play a significant role in warbler breeding. This information will assist
48 researchers and managers prioritizing conservation action and will inform upcoming species
49 status determinations.

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51 *Keywords: habitat quality, change detection, conservation, Setophaga chrysoparia*

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53 INTRODUCTION

54 Habitat loss and degradation through anthropogenic landscape modification are major drivers of
55 declining global wildlife populations and serve as primary threats justifying species' listing
56 under the United States Endangered Species Act (ESA; Hanski 2011, Bairlein 2016, Thompson
57 et al. 2016, Horváth et al. 2019, Leu et al. 2019). Habitat disturbances are even more notable for
58 Neotropical migrant songbirds that travel long and costly distances between breeding and non-
59 breeding sites. In North America, the Breeding Bird Survey – a roadside census that has been
60 conducted since 1966 – shows that half of migratory bird species are declining; declines in long-
61 distance Neotropical migrants are more pronounced than those of birds migrating shorter
62 distances (see North American Breeding Bird Survey). These species depend on multiple
63 habitats at different points in space and time, and the reduction in the quality of one habitat can
64 have far-reaching consequences for overall species persistence (Robbins et al. 1989, Zitske et al.
65 2011, Taylor and Stutchbury 2015, Jackson et al. 2019). Breeding season, though a small
66 proportion of the annual cycles for many migratory birds, is significant due to the more direct
67 association with recruitment and fitness of a species (La Sorte et al. 2017). Therefore, loss and
68 fragmentation of breeding habitats in the United States and other northern locales may have
69 particularly severe ecological implications for imperiled migratory bird populations, especially
70 when breeding distribution is very restricted.

71 The Golden-cheeked Warbler (*Setophaga chrysoparia*, GCWA) is a migratory songbird listed as
72 endangered under the federal ESA that is heavily impacted by forest conversion. The species is a
73 classic habitat specialist, breeding exclusively in the Edwards Plateau of central Texas,
74 commonly referred to as the Texas Hill Country, and preferring mature, mixed Ashe-juniper and
75 oak woodlands (Pulich 1976, Ladd and Gass 1999, Long et al. 2016). These tree species provide

76 critical material for nest-building and shelter for main GCWA food sources. A wealth of
77 literature assessing the influence of habitat factors on measures of GCWA survival (i.e.,
78 presence, reproductive success, nest survival, and density) finds that forest composition, age, and
79 patch size are important to species success (Pulich 1976, Shaw and Atkinson 1990, U.S. FWS
80 1992, Jetté et al. 1998, Magness et al. 2006, Diamond 2007, Colón et al. 2019). Their specialized
81 preference for this already range-restricted forest type, as well as the high rates of habitat loss
82 from urban developments and transportation infrastructure, led to the listing of GCWA as
83 endangered by the U.S. Fish and Wildlife Service in 1990. Since listing, the threat of habitat loss
84 persists with an estimated 29% reduction in total GCWA breeding habitat between 2000-2010
85 (Duarte et al. 2013). As of 2020, a very small portion (1.5%) of Texas lands are protected or
86 managed in a way that is consistent with biodiversity conservation (GAP 1 or GAP 2, U.S.
87 Geological Survey 2019). As such, the threat of further habitat loss and degradation remains, and
88 continued monitoring and evaluation of landscapes and populations is necessary to understand
89 the progress of GCWA recovery (Eichenwald et al. 2020).

90 A mandate of the ESA (section 4(c)(2)), regular reviews of the best available science and
91 commercial information are conducted to revisit population trends, threats to recovery, and
92 accuracy of the listing. Science that demonstrates a range-wide understanding of available
93 breeding habitat conditions and distribution is critical to engaging federal action for proper
94 protections for species recovery (La Sorte et al. 2015). Though coarse, this information may be
95 used to estimate population size and viability and, in the case of habitat conversion, can also
96 serve to evaluate the status and trends of major threats to species recovery (McGowan et al.
97 2017). For GCWA, analyses are generally focused on habitat quantity, but additional nuances of
98 habitat quality may result in a more refined understanding of population dynamics and can help

99 managers prioritize habitats for conservation and restoration. Most importantly, regular updates
100 to species habitat quality, quantity, location, and use are necessary to understand longer-term
101 temporal trends for better informed conservation efforts and for consideration in regular federal
102 assessments revisiting species listing (and other) decisions. As such, up-to-date spatiotemporal
103 trends in both the quality and quantity of species habitat at larger ecological scales are important
104 for informing conservation management and supporting continued protections for threatened and
105 endangered species.

106 The last review for GCWA was in 2014 and since then, there have been questions regarding
107 species recovery and listing status. Currently available science on GCWA breeding habitat
108 quantity assesses temporal trends on short timeframes (no more than a decade) and is now a
109 decade out-of-date (Duarte et al. 2013). Additionally, available analyses of habitat quality are
110 restricted to fractions of the breeding range (Loomis Austin 2008, Heger and Hayes 2013). There
111 is a need for an amended breeding habitat assessment to reflect recent landscape changes and
112 data availability as well as to inform upcoming species status assessments and the next steps in
113 conservation planning.

