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Original Article

Spatial and Temporal Distribution of Oak Wilt in Golden-Cheeked Warbler Habitat

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ABSTRACT Research suggests the presence of oak wilt in Ashe juniper–oak (*Juniperus ashei*–*Quercus* spp.) woodland has a negative effect on habitat selection and quality for the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*). We used aerial imagery and an occupancy model to estimate the amount of golden-cheeked warbler habitat within our study region in Texas, USA, that was affected by oak wilt over a 10-year timeframe, 2008–2018, and to assess the current probability of warbler occupancy in areas affected by oak wilt prior to 1983. We also quantified vegetation characteristics to assess regeneration in areas affected by the disease. Our results indicate that oak wilt frequently occurs in golden-cheeked warbler habitat and will continue to spread into warbler habitat in the coming years. We estimated that 6.9% of golden-cheeked warbler habitat within our study region in the southwestern portion of the warbler's range was affected by oak wilt in 2008. By 2018, we predict that 13.3% of golden-cheeked warbler habitat will be affected by the disease. Areas affected by oak wilt prior to 1983 were less likely to be classified as current potential warbler habitat than were unaffected areas. We found no differences between the understory vegetation of affected and unaffected areas but, in general, oaks were more common in the overstory than in the understory, suggesting that species composition in affected areas may shift following an outbreak of oak wilt. Future management efforts should address the threat oak wilt poses to golden-cheeked warblers by incorporating applicable preventative measures. © 2014 The Wildlife Society.

KEY WORDS distribution, endangered species, forest pathogen, golden-cheeked warbler, oak wilt, regeneration, *Setophaga chrysoparia*.

The federally endangered golden-cheeked warbler (*Setophaga chrysoparia*) is a Neotropical migrant restricted to the Ashe juniper–oak (*Juniperus ashei*–*Quercus* spp.) woodlands of central Texas, USA, during the breeding season (Ladd and Gass 1999). Stewart et al. (2014) found that oak wilt negatively influences habitat selection and quality for golden-cheeked warblers, likely as a result of reduced cover in susceptible oak species. However, additional data examining the current and future extent of oak wilt within golden-cheeked warbler habitat are necessary to assess the full scope of this potential problem.

Oak wilt is a broadly distributed forest pathogen that can cause substantial modifications to vegetation; therefore, its presence on the landscape may have negative consequences for forest-dwelling songbirds (Kendeigh 1982, Rabenold et al. 1998, Tingley et al. 2002, Smith and Stephen 2005, Monahan and Koenig 2006). The disease is caused by infection by a fungus (*Ceratocystis fagacearum*) that causes blockages to form in the vascular tissues of the host (Gibbs and French 1980). Although oak wilt can occur in all oak species (*Quercus* spp.), its effects are most pronounced in red oaks (subgenus *Erythrobalanus*) and live oaks such as Texas live oak (*Q. fusiformis*). These particular species are highly susceptible to the disease and usually die within 1–6 months post-infection (Appel 1995). Oak wilt disease centers form when fungal spores are transmitted overland to a new host tree by one of several species of beetle in the Nitidulidae family (Gibbs and French 1980, Juzwick and French 1983). Once a host tree has become infected, the pathogen can spread to adjacent trees via interconnected root systems. A concentration of oaks destroyed by oak wilt and their actively infected neighbors are collectively referred to as an oak wilt center. Oak wilt centers can expand quickly (<45 m/yr) through otherwise healthy forest, usually leaving <20% of susceptible trees alive (Appel et al. 1989). There is some debate concerning the origin of oak wilt, but the available evidence suggests that its incidence has increased considerably within Texas since the 1910s, likely because of altered species composition, increased density, and

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decreased isolation of forest stands caused by changing land-management practices (Appel 1995, Juzwik et al. 2008).

Oak wilt has been identified throughout the eastern and central portions of the United States as far south as Texas where it occurs in 30 of the 35 counties occupied by the golden-cheeked warbler (Fig. 1; Texas Forest Service 2009, O'Brien et al. 2011). Appel and Camilli (2010) found that 12% ($n = 60$) of oak wilt disease centers on the Fort Hood Military Reservation were located in golden-cheeked warbler habitat. However, the incidence of oak wilt varies across the range of the disease (Gibbs and French 1980) and likely varies within Texas because of regional differences in soil type, tree species composition, tree size, and tree density (Gibbs and French 1980, Menges and Kuntz 1985, Appel et al. 1989, Bruhn et al. 1991).

Oak wilt may result in short-term changes to affected forest including reduced total canopy cover, reduced canopy cover in susceptible species, shifts in species composition, decreased live tree density, and increased edge (Appel et al. 1989, Stewart et al. 2014). Such changes are likely to be detrimental to the golden-cheeked warbler because it is a species typically found in areas of high canopy cover (Ladd and Gass 1999) whose presence has been positively correlated with increased distance to edge, oak density, and percent oak composition (Wahl et al. 1990, DeBoer and Diamond 2006, Klassen et al. 2012). Additionally, golden-cheeked warbler patch occupancy probabilities have been positively correlated with patch size and percent surrounding woodland composition (Magness et al. 2006, Collier et al. 2012). Therefore, fragmentation of habitat caused by oak wilt could decrease the suitability of areas not directly affected by the disease.

