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Amphibians and Large, Infrequent Forest Disturbances: An Extreme Wind Event Facilitates Habitat Creation and Anuran Breeding

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***Abstract*.—Large, catastrophic wind disturbances are historically common across the Coastal Plain of the southeastern United States, a region which harbors one of the planet's most speciose regions for amphibian taxa. Links between such disturbances and the amphibians they potentially impact, however, have received little focus, and studies addressing these impacts are often limited by an inability to compare post-disturbance survey data to pre-disturbance conditions at the same sites. I conducted habitat and anuran surveys following an intense tornadic disturbance in 2011 within a series of transects in the upper Coastal Plain of central Alabama that has been studied continuously since 2009, with the purpose of examining the effects of catastrophic wind events. These surveys revealed that several Southern Toads (*Anaxyrus terrestris*) appeared to have been killed due to storm impacts, while Cope's Gray Treefrogs (*Hyla chrysoscelis*) began breeding in the storm-damaged area immediately following the storm. This was the first instance of anuran breeding activity; none had occurred during the preceding three years in this transect. Breeding activity in *H. chrysoscelis* was facilitated by the creation of multiple, isolated pools via debris scouring as a direct result of the tornado. Although extreme wind events are often stochastic and infrequent, these results illustrate their importance for habitat creation within storm-damaged areas, and provide potentially useful information for managers charged with monitoring amphibian populations following extreme wind disturbance.**

Key Words.—amphibian; anuran; disturbance; Cope's Gray Treefrog; *Hyla chrysoscelis*; tornado; wetland; wind

Introduction

Large, catastrophic ecological disturbances are integral, yet little-understood, events in forest ecosystems. Commonly associated with infrequent disturbances such as catastrophic wildfires, windstorms, floods, or winter weather systems, these events often produce transformative and long-lasting impacts on forest structure, succession, and composition (Lorimer 1989; Foster et al. 1998; Turner et al. 1998). Windstorms such as hurricanes and tornadoes are some of the most common large disturbances present in forest ecosystems across the southeastern United States (Greenberg and McNab 1998; Peterson 2000; Duryea et al. 2007). Although the timing of these events is ultimately stochastic and typically infrequent, they are nonetheless ubiquitous in the disturbance history of individual ecosystems. For example, while over 900 strong (Enhanced Fujita Scale 3 or higher) tornadic systems have impacted the United States since 1880, the return intervals of these systems are highly variable, ranging from 10 years to several centuries, depending on location (Broyles and Crosbie 2004). Severe thunderstorm activity that generates these extreme wind disturbance events, however, is expected to increase in frequency and severity in coming decades, given current climatological trends (Garinger and Knupp 1993; Trapp et al. 2007).

The effects of such large, infrequent wind disturbances on amphibian populations have received little focus and, when studied, often show variable impacts. Greenberg (2001), for example, found no significant effect of downburst-produced canopy gaps on amphibian abundance, species richness, and diversity in a southern Appalachian hardwood forest. However, Woolbright (1991) observed significant shifts in population density for forest frogs in Puerto Rico following wind disturbance from Hurricane Hugo. The stochastic nature of such events has forced many researchers to rely on surrogate, 'undisturbed' reference habitats for the purposes of comparative analyses. Explicit comparisons of pre- and post-disturbance data from the same sites are uncommon, yet represent a more robust approach to evaluating the effects of a given disturbance (see Woolbright 1991). Such before-and-after study designs have been previously used to examine the responses of amphibians to large tropical systems (Schriever et al. 2009; Gunzburger and Hughes 2010), but such studies are lacking for extreme wind events associated with tornadic systems, due to these systems' highly stochastic nature and relatively small size.

On the evening of 27 April 2011, an unusually large and violent EF–3 (Enhanced Fujita Scale) tornado moved through a portion of the Talladega National Forest, Oakmulgee District, in Bibb and Hale Counties of west-central Alabama. Containing surface winds estimated at up to 230 km per hour, this system impacted a 1.6-km wide and 115 km long region within an existing mixed pine-hardwood forest (NOAA 2011a). This event removed approximately 100,000 m^3 of forest cover across a 600-ha portion of the Oakmulgee District (Ragland 2011). The southwestern portion of this storm's path directly impacted an existing transect in the Pine Flat area of the Oakmulgee District that has been used to study anuran populations and associated wetland habitats continuously since 2009. This portion of the storm track included some of the most intense and widespread wind damage present throughout the affected area.