114 The objective of this study was to conduct a more comprehensive spatiotemporal model of
115 GCWA breeding habitat distribution. As part of this study, we used geospatial data spanning the
116 last 25 years to 1) update range-wide dynamics in GCWA habitat quantity, 2) analyze
117 spatiotemporal patterns in habitat quality, and 3) compare findings with GCWA sightings and
118 with local protected areas for considerations of habitat use and conservation, respectively.

119

120 **METHODS**

121 This study focused on spatiotemporal changes to habitat loss and degradation for the entirety of
122 the Golden-cheeked Warbler (*Setophaga chrysoparia*, GCWA) breeding range. Breeding and
123 nesting activities are confined to central Texas, USA where ideal habitat varies in density and
124 cover. Generally, habitat is more common in the southern and eastern regions of the range.
125 Nesting habitat is generally defined by the tree species composition. Warblers nest in habitat
126 made up of mature Ashe-juniper and a combination of other species such as live oak (*Quercus*
127 *fusiformis*), Shallow-lobed oak (*Quercus breviloba*), Texas oak (*Q. buckleyi*), post oak (*Q.*
128 *stellata*), blackjack oak (*Q. marilandica*), Lacey oak (*Q. glaucoides*), shin oak (*Q. sinuata*),
129 sugarberry (*Celtis laevigata*), Texas ash (*Fraxinus texensis*), Nuttall's oak (*Quercus taxana*),
130 cedar elm (*Ulmus crassifolia*), escarpment cherry (*Prunus serotina* var. *eximia*), pecan (*Carya*
131 *illinoensis*), and little walnut (*Juglans microcarpa*) (U.S. FWS 1992, Texas Parks and Wildlife
132 Dept). Quality habitat generally occurs in forest patches at least 100 hectares in size with
133 moderate to high density of older trees. Forests with greater variation in tree height, greater
134 average tree height, and greater density of deciduous oaks are also associated with higher
135 densities of GCWA (Wahl et al. 1990).

136

137 **Data Acquisition**

138 All spatial datasets used are publicly available and were analyzed with relation to GCWA range
139 as defined by the U.S. Geological Survey's Gap Analysis Program (Table 1). Data were acquired
140 in the summer of 2020 and analyzed using ArcPro v 2.3 (Esri, USA).

141

142 **Spatial Analyses**

143 Habitat Disturbance

144 Google Earth Engine implementation of the LandTrendr algorithm (Kennedy et al. 2018) was
145 used to identify loss of habitat within the GCWA breeding range between 1985 and 2018 from
146 Landsat imagery via breakpoints in temporal trends of NDVI (see Eichenwald et al. 2020).
147 Habitat loss was defined as the area where one habitat was degraded quickly over a short period
148 of time (including from natural or prescribed burns). For each year, we calculated the area of
149 disturbed and undisturbed habitat throughout the entire breeding range, in urban and non-urban
150 portions of the range, and in the metropolitan areas of Austin and San Antonio separately as
151 defined by U.S. Census urban area boundaries. We conducted identical calculations with forest
152 loss data from the National Land Cover Database to corroborate the analysis.

153

154 Habitat Quality

155 We applied a previously developed habitat assessment framework to determine location and
156 acreage of quality GCWA habitat for the entire breeding range in 1985 and the most current year
157 of the National Land Cover Dataset (2016, Heger and Hayes 2013). Coarser-resolution (250m)
158 models of historical land use and land cover for the contiguous U.S. were used for estimating
159 habitat in 1985 (Sohl et al. 2018). To account for differences in data resolution, the land cover
160 data from 1985 were resampled and masked by historic forest disturbance data (NLCD 2016)
161 assuming that all pixels labeled as either a) never experiencing a disturbance or b) experiencing a
162 disturbance after 1985 were forested in 1985. The framework for scoring habitat suitability is
163 based on a large body of literature citing forest composition, landscape fragmentation, and edge
164 effects as related to GCWA presence, survival and breeding success (e.g., Pulich 1976, U.S.

165 FWS 1992, Jetté et al. 1998, Ladd and Gass 1999, Magness et al. 2006, Peak 2007, Long et al.
166 2016, Reidy et al. 2017, Reidy et al. 2018, Colón et al. 2019). Additionally, Heger and Hayes
167 tested multiple models and confirmed that an evergreen and mixed forest-based model performed
168 better than models using only evergreen or mixed forest types. Habitats of highest quality are
169 intact mixed or evergreen forest cores. Factors and criteria used for scoring habitat quality
170 include:

171 Forest type: where mixed or evergreen forest types and deciduous forest within 100m of
172 mixed/evergreen forest received a 1. All other land cover types received a 0.

173 Landscape context: neighborhood statistics were used to determine the percent of forest land
174 cover in a 210m radius. Areas that were 80-100% forested received highest score (4) and areas 0-
175 20% forested the lowest (0).