Previous research suggests that vegetation changes caused by oak wilt could last well into the future. Menges and Loucks (1984) predicted that oak wilt will cause stand composition to shift away from red oaks toward other species such as black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), and various species of white oak (subgenus *Leucobalanus*) in Wisconsin, USA. This tendency has been documented in stands affected by other pathogens such as chestnut blight, white pine blister rust, beech bark disease, and various fungal root infections (Castello et al. 1995). Alternatively, Tryon et al. (1983) found no significant change in stand composition post-oak wilt in West Virginia, USA. If oak wilt results in long-term changes to vegetation, it may have lasting impacts on golden-cheeked warblers' use of affected areas.

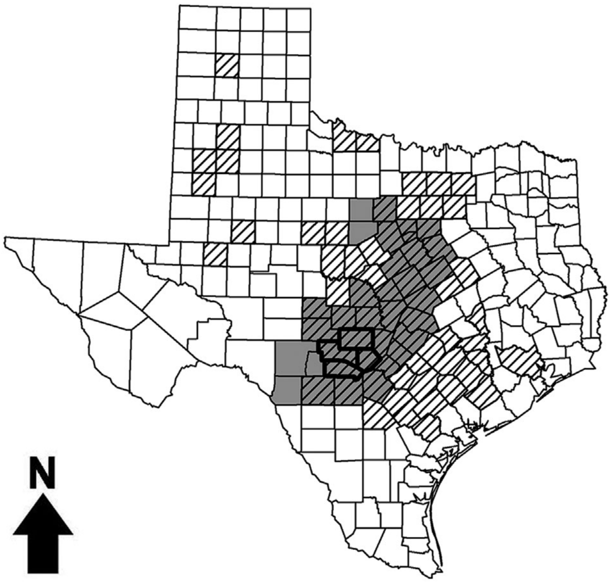

Figure 1. The breeding range of the golden-cheeked warbler (gray), Texas (USA) counties with confirmed cases of oak wilt (slashed, Texas Forest Service 2009), and study region (in bold) encompassing (clockwise from top) Gillespie, Kendall, Bandera, and Kerr counties, Texas. Oak wilt has been confirmed in 30 of the 35 counties where golden-cheeked warblers breed.

We used digital ortho-imagery and an occupancy model to estimate the amount of golden-cheeked warbler habitat affected by oak wilt in 2008 and to predict the amount of golden-cheeked warbler habitat likely to be affected by oak wilt by 2018. We assessed the effects of historical oak wilt on current probability of golden-cheeked warbler occupancy using aerial photography taken in 1982–1983. We predicted that current patch occupancy probability is negatively influenced by the historical presence of oak wilt. To assess the potential for oak wilt to cause long-term changes to vegetation, we compared characteristics of regenerating forest with adjacent unaffected forest. We predicted that the understory of regenerating forest would consist of a more open condition with fewer susceptible oaks, more Ashe juniper, and more white oaks than the understory of unaffected forest.

STUDY AREA

We conducted our study in Bandera, Gillespie, Kendall, and Kerr counties, Texas, located in the southwestern portion of the golden-cheeked warbler's range (Fig. 1). Located on the Edwards Plateau, these counties were characterized by limestone hills separated by broad, flat valleys or canyons. Elevation ranged from approximately 300 m to 750 m. Common vegetation communities included oak savanna and Ashe-juniper woodland (Diamond 1997). Collier et al. (2012) estimated that approximately 314,000 ha of golden-cheeked warbler habitat existed in these 4 counties. Oak wilt was widespread throughout the southern portion of Gillespie County, the western portion of Kendall County, and the eastern portions of Bandera and Kerr counties. The Texas Forest Service estimates that oak wilt had affected $\geq$32,030 ha in these 4 counties by 2009 (J. Zhu, Texas Forest Service, unpublished data).

METHODS

Present and Future Extent of Oak Wilt in Golden-Cheeked Warbler Habitat

To estimate the present extent of oak wilt within our study region, we used ArcMap 9.3 to remotely delineate potential oak wilt centers using the most recent high-resolution imagery available, Texas Natural Resource Information System 2008 leaf-on color infrared 0.5-m digital ortho-imagery (Ulliman and French 1977, Appel and

Maggio 1984, Everitt et al. 1999, Appel and Camilli 2010). We delineated all potential oak wilt centers visible within 96 1-km^2 sample squares that we systematically selected from a grid covering our 4-county study region. For the purposes of our delineations, we defined a potential oak wilt center as an area containing ≥ 3 dead or dying trees spaced apart ≤ 20 m (Appel et al. 1989). Once we had delineated all potential oak wilt centers within our sample squares using the 2008 imagery, we used National Agriculture Imagery Program 2010 leaf-on color infrared 1.0-m digital ortho-imagery to confirm that each potential oak wilt center represented an area of actual tree mortality as opposed to temporary defoliation. If a potential oak wilt center did not meet our criteria on the 2010 imagery, we dropped it from our data set.