The coincidence of a severe tornado occurring on the aforementioned transect presents a rare opportunity to directly examine the effects of a large, infrequent forest disturbance on anuran populations and to compare post-disturbance observations to multiple years of pre-disturbance data. In addition, high-resolution orthoimagery collected immediately following this storm (NOAA 2011b) provides the means to analyze spatial patterns of breeding habitat alteration. Specifically, I couple geospatial analyses with post-disturbance field surveys to analyze patterns of tornado induced formation of scour pools and subsequent colonization of pools by breeding anurans. I discuss potential implications of these observations for amphibians and forest management within the context of intense, infrequent disturbances.

Materials and Methods

Anuran surveys.—I commenced anuran surveys in the Oakmulgee District of Bibb and Hale Counties of west-central Alabama in February 2009 as part of a larger study investigating the response of breeding anuran assemblages to forest management in the upper Gulf Coastal Plain (Smith 2011). I established three transects (each approximately 1 km in length) within midslope and bottomland forest habitat directly adjacent to an unnamed, third-order tributary of Fivemile Creek (Table 1). Forest types within this area ranged from extensive Longleaf Pine (*Pinus palustris*) forest in midslope and ridgetop areas to large stands of Black Tupelo (*Nyssa sylvatica*) along creek bottoms. Two of these transects were located adjacent to actively-maintained beaver impoundments, while the third was located adjacent to a former, drained beaver impoundment transitioning back to forest habitat.

I surveyed each transect approximately twice per month, from February to July, for breeding anurans and the presence/condition of aquatic habitat. I inventoried aquatic habitat (defined as ephemeral pools of standing water separate from the main channels of permanent streams) by walking each transect and documenting the location of each habitat feature within approximately 20 meters of the transect centerline (a gated forest road). Anuran surveys consisted of nocturnal, auditory call surveys following the guidelines and abundance indices recommended by Weir and Mossman (2005). When calling anurans were detected, I performed diurnal surveys of the associated aquatic habitats for the presence of anuran egg masses to confirm breeding activity. I performed the final anuran call survey preceding the disturbance event on 11 April 2011.

Post-disturbance surveys.—I performed an initial visual survey of each transect on 30 April 2011. Surveys consisted of walking each transect and documenting the location and type of aquatic habitat present within each transect, similar to pre-disturbance surveys. Following these initial surveys, I performed standard surveys (as described above) weekly to monitor aquatic habitat for evidence of successful anuran breeding. I continued these surveys through September 2011. Newly created pools had dried by then and the U.S. Department of Agriculture Forest Service began salvage logging activities, preventing site access.

Only one of the three transects had storm damage. This transect was located directly in the path of the tornado, in an area estimated to have experienced EF-3 scale wind damage (NOAA 2011a). The other two transects did not receive significant habitat disturbance at any point throughout the three-year study period, effectively creating a before-after control-impact (BACI) study design. I used linear mixed-effects models in Minitab v16 (Minitab, Inc., State College, Pennsylvania, USA) to examine the effects of disturbance on species richness and pool count, with disturbance (impacted and

Table 1. Transect location, pool counts, and species observed from 2009 to 2011 in the Oakmulgee District. Geographic coordinates refer to latitude/longitude for each transect's starting point (western terminus) and ending point (eastern terminus) along an unnamed tributary of Fivemile Creek. The transect labeled "disturbed" refers to the area impacted by tornadic winds in 2011.