176 Edge effect: scores were docked 1 if they were within 100m of the forest edge.

177 For each dataset, we calculated the amount of habitat by score throughout the entire breeding
178 range. Descriptive statistics were also generated to compare results in urban areas and
179 specifically for Austin and San Antonio metropolitan areas.

180

181 Hotspot Analysis

182 Occurrence data from open-source community science databases (iNaturalist and eBird) were
183 used to assess hotspots in GCWA sightings. Point locations were grouped by date: sightings
184 prior to 1995 (n = 647) were considered more closely linked to historic landscape patterns and
185 sightings after 2010 (n = 14,568) may give more insight on current spatial patterns. Sightings

186 during breeding season (April to August) were used. Additionally, only non-duplicate points
187 representing live observations were used if they were associated with an observation date and a
188 meaningful latitude and longitude (not the centroid of the state or county). Kernel density was
189 used to calculate density of GCWA sighting per square kilometer, with the top quartile of density
190 values representing ‘hotspots’ for GCWA nesting. Centrality and directional distribution of
191 sightings were also compared between the two time periods. We have high confidence in
192 drawing conclusions about breeding location based on sighting location because a warbler’s
193 range is on average a 100-m radius around its nest, depending on the quality of habitat (Reidy et
194 al. 2018).

195

196 Protected Areas Overlay

197 Community science data and results from habitat quantity and quality analyses were used in
198 overlays to calculate descriptive statistics based on other landscape designations and coverages
199 from the protected areas database of the U.S. (PADUS v 2.0). We used U.S. Geological Survey’s
200 Gap Analysis Program (GAP) codes, which are specific to the management intent to conserve
201 biodiversity. GAP 1 and 2 areas are managed in ways typically consistent with conservation and
202 are considered ‘protected’ in this context.

203

204 **RESULTS**

205 Before 1985, 25.64% of Golden-cheeked Warbler (GCWA) breeding range was covered by
206 forest lands (over 4.54 million acres). Between 1985 and 2016, 13% of all forests within the
207 warbler’s breeding range were converted to other land uses (Figure 1). Forest conversion was

208 more extreme in parts of the range in metropolitan areas, with 24% forest loss in the Austin
209 metropolitan area and 32% loss in the San Antonio metropolitan area. Generally, for all regions,
210 there were greater rates of decline in more recent years. Habitat quality also declined during this
211 time period throughout the breeding range (Figure 2). In the 1980s, over one-tenth of the forested
212 habitat within GCWA breeding range was intact mixed or evergreen core forests. In 2016, high
213 quality habitat made up 5% of the breeding range, indicating a 45% decrease in the highest
214 quality breeding habitat (Figure 3). Remaining quality habitat is more fragmented, with
215 significantly smaller patch sizes than in 1985 (Figure 4; $t = 1.96$, p value < 0.001). Generally,
216 quality habitat is more concentrated along the southeastern extent of the breeding range and
217 some forested areas to the northwest of Austin and in the northern parts of the breeding range
218 have improved since 1985 (Figure 2). Habitats within protected areas (i.e., GAP Code 1 & 2)
219 saw a less sharp decline in habitat quality from 27% to 20% of the breeding range (27%
220 decrease; Figure 3). However, protected habitats currently represent only 10% of all highest-
221 quality habitat in the breeding range.

222 GCWA sightings were generally spatially coincident with habitat quality. In the 1980s, 39% of
223 sightings were in high-quality habitat. As of 2020, sightings in high-quality habitat had dropped
224 to 28%, but this is still disproportionately high given that only 5% of the breeding range consists
225 of high-quality breeding habitat. The proportion of sightings in protected areas in the breeding
226 range has increased dramatically from 5% of sightings before 1995 to 59% after 2010. There
227 were small, localized shifts in the location of GCWA sighting hotspots between the 1980s and
228 2020, but breeding range-wide, the distribution of hotspots (centrality and dispersion) remains
229 the same (Figure 4). Sightings were once very concentrated to the southeastern portions of the
230 range, but are now less concentrated, with a few hotspots formed in western parts of the range.

231 Parks in and around San Antonio metropolitan area and Lost Maples Natural Area continue to be
232 hotspots for sightings. All but one of the hotspots were associated with a protected area (Figure
233 4).

234

235 **DISCUSSION**

236 We quantified the absolute change in forest cover within Golden-cheeked Warbler (GCWA)
237 breeding range and changes in breeding habitat quality over a 30-year period. Overall, we
238 estimated a 13% loss in breeding habitat with high spatial heterogeneity in landscape conversion
239 closely tied to human developments. This value is lower than other estimates and may be
240 reflective of changing forest dynamics that occur over the longer-term study period- this would
241 support our findings that greater decline has occurred in more recent years (Groce et al. 2010,
242 Duarte et al. 2013). Additionally, drastic declines in habitat quality suggest that 13% is an
243 underestimation of effective habitat loss as degradation may impact the ecological viability of
244 remaining forests for GCWA nesting. The amount of intact core forest habitat fell 45% in the 30-
245 year period leaving quality breeding sites concentrated along the southeastern extent of the
246 breeding range and in protected areas.