We assessed the accuracy of our delineations by visiting private properties that were at least partially located within 13 (14%, $n = 96$) of our sample squares in June 2010. We ground-truthed 26 likely oak wilt centers to confirm the presence and cause of mortality. We used foliar symptoms, including veinal necrosis and vein banding, as indicators of active infection and ≥ 80% mortality of susceptible species as an indicator of past infection by *C. fagacearum* (Appel and Maggio 1984, Appel et al. 1989). We confirmed mortality at 100% ($n = 26$) of likely oak wilt centers and attributed all but one (96%, 25 of 26) of the mortality centers to oak wilt. We also walked transects spaced every 100 m across each property to locate any additional oak wilt centers that were not visible on the 2008 imagery. We covered 1,623 ha and located 11 new oak wilt centers; therefore, our technique enabled us to remotely identify 69% (25 of 36) of the oak wilt centers that were actually present. Of the oak wilt centers we missed, 91% (10 of 11) were <0.4 ha in size; 39% (14 of 36) of all centers that were actually present were <0.4 ha in size.

We used our delineations of oak wilt centers to identify areas of potential golden-cheeked warbler habitat affected by the disease in 2008. To identify habitat, we used a spatially explicit golden-cheeked warbler occupancy model described by Collier et al. (2012). Collier et al. used 2007 and 2008 LANDSAT 5 imagery to delineate woodland patches using ArcMap 9.2, and then performed an unsupervised classification to separate patches of potential golden-cheeked warbler habitat (juniper–oak woodland) from unsuitable areas such as contiguous patches of oak or juniper (Collier et al. 2012). Collier et al. used 2001 National Land Cover Data to mask any cover types (e.g., urban areas) misclassified as forest and then deleted pixels that intersected roads depicted by the Texas Strategic Mapping Program. The authors used patch size, percent surrounding woodland composition, and spatial location (latitude and longitude) to assign a probability (0 to 1) of golden-cheeked warbler occupancy to each patch. Collier et al. (2012) used a scoring classifier to validate their model by comparing survey detections with occupancy predictions. The resulting area under curve estimate (0.91) indicates that the model predicts reality with a high degree of accuracy.

We used the oak wilt centers delineated on the 2008 imagery to create a spatial model predicting the amount of golden-cheeked warbler habitat at risk of being affected by oak wilt by 2018. We chose a 10-year timeframe because it was long enough to show change but short enough to provide an estimate relevant to current management efforts. We ran a supervised classification on 2008 natural color 0.5-m ortho-imagery using ArcMap 9.3 to identify all areas within each of our 96 sample squares that could be susceptible to oak wilt (i.e., areas with trees; Fig. 2). To increase the accuracy of the classification, we manually deleted all areas misclassified as trees (e.g., cropland). Based on average oak-wilt-center expansion rates of 11–16 m/year observed by Appel et al. (1989) within our study region, we simulated yearly spread by placing a conservative 10-m buffer around each oak wilt center; then we removed all areas within the buffer that the supervised classification did not identify as trees. We

Figure 2. Example of an oak wilt center in Texas, USA, identified on 2008 digital ortho-imagery (left). The picture at right depicts the delineated boundary of the same oak wilt center in 2008 (red outline) and the predicted boundary of the center in 2018 (green outline). Successive color bands show the extent of expansion each year, 2008–2018. Oak wilt does not spread across agricultural fields and other land-cover types without trees.

completed 10 iterations of this procedure to simulate 10 years of oak wilt spread. To account for oak wilt that may spread into our sample squares from adjacent areas, we completed the same procedure for all areas within 100 m of each sample square. This provided us with a depiction of forest likely to be affected by oak wilt in 2018. Following the criteria we used to delineate oak wilt centers on the 2008 imagery, we delineated the predicted 2018 oak wilt centers within each of our sample squares (Fig. 2).

We assessed the accuracy of our predictions by comparing the extent of 19 oak wilt centers delineated during ground-truthing in 2010 to their predicted extent in year 2 of our simulation (equivalent to 2010). Of the total area within predicted oak wilt centers, 67% (57 of 84 ha) was located within the boundaries of an actual ground-truthed center. Of the total area within actual oak wilt centers, 78% (57 of 73 ha) was predicted to contain oak wilt by our simulation.