Transect	Starting Coordinates	Ending Coordinates	Year	# pools	Species Observed
Undisturbed	32.90671, -87.39526	32.90885, -87.38944	2009	4	*Acris crepitans, Anaxyrus terrestris, Hyla avivoca, Hyla chrysoscelis, Hyla cinerea, Lithobates catesbeianus, Lithobates clamitans*
			2010	4	*Acris crepitans, Hyla avivoca, Hyla chrysoscelis, Hyla cinerea, Lithobates catesbeianus, Lithobates clamitans*
			2011 (Post-disturbance)*	4	*Acris crepitans, Hyla avivoca, Hyla chrysoscelis, Hyla cinerea, Lithobates catesbeianus, Lithobates clamitans*
Undisturbed	32.90370, -87.40700	32.90329, -87.39991	2009	5	*Acris crepitans, Anaxyrus terrestris, Hyla avivoca, Hyla chrysoscelis, Hyla cinerea, Lithobates catesbeianus, Lithobates clamitans*
			2010	5	*Acris crepitans, Hyla avivoca, Hyla chrysoscelis, Hyla cinerea, Lithobates catesbeianus, Lithobates clamitans*
			2011 (Post-disturbance)*	5	*Acris crepitans, Hyla avivoca, Hyla chrysoscelis, Hyla cinerea, Lithobates catesbeianus, Lithobates clamitans*
Disturbed	32.91096, -87.44071	32.91163, -87.43043	2009	1	*Lithobates clamitans*
			2010	1	*Lithobates clamitans*
			2011 (Post-disturbance)*	16	*Acris crepitans, Anaxyrus terrestris, Hyla chrysoscelis, Lithobates clamitans*

*visits performed as weekly surveys, rather than twice-monthly pre-disturbance survey visits

control) and year (2009, 2010, and 2011) as fixed effects. I included transect as a random effect, and ln-transformed counts (species and pools) prior to model construction. Emphasis was placed on tests of the interaction term (year × disturbance) due to this term's value in a BACI design (Underwood 1994; McDonald et al. 2000); tests of main effects are therefore not reported hereafter. I used a significance level of $\alpha = 0.05$ for all statistical analyses.

Geospatial analyses.—I used a combination of data collected in the field and digital datasets prepared by the National Oceanic and Atmospheric Administration (NOAA) to examine spatial patterns of newly-created aquatic habitat within the storm-damaged transect. I mapped the location of each newly-created habitat feature within this transect in ArcGIS v.10.1 (Esri, Redlands, California, USA) using geographic coordinates collected using a Garmin 60CS handheld GPS unit (approx. 3–4 meters accuracy; Garmin International Inc., Olathe, Kansas, USA). I overlaid these points with a digital elevation model (10 m resolution) of the study area produced by the U.S. Geologic Survey (USGS) and high-resolution (25-cm ground sample distance) digital orthoimagery produced during post-disturbance aerial surveys by the National Geodetic Survey of NOAA (NOAA 2011b).

I obtained wind and terrain vectors at the location of each newly-created breeding site using this dataset in order to test the hypothesis that interactions between wind and terrain promote debris scouring of topsoil and, subsequently, pool creation. I estimated direction (azimuth) of wind vectors by examining the pattern of treefall and direction of topsoil scouring (indicators of wind direction) at each pool via field visits and examination of the digital orthoimagery. I obtained the direction (azimuth) of terrain vectors at each pool location by performing an aspect analysis on the USGS digital elevation model in the Spatial Analyst extension of ArcGIS v.10.1. I verified terrain aspect in the field.

I overlaid a set of 16 random points (equivalent to the number of actual aquatic habitat features present following disturbance) across the same spatial extent of the storm-damaged transect in ArcGIS v.10.1 to determine if the relationship between wind and terrain vectors at newly-created pools was significantly different from that expected due to random chance. I recorded the azimuth of wind and terrain vectors at each of these random points, and calculated the absolute difference (degrees) between vectors for both newly-created pools and random points. I compared differences between these groups using a Student's t-test (α = 0.05) in Minitab v.16. A significant difference between wind and terrain vector angles from scour pools and random points indicates nonrandom interactions between wind and terrain in creating pools. Due to a low sample size of newly-formed pools, I performed 100 bootstrap samples of this dataset and compared the observed t statistic for the actual dataset to the resulting distribution of t statistics from resampling to further assess significance.