247 Human impact is on the rise in Texas landscapes and may compromise habitat quality. In recent
248 years, Texas has had the largest increases in population of any state in the U.S. (U.S. Census
249 Bureau 2020). In the 30-year period that was studied, the population grew 73.9% and growth is
250 projected to continue at a steady rate to 2050 (88.3% increase in the next three decades; Texas
251 Demographic Center 2019). Within GCWA breeding range, at least four counties are projected
252 to see population increases of over 100% by 2050, all of which coincide with areas of quality

253 habitat in the southeastern parts of the range: Williamson, Hayes, Comal, and Kendall counties.
254 Increased development pressures in the Texas Hill Country could continue to drive the trends of
255 GCWA habitat disturbance and degradation. Our data indicate that quality forests have
256 undergone fragmentation resulting in smaller habitat patches. Similar trends have been reported
257 more specifically for Ashe-juniper distributions across the state due to an increase in pastureland
258 and development (Diamond 1997). A reduction in canopy cover can lead to decreased nest
259 success for forest songbirds (Martin and Roper 1988, Trzcinski et al. 1999, Twedt et al. 2001).
260 Canopy cover is also essential to conceal GCWA nests located in the mid-story to upper
261 canopies of trees, thus reducing the probability of nest predation and parasitism (Reidy et al.
262 2008). Additionally, fragmentation of breeding habitat may represent barriers to dispersal of
263 birds and important genetic material (Lindsay et al. 2008). Hence, there is already evidence of
264 notable genetic differentiation among populations of GCWA, having important implications for
265 management of species like GCWA that are relatively vagile, but highly specialized in their
266 habitat preferences. Restoration and protection of connected patches may be the best option for
267 conserving or recovering such species (Young and Clarke 2000).

268 We found that only 10% of the highest quality forest habitat are in protected areas, creating both
269 challenges and opportunities. These lands, because they are managed in ways consistent with
270 biodiversity conservation, generally represent higher quality habitats with fewer human
271 disturbances (Rosa and Malcom 2020). Our findings indicate that protected areas within GCWA
272 breeding range also exhibited declines in quality, but degradation was buffered relative to the
273 overall range. As human populations grow and landscape conversion continues, protected areas
274 are expected to grow in importance. Nearly all (17 out of 18) of GCWA sighting hotspots from
275 our analysis were associated with a protected area. Additionally, the proportion of sightings that

276 occurred on protected areas saw a significant increase. It should be noted that public lands may
277 have a higher proportion of sighting simply due to their accessibility to observers. However, a
278 preliminary analysis of GCWA occupancy models from Morrison et al. (2010) also demonstrates
279 the importance of protected areas to GCWA success: areas with at least 70% probability of
280 occupancy make up 13% of the breeding range, but 62% of protected areas. Public protected
281 areas can play a central role in habitat conservation efforts because they are more amenable to
282 the application of broad-scale management strategies that more closely align with species
283 conservation. However, the extent to which public protected areas can benefit migratory bird
284 populations depends on how well protected areas are represented within the breeding range (La
285 Sorte et al. 2015). Currently, areas managed for conservation (GAP status 1 and 2) represent
286 3.23% of the breeding range. Lands with more intermediate mandates (GAP 3) provide a higher
287 degree of flexibility for the implementation of management recommendations more closely
288 aligned with maintaining biodiversity. However, these lands are also limited in the state of Texas
289 (1.71%). Expansion of protections to key habitats would require that resources be spent in
290 agency land acquisition or in private lands conservation.

291 Our findings demonstrate a need for strengthening current conservation measures and expanding
292 upon protections for GCWA habitat to ensure greater breeding success and, ultimately, species
293 recovery. Newer proposals to protect at least 30% of U.S. lands and waters by 2030 to address
294 the biodiversity and climate crises may provide additional opportunities for land designations
295 and conservation efforts for imperiled species like GCWA (Exec Order No 14008 2021, CA
296 Exec Order N-82-20 2020). While a majority of GCWA habitat conservation dollars have been
297 spent conserving GCWA breeding habitat on the outskirts of the cities of Austin and San
298 Antonio, our findings support previous work demonstrating higher rates of habitat conversion

299 near metropolitan areas (Duarte et al. 2013). Given the scarcity of public lands, the distribution
300 of intact forest habitat, and the relatively high amount of habitat loss and degradation occurring
301 in and around metropolitan areas, future GCWA habitat conservation efforts should be more
302 focused on supporting current protected areas and expanding protections to quality habitats in the
303 Balcones Canyonlands and Fort Hood areas and regions west of San Antonio and Fort Worth.
304 Additionally, projected species distribution models reflecting climate change impacts on tree
305 species indicate that the Texas Hill Country will continue to be a stronghold for Ashe-juniper
306 (with potential for population stabilization and maybe even increase/spread to the northeast;
307 McKenney et al. 2007). This suggests that efforts to conserve or restore quality GCWA habitat
308 will have long-term benefits.