We quantified the amount of golden-cheeked warbler habitat affected by oak wilt in 2008 and the amount affected by 2018 in 4 categories of occupancy probability: low (>0 to <0.25), medium (≥ 0.25 to <0.75), high (≥ 0.75), and all. We defined these categories based on the occupancy probability of patches where Stewart et al. (2014) located territories (L. R. Stewart, unpublished data). In that study, no occupied patches ($n = 24$) had a probability of occupancy <0.25, 33% (8 of 24) had a probability of occupancy between 0.25 and 0.75, and 67% (16 of 24) had an occupancy probability ≥ 0.75. We calculated the percent of each habitat category within our sample squares that overlapped our 2008 oak wilt centers and the percent that overlapped our predicted 2018 oak wilt centers. We extrapolated these percentages to our entire study region to estimate the total area of each habitat category affected by oak wilt in 2008 and in 2018.

To account for the effects of habitat fragmentation, we re-ran the model described by Collier et al. (2012) twice to assess changes in patch occupancy probability caused by the spread of oak wilt within our 96 sample squares (McFarland et al. 2012). First, we removed forest located within the boundaries of our 2008 oak wilt centers from the Collier et al. (2012) habitat patch data set. We then ran the model to reassess current (2008) occupancy probability of patches within our study region. We repeated this procedure using our predicted 2018 oak wilt centers to reassess future (2018) occupancy probability. We calculated the revised percent of each habitat category (defined in the preceding paragraph) within our sample squares that overlapped our 2008 oak wilt centers and the revised percent that overlapped our predicted 2018 oak wilt centers. We extrapolated these percentages to our entire study region to produce an estimate of the total area of each habitat category affected by oak wilt in 2008 and in 2018 that accounts for habitat fragmentation. This assessment is based on the assumption that woodland becomes unsuitable for golden-cheeked warblers once it has been affected by oak wilt. Stewart et al. (2014) found that golden-cheeked warblers within our study region rarely place a substantial portion of their territories within oak wilt centers. Therefore, our assessment of fragmentation represents a plausible worst-case scenario regarding habitat loss caused by oak wilt spread.

The Effect of Historical Oak Wilt on Current Occupancy Probability

We used ArcMap 9.3 to remotely delineate potential oak wilt centers visible on color infrared aerial photography taken on 3 flight lines in the early 1980s: Kerrville to Bandera, Texas, taken on 27 and 28 July 1982; Fredericksburg to Johnson City, Texas, taken on 27 July 1982; and Fredericksburg to Comfort, Texas, taken on 26 July 1982 and 21 August 1983 (Fig. 3). We delineated all potential oak wilt centers visible within 46 1-km^2 sample squares that we systematically selected from a grid covering the photographed areas. Appel and Maggio (1984) delineated oak wilt centers on this imagery using a similar protocol; oak wilt was the likely cause of mortality for 86% ($n = 43$) of centers they ground-truthed from February through September 1983. We also visually delineated all unaffected forest present within our sample squares and then removed areas with oak wilt visible on 2008 0.5-m color infrared ortho-imagery. This left us with a representation of historical forest that, based on available information, has never been affected by oak wilt.

For each sample square, we calculated the proportion of the area in historical oak wilt centers and the proportion of the area in unaffected forest that was identified as current warbler habitat by Collier et al. (2012). We excluded sample squares with no oak wilt centers from this analysis. We analyzed our data in 3 categories of habitat occupancy probability: low (<0.25), high (≥ 0.75), and all. To control for possible differences across our study region, we used a paired analysis that matched the proportion of historical centers containing current habitat to the proportion of unaffected forest containing current habitat by sample square. Because our data were not normally distributed, we used 1-tailed Wilcoxon paired-sample tests (Zar 1996:167) to evaluate

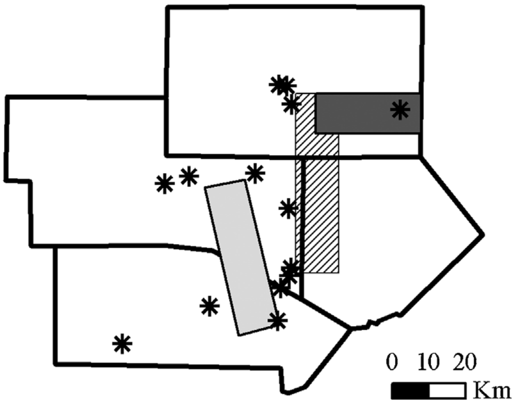

Figure 3. Study region encompassing (clockwise from top) Gillespie, Kendall, Bandera, and Kerr counties, Texas, USA. We used aerial photography taken along three flightlines, Fredericksburg to Johnson City (dark gray); Fredericksburg to Comfort (slashed); and Kerrville to Bandera (light gray), in 1982 and 1983 to assess the effects of historic oak wilt on probability of warbler occupancy in 2008. We assessed regeneration of forest affected by oak wilt at 14 study sites (asterisks) using vegetation measurements taken in 2011.

our prediction that the proportion of area currently identified as golden-cheeked warbler habitat would be less in historical oak wilt centers than in unaffected forest. If the mean current occupancy probability was greater in affected areas than in unaffected areas, we used a 2-tailed Wilcoxon paired-sample test to test for statistical significance (Zar 1996:167).