Results

The tornadic system produced significant physical changes in forest cover within the storm-impacted transect, removing all canopy cover and, in most cases, removing vegetation down to the ground layer. By contrast, the other two transects exhibited no change in forest structure (Fig. 1). Coarse woody debris mobilized by the wind event collected in large piles within the storm-damaged transect, particularly at the base of embankments and standing but heavily-damaged trees. Three dead Southern Toads (*Anaxyrus terrestris*) were found within these debris piles during immediate post-disturbance surveys (Fig. 2a). All had significant physical trauma to the head and neck. I observed no mortality in the two transects not impacted by the storm.

Debris piles also resulted in the creation of numerous isolated pools within the storm-damaged transect via topsoil scouring (Fig. 2b). The interaction term (year × disturbance) was significant for pool count ($F_{1,8)}$ = 9.449, P = 0.028), indicating an effect of the tornado on the abundance of aquatic habitat. Specifically, I recorded 16 pools immediately following the disturbance event in the tornado-impacted transect, fifteen of which were not present during the preceding two years of habitat surveys (Table 1). By contrast, I detected no new pools or other forms of aquatic habitat following the disturbance event in the other two transects outside of the storm's path. Four (25%) of the new pools occurred close enough to the forest road bisecting the transect to experience some minor anthropogenic modification (widening) as a result of road clearing in preparation for salvage logging in summer 2011. The other

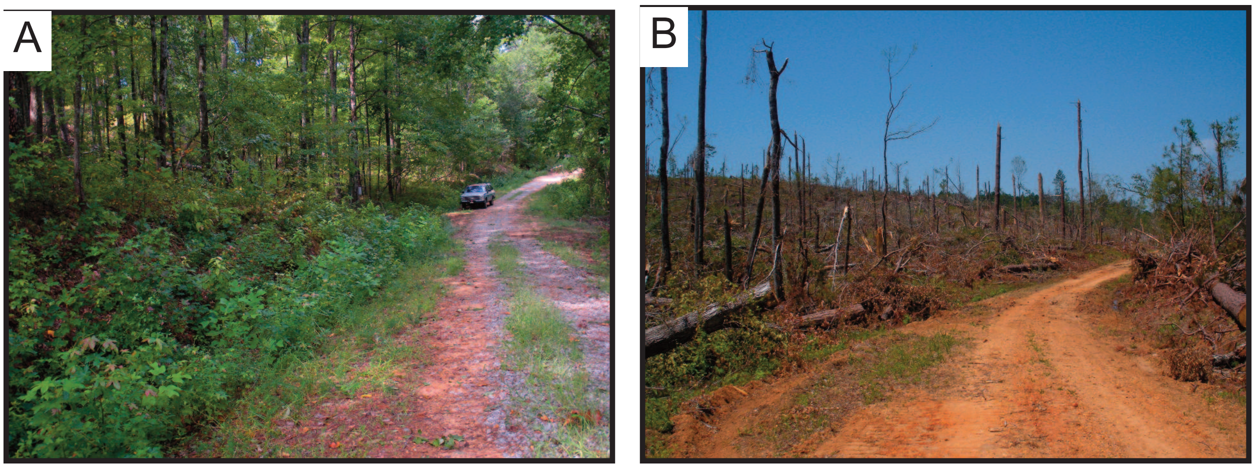

Figure 1. Forest habitat (A) in an undisturbed transect and (B) in the disturbed transect at the same time period in spring 2011. (Photographed by Walter H. Smith).