309 We recognize the limitations of the analysis which equate all available mixed or evergreen
310 forests within the breeding range, and not strictly those with Ashe-juniper components, as
311 potentially suitable habitat for GCWA nesting. This is mainly due to current publicly available
312 data sources and lack of LiDAR or other advanced geospatial datasets that would clarify spectral
313 or structural differences in forest composition. Regardless, overall classification accuracies of the
314 habitat loss dataset followed methods that average a mean absolute error of less than 3%
315 (Kennedy et al. 2018). Additionally, datasets used for assessing habitat quality, though they
316 represent the most current version available, are already out of date. Collectively, this indicates
317 that our estimates for available habitat may be more liberal than in actuality. In the context of
318 federal species listing and review, landscape change analyses, habitat identification and
319 classification, and the characterization of trends over time must be considered. We selected
320 metrics that are easily applied to larger scales and interpretable to a wide audience of resource
321 managers and policy makers, regardless of biogeographic, ecological, or geospatial expertise and

322 training. Nonetheless, selection of metrics may in some cases influence how landscape change is
323 quantified and interpreted, particularly when the analysis is focused on characterizing or
324 understanding underlying landscape processes and species modeling.

325 Human landscape modification is likely to continue in the Texas Hill Country, but conservation
326 and land management actions can be taken to minimize further habitat loss and degradation in
327 GCWA breeding range. This information will assist researchers and managers in prioritizing
328 range-wide breeding habitat conservation efforts and highlights the significant role land
329 management for conservation biodiversity plays on the landscape. There remains a need to grow
330 the network of protected areas for GCWA restoration. Further, continued regular spatiotemporal
331 assessments of habitat quantity and quality are necessary to assess changes to species potential
332 for persistence and extrapolate population viability given these dynamics.

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334

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459 **TABLES**

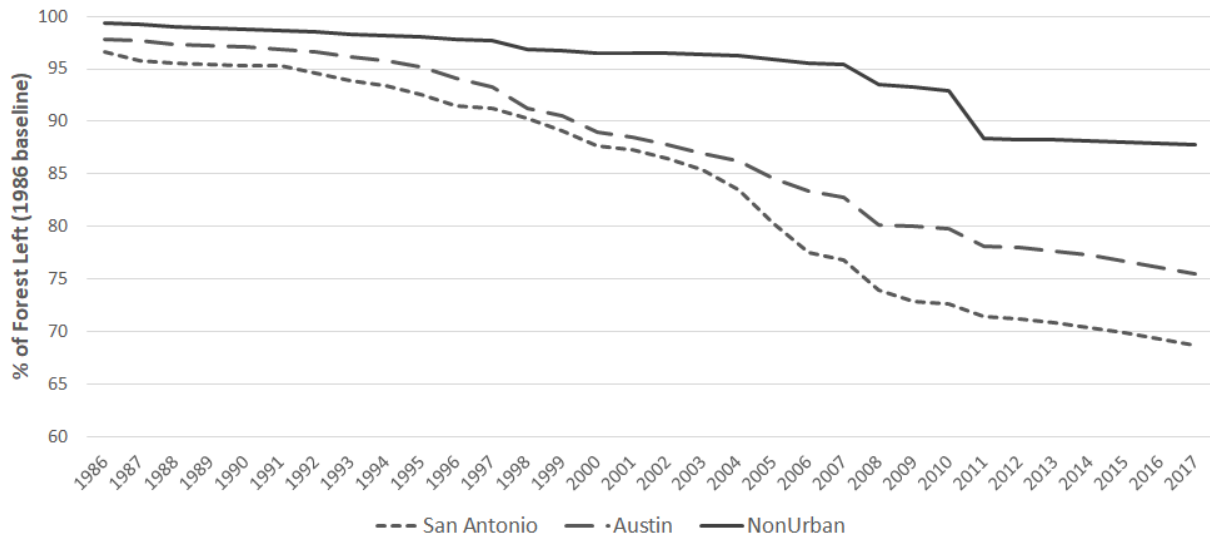
460 Table 1. Data acquired for spatiotemporal analyses on habitat disturbance, quality, and sightings.

Data	Source	Temporal Resolution	Spatial Resolution	Analysis
Landscape change	Eichenwald et al. 2020	1985-2018	30m	Habitat disturbance
Forest Change	MRLC National Land Cover Database	1985-2016	30m	Habitat disturbance
Modeled historic land use	Sohl et al. 2018	1985	250m	Habitat quality
NLCD	MRLC	2016	30m	Habitat quality
Warbler sightings	iNaturalist & eBird	1934-2020	point	Sighting Hotspots
Protected Areas	U.S. Geological Survey	2019	vector	All
Urban areas	U.S. Census	2019	vector	Habitat disturbance