Effects on Future Stand Composition

To assess the regeneration of vegetation within oak wilt centers, we collected data from 14 study sites in conjunction with our study of golden-cheeked warbler habitat selection and quality (Stewart et al. 2014) in May and June of 2011 (Fig. 3). We selected study sites using a Geographic Information Systems shape-file depicting oak wilt centers identified by the Texas Forest Service either during aerial surveys conducted in the mid-1990s or during opportunistic visits to private properties that began in 1991 (J. Zhu, unpublished data). We randomly selected an oak wilt center from the shape-file and then accepted or rejected the location as a study site based on 2 criteria. First, the oak wilt center had to be ≥4 ha in size. Appel et al. (1989) observed mean oak wilt expansion rates of 11–16 m/year in our study region. Thus, a center ≥4 ha in size has likely been present for >6 years, enough time for regeneration to have begun. The second criterion was that each oak wilt center was adjacent to ≥20 ha of unaffected forest, the minimum patch size required for golden-cheeked warblers to successfully reproduce (Butcher et al. 2010). Aside from the size of the forested area, the potential for golden-cheeked occupancy did not influence whether we accepted a potential site. If we rejected the location as a study site or if a landowner denied us access to their property, we randomly selected another oak wilt center for consideration. Because we replaced study sites that landowners denied us access to with others selected using identical criteria, we assumed inaccessible potential study sites to be missing at random (Stevens and Jensen 2007, Collier et al. 2012). Each of our study sites included the oak wilt center identified from the shape-file plus all unaffected forest within 400 m of the center's boundary, as permitted by private property lines. If a study site contained multiple oak wilt centers spaced <400 m from one another, we considered the site to encompass the centers, the unaffected forest between them, and unaffected forest within 400 m of the outermost centers.

We identified all oak wilt centers that were present by walking transects that were spaced every 100 m across each study site between 16 March and 1 June 2011. Upon completion of the transect surveys, we returned to map the boundaries of the oak wilt centers we had encountered using handheld Global Positioning System units. We used the points to create polygons in ArcMap 9.3 depicting the extent of each oak wilt center.

We took vegetation measurements at 150 randomly selected points in oak wilt centers and at 150 randomly selected points in unaffected forest at each study site. We spaced points ≥20 m from one another to avoid measuring vegetation at multiple locations containing the same individual trees (Gilman and Watson 1994, Jennings et al. 1999). At each point, we recorded all species present within 1 m of the sampling point that were <3 m and all species that were >3 m in height.

To control for regional variation in vegetation characteristics, we used a paired analysis that matched data collected from oak wilt centers to data collected from unaffected forest by study site. We used 2-tailed Wilcoxon paired-sample tests (Zar 1996:167) to evaluate our hypotheses that the proportion of points with all woody vegetation, susceptible oaks, less susceptible oaks, and Ashe juniper in the understory would differ between oak wilt centers and unaffected forest. We also used 1-tailed Wilcoxon paired-sample tests to evaluate differences between the understory and the overstory for the aforementioned vegetation categories in oak wilt centers and in unaffected forest (Zar 1996:167).

RESULTS

Present and Future Extent of Oak Wilt

We identified 158 mortality centers located in 54% (52 of 96) of our sample squares using the 2008 imagery. Of the total area within our sample squares, 7.7% (743 of 9,613 ha) was affected by oak wilt. We extrapolated this proportion to our entire study region and found that 73,091 ha were likely to have been affected by oak wilt in 2008. Our simulation predicted that by 2018, 16.0% (1,536 of 9,613 ha) of the total area within our sample squares would be affected by oak wilt; 2.1 times the amount of oak wilt present in 2008 and an increase of 77,921 ha across the study region.

In 2008, 3,299 ha of potential golden-cheeked warbler habitat were present within our sample squares, 6.9% (227 ha) of which was affected by oak wilt. Our simulation predicted that by 2018, 13.3% (439 of 3,299 ha) of potential habitat would be affected by oak wilt, 1.9 times the amount present in 2008. We extrapolated these proportions to our study region and found that 22,326 ha of potential habitat were likely to have been affected by oak wilt in 2008 and an additional 20,847 ha are at risk of being affected by 2018. Our simulation predicted the largest percent increase in affected area would occur in woodland patches with a low probability of occupancy (0 to <0.25; Table 1). The lowest

Table 1. Estimated percent of golden-cheeked warbler habitat affected by oak wilt within sample squares and the estimated area affected by oak wilt across our study region of Bandera, Kendall, Kerr, and Gillespie counties, Texas, USA, in 2008 and by 2018.