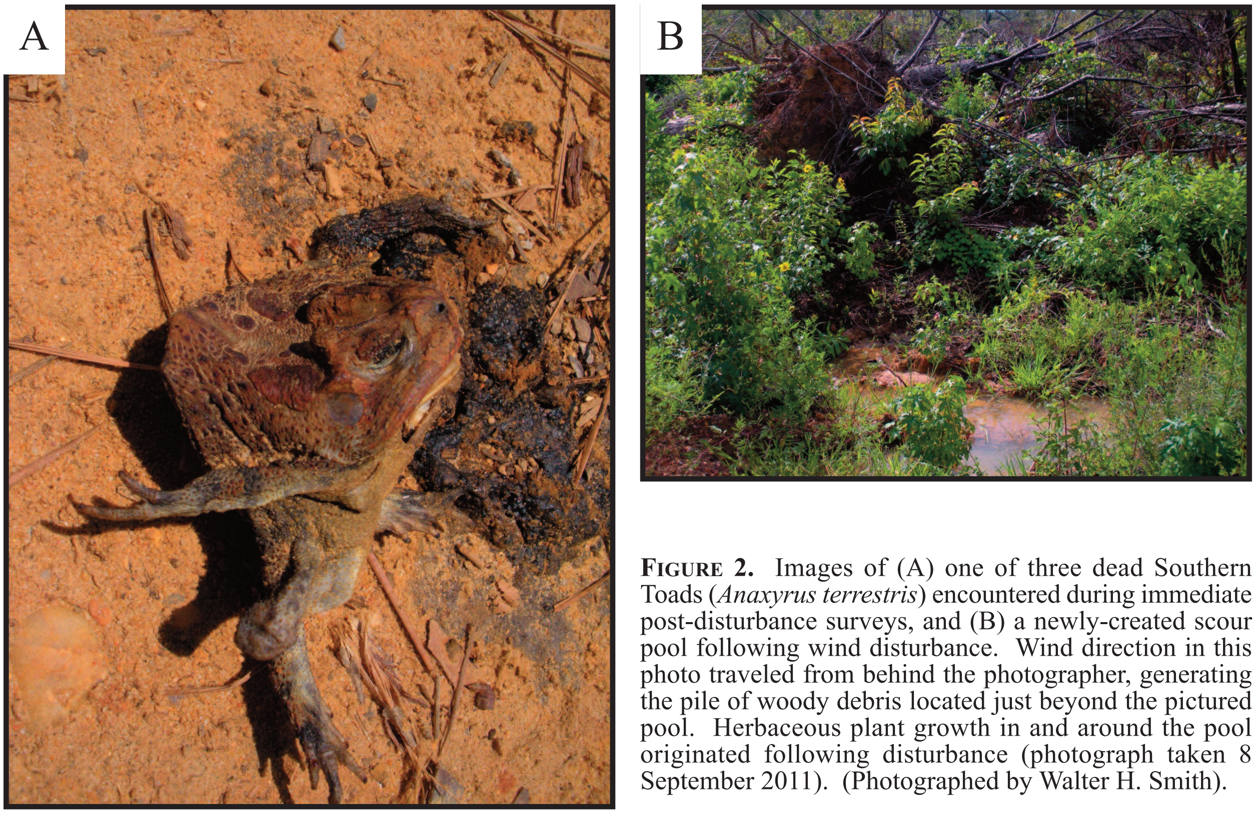

Figure 2. Images of (A) one of three dead Southern Toads (*Anaxyrus terrestris*) encountered during immediate post-disturbance surveys, and (B) a newly-created scour pool following wind disturbance. Wind direction in this photo traveled from behind the photographer, generating the pile of woody debris located just beyond the pictured pool. Herbaceous plant growth in and around the pool originated following disturbance (photograph taken 8 September 2011). (Photographed by Walter H. Smith).

pools, however, occurred far from this roadbed and did not experience changes beyond the initial debris scouring.

Similarly, the interaction term was significant for species count ($F_{1,8}$ = 12.050, P = 0.018), indicating an effect of the tornado on anuran populations. The most significant change in species count occurred in the tornado-disturbed transect, in which three species were recorded following disturbance that had not been recorded in the years prior. These species were the Northern Cricket Frog (*Acris crepitans*), Southern Toad (*Anaxyrus terrestris*), and Cope's Gray Treefrog (*Hyla chrysoscelis*; Table 1). Within two days of the disturbance event, I encountered *H. chrysoscelis* egg masses within newly-created pools in this transect and eventually found breeding activity in 10 of 16 pools. These were the first observations of anuran breeding within this transect over the three years of survey efforts (Fig. 3).

Egg mass counts from this transect totaled 53 clutches. Average clutch size for *H. chrysoscelis* is 30–40 eggs per clutch (Wright 1932; Greer 2008), so total egg deposition at this site may have summed to 1,590–2,120 individual eggs. Larvae exhibited typical development for *H. chrysoscelis* throughout the survey period, and all pools were empty of larvae by 8 September 2011. Pools subsequently dried, with all pools dry by 25 September 2011 (Fig. 4).