Breeding range U.S. Geological Survey GAP 2001 vector Study area

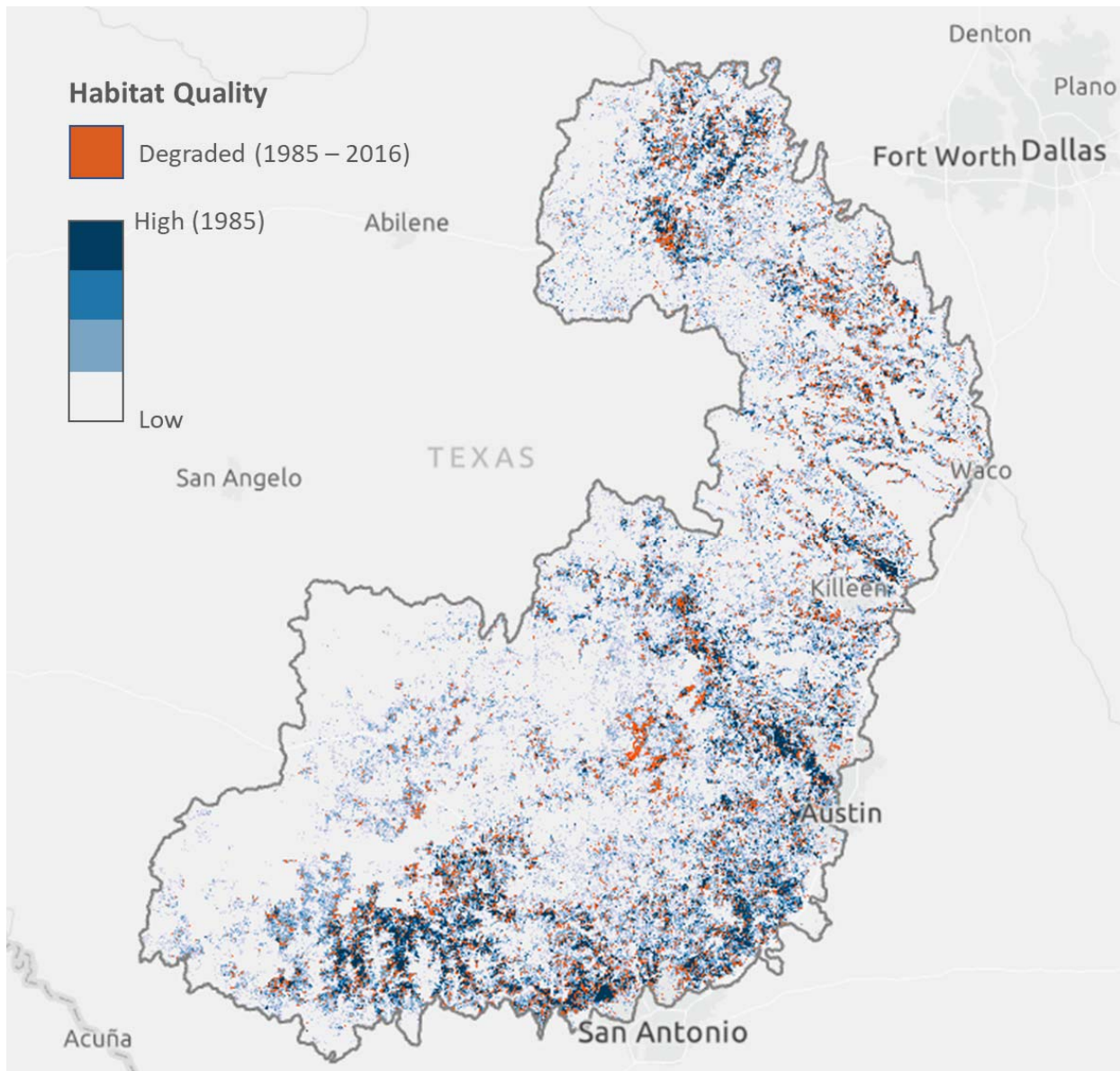
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FIGURES



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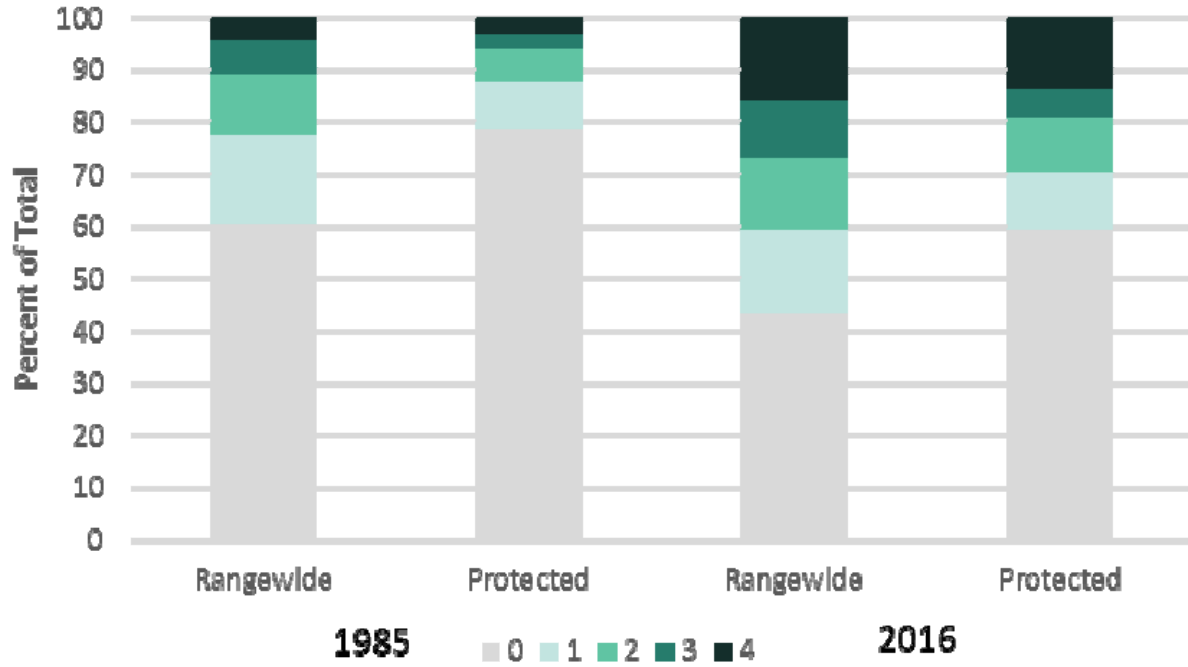
Figure 2