Occupancy probability	Ha all habitat in squares (*n*)	Squares (%)	Region (ha)	Squares (%)	Region (ha)	Increase (%)	Regional increase (ha)
		2008		2018		2008–2018	
<0.25	423	9.6	4,012	22.7	9,432	135	5,420
0.25–0.75	484	14.7	6,996	30.4	14,491	107	7,495
≥0.75	2,392	4.8	11,318	8.1	19,250	70	7,932
All habitat	3,299	6.9	22,326	13.3	43,173	93	20,847

percent increase was predicted to occur in woodland patches with high probability of occupancy ($\geq$0.75), but because patches with high probability of occupancy comprised 51% all affected potential habitat in 2008, these areas contained the highest total number of hectares at risk.

When we accounted for fragmentation of habitat caused by the presence of oak wilt on the landscape, we found that 21,233 ha of potential golden-cheeked warbler habitat were at risk of being affected between 2008 and 2018, 0.7% more total habitat than was directly affected by oak wilt (Table 2). The greatest absolute loss occurred in woodland patches with high probability of occupancy ($\geq$0.75) and the greatest percent loss occurred in patches with an intermediate probability of occupancy (0.25 to <0.75).

The Effect of Historical Oak Wilt on Current Occupancy Probability

Using the 1982–1983 aerial imagery, we identified 51 oak wilt centers on 48% (22 of 46) of our sample squares. Of the total area inside our sample squares, 1.2% (57 of 4,603 ha) was affected by oak wilt. Using the 2008 imagery, we located 72 oak wilt centers on 63% (29 of 46) of our sample squares. Oak wilt centers were located on 4.1% (187 of 4,603 ha) of the total area within the sample squares in 2008; 3.3 times the amount present in 1982–1983. The change in area affected by oak wilt varied by flight-line (Table 3). Of the sample squares where oak wilt occurred in 1982–1983, 77.3% (17 of 22) contained oak wilt in 2008 and 13.7% (7 of 51) of the individual centers were still visible. Of the squares where we located oak wilt in 2008, 37.9% (11 of 29) did not contain oak wilt in the early 1980s.

The effect of historical oak wilt on current occupancy probability varied among habitat categories (Table 4). We found no difference in the proportion of habitat present between historical oak wilt centers and unaffected forest when we considered all habitat and habitat with occupancy probability $\geq$0.75. The proportion of forest currently composed of habitat with $\geq$0.25 occupancy probability was 71% less in historical oak wilt centers.

Effects on Future Stand Composition

Ashe juniper was the most common overstory and understory species in oak wilt centers and in unaffected forest. We found no difference in the proportion of points with understory vegetation between oak wilt centers and unaffected forest. We also found no difference in the proportion of understory

Table 2. Area (ha) of golden-cheeked warbler habitat not affected by oak wilt within our sample squares and across our study region in Bandera, Kendall, Kerr, and Gillespie counties, Texas, USA, in 2008 and by 2018. Changes to the amount of potential habitat are attributed both to the presence of oak wilt and to fragmentation of otherwise unaffected habitat.

Occupancy probability (%)	Squares (ha)	Region (ha)	Squares (ha)	Region (ha)	Area lost in region (ha)	Area lost (%)
	2008		2018		2008 to 2018	
$0 < p < 25$	410	40,287	371	36,432	3,855	9.6
$25 \leq p < 75$	398	39,134	322	31,616	7,518	19.2
$p \geq 75$	2,246	220,864	2,146	211,004	9,860	4.4
All potential habitat	3,054	300,285	2,838	279,052	21,233	7.1

Table 3. Percent of sample squares containing oak wilt centers in 1982–1983 and in 2008 in our study region in Bandera, Kendall, Kerr, and Gillespie counties, Texas, USA, percent of total area within sample squares containing oak wilt in 1982–1983 and in 2008, and percent change in area with oak wilt between 1982–1983 and 2008. Results are presented for each flight-line (Fredericksburg to Johnson City [F–JC], Fredericksburg to Comfort [F–C], and Kerrville to Bandera [K–B]), where aerial photography was taken in 1982-1983 as well as for all 3 flight-lines combined (all).

	Squares with oak wilt (%)			Area with oak wilt (%)			
Flight-line	1982–1983	2008	*n* (squares)	1982–83	2008	*n* (ha)	Increase (%)[a] 1982–1983 to 2008
F–JC	8.3	50.0	12	<0.001	1.1	1,200	15,964
F–C	52.9	82.4	17	0.3	9.1	1,701	2,721
K–B	70.6	52.9	17	3.0	1.1	1,702	−63
All	47.8	63.0	46	1.2	4.1	4,603	229

[a] Reported percentages are rounded from actual values, we calculated percent increase using actual values.

Table 4. Mean proportion of forest in our study region in Bandera, Kendall, Kerr, and Gillespie counties, Texas, USA, affected by oak wilt in 1982–1983 and the mean proportion unaffected forest in 1982–1983 that contained golden-cheeked warbler habitat with low (<0.25) and high ($\geq$0.75) probabilities of occupancy in 2008, the mean and standard deviation of the difference between the two calculated as proportion habitat in affected minus the proportion habitat in unaffected, and results of Wilcoxon paired-sample tests ($n = 22$).