Spatial analyses indicated a non-random pattern of pool creation across the storm-damaged transect. Specifically, angles of difference between wind and terrain vectors at pools created by debris scours were significantly greater than random differences (t = -3.53, df = 30, P < 0.001; resampling P = 0.01, 100 resamples). Data for this analysis were normally distributed (P = 0.571 Shapiro-Wilk Normality Test). This significant difference indicates that interactions between wind direction and terrain at the location of scour pools exhibited greater resistance than those present at random points across the same landscape.

Discussion

Large, infrequent forest disturbances produce intense and transformative impacts on forest composition and health through the large-scale removal of forest cover. In the Oakmulgee District, impacts from an intense mesocyclone resulted in the removal of forest cover down to

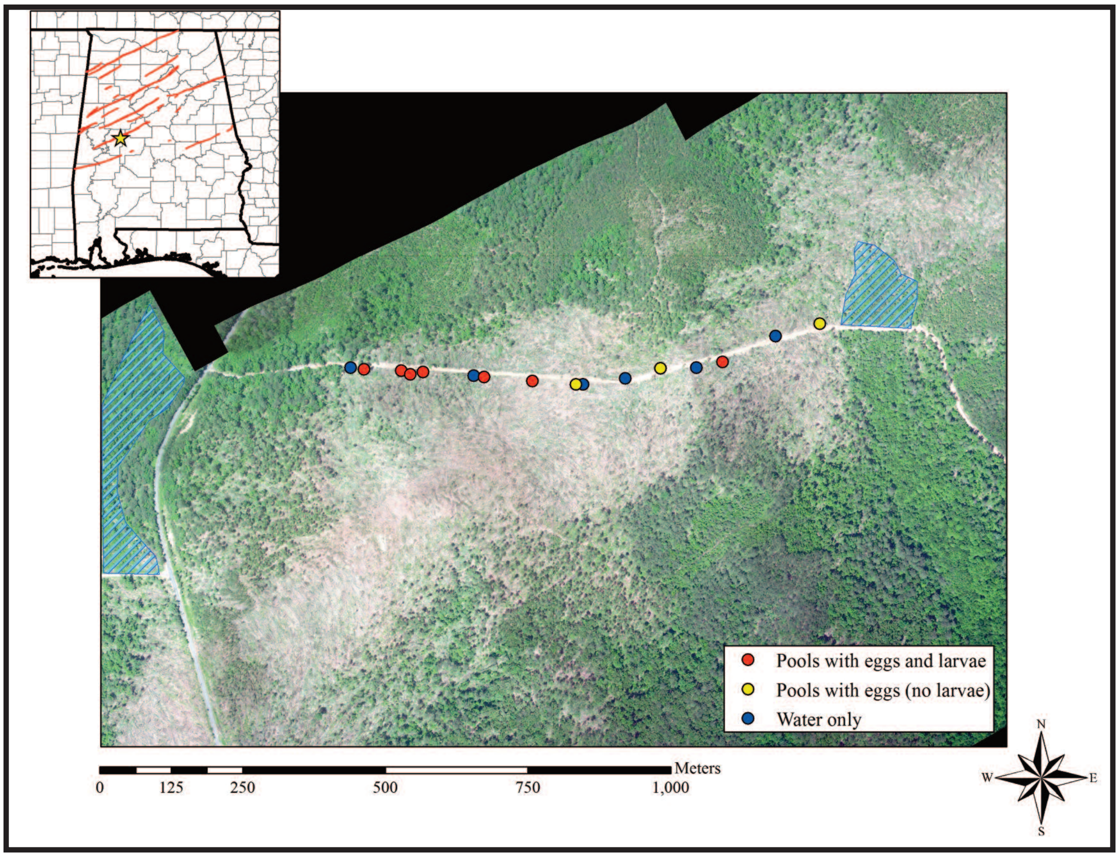

Figure 3. Location and condition (eggs present, larvae present, water only) for 16 ephemeral pools following wind disturbance in a transect studied continuously since 2009. The light-colored band in the center of the photo indicates deforestation from wind disturbance in 2011. Blue cross-hatched areas represent the location of abandoned, unmaintained beaver ponds within the study region. Inset image denotes the location (starred symbol) of the study site with respect to additional tornado locations on 27 April 2011. Tornado track data and site orthoimagery were sourced from the National Oceanic and Atmospheric Administration (NOAA 2011b).