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Figure 3

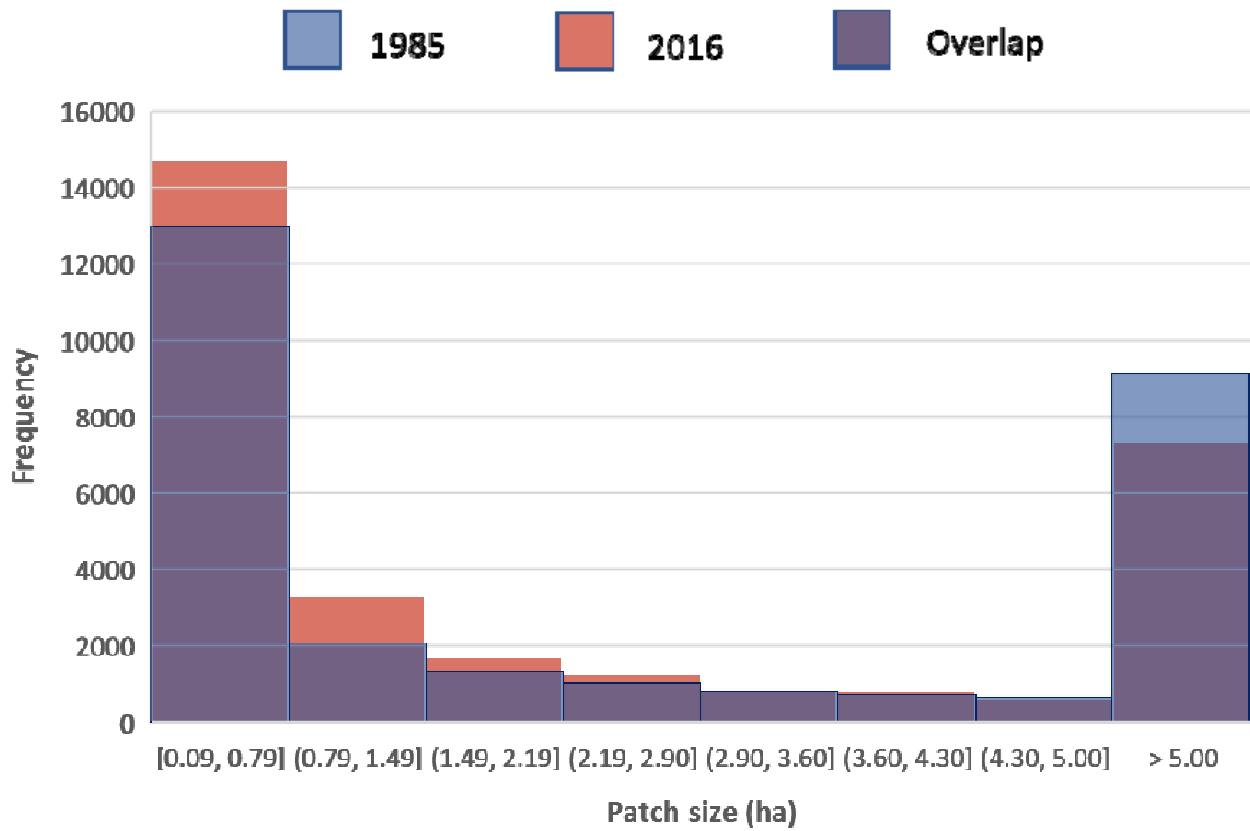


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Figure 4



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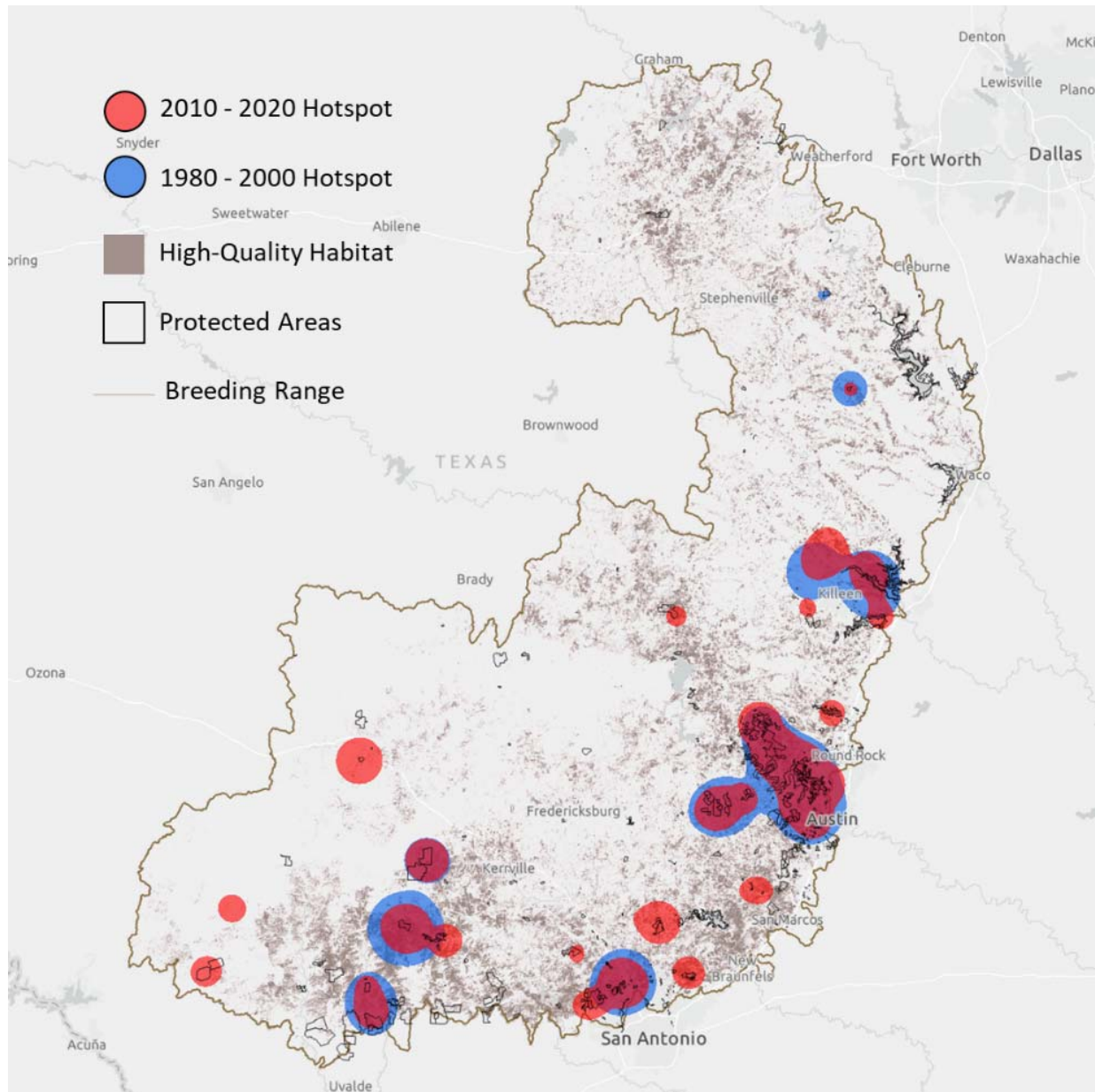
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Figure 5



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496 **FIGURE CAPTIONS**

497 Figure 1. Annual declines in forested land cover relative to a 1985 baseline for portions of the
498 Golden-cheeked Warbler breeding range that fall outside of urban boundaries and portions that
499 fall within the urban boundaries of San Antonio and Austin, respectively.

500

501 Figure 2. A map of overall change in Golden-cheeked Warbler breeding habitat quality between
502 1985 and 2016. Blues indicate areas of lower-quality habitat in 1985, white indicates high-
503 quality habitat in 1985, and red indicates high-quality habitat areas that experienced a decline in
504 habitat quality between 1985 and 2016.

505

506 Figure 3. Percent of the Golden-cheeked Warbler breeding range by habitat quality value (0 =
507 low quality, 4 = high quality) for habitats throughout the entire range and for habitats that fall
508 inside protected areas managed for biodiversity conservation (U.S. Geological Survey's
509 Protected Areas Database of the U.S., GAP codes 1 and 2) for 1985 and 2016, respectively.

510

511 Figure 4. Histograms showing frequency of patch size for high quality habitat areas in 1985
512 (blue) and 2016 (red) indicate habitat fragmentation over the time period. Means of the two
513 groups were significantly different at $\alpha = 0.05$ (p value <0.001).

514

515 Figure 5. A map comparing locations of high-quality habitat in 2016, protected areas managed
516 for biodiversity conservation (U.S. Geological Survey's Protected Areas Database of the U.S.,

517 GAP codes 1 and 2), and hotspots for Golden-cheeked Warbler sightings between 1980 – 2000

518 (in blue) and 2010 – 2020 (in red).

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