Occupancy probability	Proportion of historical affected	Proportion of unaffected	Mean difference	SD difference	S_{21}	*P*
<0.25	0.05	0.17	−0.12	0.20	40.5	0.004
$\geq$0.75	0.03	0.07	−0.04	0.21	10.0	0.098
All	0.30	0.21	0.09	0.72	21.0	0.452

points with susceptible oaks, less susceptible oaks, or Ashe juniper between oak wilt centers and unaffected forest (Table 5).

The proportion of points with susceptible oaks in the overstory was 3.5 times that of the understory in oak wilt centers and 5.7 times that of the understory in unaffected forest (Table 6). Similarly, the proportion of points with less susceptible oaks in the overstory was 5.2 times that of the understory in affected areas and 6.6 times that of the understory in unaffected areas. We found no statistical difference in the proportion of points with Ashe juniper between the overstory and the understory in oak wilt centers and in unaffected forest. We also found no significant difference in the proportion of points with woody vegetation between the overstory and understory in oak wilt centers, but we found the proportion of points with woody vegetation was 1.6 times higher in the overstory than in the understory of unaffected forest.

DISCUSSION

We found that the percent of golden-cheeked warbler habitat affected by oak wilt in 2008 was roughly equivalent to the percent of the landscape as a whole that was affected by the disease. This result suggests that oak wilt may actually occur in warbler habitat less frequently than in other forest types (e.g., oak savanna) because our landscape assessment included all areas within our sample squares, including places oak wilt could not occur such as agricultural fields, grasslands, and other areas lacking oaks. Appel and Camilli (2010) suggest that oak wilt is more likely to occur in forest with a higher proportion of oak relative to Ashe juniper than in forest used by golden-cheeked warblers at their study sites on the Fort Hood Military Reservation. Despite this, we found that oak wilt frequently occurred in golden-cheeked warbler habitat. We predict that the amount of habitat affected by oak wilt will nearly double by 2018, with the greatest increase occurring in the areas with the highest probability of occupancy. When we accounted for the additional effect of fragmentation, less potential habitat was lost from the category with the lowest probability of occupancy and more was lost from potential habitat with high probability of occupancy. This outcome was likely caused by a downward shift in occupancy probability in patches fragmented by oak wilt. Because many patches of potential habitat were not completely contained within our sample squares, oak wilt may have caused additional fragmentation not accounted for in our estimates. Thus, the losses we attributed to fragmentation should be considered to be a conservative estimate. Previous studies have suggested that urbanization and agricultural practices are the main causes of loss and degradation of warbler habitat (Wahl et al. 1990); oak wilt may be a third contributor given the frequency at which it occurs in golden-cheeked warbler habitat and its negative influence on habitat selection and quality (Stewart et al. 2014).

Several factors that we could not account for in our 10-year simulation may influence the rate of oak wilt spread and, thus, the amount of warbler habitat potentially impacted by

Table 5. Mean proportion of sample points with susceptible oak species, less susceptible oak species, Ashe juniper, and all woody species <3 m in height; the mean and standard deviation of the difference between the two calculated as the proportion of points in affected areas minus the proportion of points in unaffected areas; and results of Wilcoxon paired-sample tests (*n* = 14). Samples were taken from 14 study sites in Bandera, Kendall, Kerr, and Gillespie counties, Texas, USA, during 2011.

Species	Proportion of affected	Proportion of unaffected	Mean difference	SD	*S*	*P*
Susceptible oaks	0.04	0.03	−0.01	0.05	20.5	0.217
Less susceptible oaks	0.007	0.008	−0.001	0.01	4.5	0.695
Ashe juniper	0.18	0.22	0.04	0.14	10.5	0.542
All woody species	0.31	0.30	−0.01	0.14	1.5	0.952

Table 6. Mean proportion of sample points with susceptible oak species, less susceptible oak species, Ashe juniper, and all woody species in the understory (<3 m in ht) and the overstory (>3 m in ht); the mean and standard deviation of the difference between the two calculated as the proportion of understory points minus the proportion of overstory points; and results of Wilcoxon paired-sample tests for affected and unaffected portions of study sites (*n* = 14). Samples were taken from 14 study sites in Bandera, Kendall, Kerr, and Gillespie counties, Texas, USA, during 2011.

Species	Proportion of understory	Proportion of overstory	Mean difference[a]	SD	*S*	*P*
Affected						
Susceptible oaks	0.04	0.14	−0.10	0.10	41.5	0.007
Less susceptible oaks	0.007	0.036	−0.030	0.043	33.0	0.007
Ashe juniper	0.18	0.17	0.01	0.17	−7.5	0.636
All woody species	0.31	0.41	−0.10	0.19	24.5	0.135
Unaffected						
Susceptible oaks	0.03	0.17	−0.15	0.06	52.5	<0.001
Less susceptible oaks	0.008	0.053	−0.045	0.050	43.5	0.004
Ashe juniper	0.22	0.27	−0.05	0.16	2.5	0.903
All woody species	0.30	0.49	−0.19	0.19	44.5	0.003

[a] Reported proportions are rounded from actual values, we calculated mean difference using actual values.

the disease. In instances where specific information was lacking, we went with the most conservative option. First, our model works on the assumption that oak wilt expands locally at a constant rate of 10 m/year. Appel et al. (1989) observed mean expansion rates of 11–16 m/year with a maximum of 45 m/year in central Texas. Therefore, it is likely that more total area and thus more warbler habitat will be affected by oak wilt over the next 10 years than our model predicts. The moderate error of omission revealed by our ground-truthing may also contribute to an underestimation of area affected by oak wilt. A second assumption in our model is that oak wilt only spreads locally via interconnected root systems. However, oak wilt can also be vectored over longer distances by several species of Nitidulid beetle (Gibbs and French 1980, Juzwick and French 1983). Vectored spread always initiates with an infected red oak because *C. fagacearum* does not form reproductive mats on live or white oaks (Appel 1995). Appel (1995) described the relationship between *C. fagacearum* and its vector as inefficient, leading to low rates of new center formation. Stewart et al. (2014) found that live oak canopy cover in oak wilt centers and in adjacent unaffected forest was ≥4 times greater than canopy cover in species susceptible to fungal mat formation (Texas red oak [*Q. texana*] and blackjack oak [*Q. marilandica*]). Given the relative abundance of live oaks within our study sites and oak wilt's inefficient relationship with its vector, we assumed the amount of forest affected by vectored spread would be negligible over the 10-year period of our simulation. Our third assumption, that all trees identified by supervised classification were species susceptible to oak wilt, could have resulted in some overestimation of spread. The supervised classification successfully distinguished between areas with and without trees but did not differentiate between tree species. Thus, some forested areas composed of unsusceptible species such as Ashe juniper or mesquite (*Prosopis* spp.) may have been incorrectly predicted to contain oak wilt by 2018. This may explain why some areas that fell within the boundaries of oak wilt centers in year 2 of our simulation did not actually contain oak wilt on the ground.

We found that how habitat was categorized influenced our assessment of the effect of historical oak wilt on current occupancy probability. The tendency of oak wilt to reduce the total number of trees but to infrequently remove all trees may provide an explanation. Because only certain types of trees are susceptible to oak wilt, areas affected by the disease are often still forested and thus may be identified as warbler habitat despite historical infection. However, areas where oak wilt occurred historically are likely to be more fragmented and contain fewer trees than unaffected areas. Because previous studies have found a positively correlated probability of warbler occupancy with patch size and surrounding percent woodland composition, the more open condition resulting from loss of oaks may decrease the occupancy probability of affected areas, resulting in the variation we observed (Magness et al. 2006, Collier et al. 2012).

We found no differences in understory vegetation between affected and unaffected portions of our study sites. However, we did find that understory oaks were rather uncommon in general, while Ashe juniper was the most frequently observed species. Oaks were 3.5–5.7 times more common in the overstory than the understory, while the proportion of points with Ashe juniper was not significantly different between the two. Recent studies have suggested that live and red oaks are not recruiting to adulthood in the savannas and Ashe juniper–oak woodlands of the Edwards Plateau (Russell and Fowler 1999, 2002). This may be due to high seed and seedling mortality rates caused by changes in land management practices since the 1930s that have resulted in increased browsing by white-tailed deer (*Odocoileus virginianus*) and decreased fire frequency (Russell and Fowler 1999, 2002). This suggests that as mature oaks are removed from the forest by a variety of factors, of which only one is oak wilt, species composition will shift toward Ashe juniper (USFWS 1990, Russell and Fowler 2002). Over time, loss of oaks from Ashe juniper–oak woodland would have negative consequences for golden-cheeked warblers because oaks are a necessary component of their breeding habitat (USFWS 1990, Ladd and Gass 1999, Groce et al. 2010).

MANAGEMENT IMPLICATIONS

Our results suggest that oak wilt is widespread throughout our study region and frequently occurs within golden-cheeked warbler habitat. Further, large areas of potential golden-cheeked warbler habitat are at risk of becoming affected by the disease as oak wilt spreads across the landscape. Therefore, oak wilt should be considered as a factor when evaluating the status of threats to the golden-cheeked warbler. Future management efforts should address the threat oak wilt poses to golden-cheeked warblers by incorporating applicable preventative measures. We recommend that techniques such as trenching and chemical control be employed to stop or slow local spread of the disease within golden-cheeked warbler habitat. However, we do not recommend that local oak wilt control measures be employed for all areas affected by the disease because this strategy is likely to produce little benefit to the warbler since the majority of oak wilt centers occur outside of golden-cheeked warbler habitat. To control oak wilt on a larger scale, efforts should focus on preventing the formation of new infection centers.

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