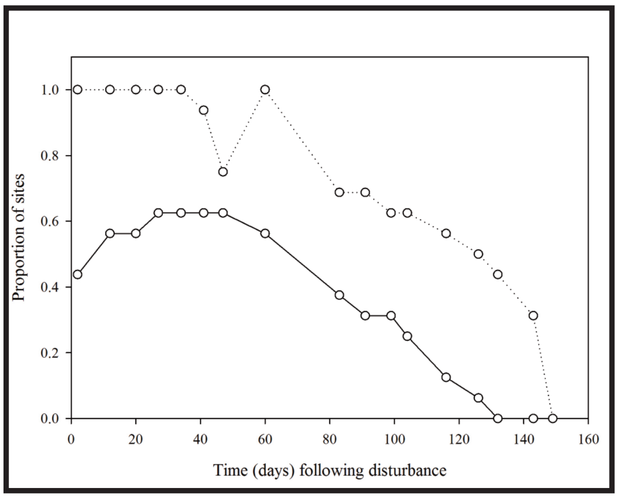

Figure 4. Proportion of ephemeral pools (n = 16) containing water (dotted line) and *Hyla chrysoscelis* eggs or larvae (solid line) over time following tornadic disturbance in the Oakmulgee District in 2011. Open circles denote individual sampling occasions.

bare topsoil, including not only mature trees but also smaller woody and herbaceous vegetation. This resulted in mobilization of large amounts of organic matter which, while airborne for only a matter of seconds, produced large piles of woody debris and associated debris scour paths across the ground surface. This immediate damage and topsoil gouging by debris is consistent with known impacts from EF-3 scale and higher tornadic systems, as evidenced from previous surveys and studies (Marshall 2002; Karstens et al. 2010; NOAA 2012). Post-disturbance surveys found evidence of direct effects of the tornado on anuran mortality and indirect effects through the creation of breeding pools in scoured areas.

Although anuran mortality was not a primary focus of this study, examination of the dead toads (*A. terrestris*) found lodged in woody debris indicated direct lethal effects by trauma.

Mortality probably did not cause demographic changes in populations of *A. terrestris* due to the study site's small size and location far from any established breeding sites of *A. terrestris*. However, storm-induced mortality was almost certainly underestimated because most debris piles were either inaccessible due to safety considerations or could not be surveyed without the use of heavy equipment.

In contrast to mortality, indirect impacts involving the creation of anuran breeding habitat caused the largest changes between pre- and post-disturbance conditions. Specifically, the creation of potholes and debris scours by tornadic winds and associated debris mobilization formed ephemeral, yet highly abundant, pools of standing water across the impacted landscape. Cope's Gray Treefrogs bred in these new pools, in a transect which had previously lacked anuran breeding activity other than two observations of calling Bronze Frogs (*Lithobates clamitans*) throughout 32 hours of observation during the preceding two years.

H. chrysoscelis will breed in isolated pools in highly disturbed habitats. Hillis et al. (1987), for example, found this species to use flooded furrows of cornfields in Kansas as sites of egg deposition, and roadside ditches or other anthropogenically-created pools are a commonly-cited location for both calling and egg deposition for this species (Mount 1975; Greer 2008). Experimental work, in fact, shows a preference for open-canopy breeding sites in Gray Treefrogs (*H. versicolor*) subjected to anthropogenic forest disturbance (Hocking and Semlitsch 2007). The observations of *H. chrysoscelis* colonizing and breeding in isolated pools within a recently-disturbed habitat, as reported here, are not surprising. However, these results are notable in that they highlight the role of large, catastrophic wind disturbance events in facilitating the establishment of amphibian breeding sites within a forest ecosystem.

These data additionally show that anurans not only used scour pools for egg deposition, but tadpoles were able to successfully complete their development prior to pool desiccation. The extent of new recruitment in response to tornado-altered habitat may be substantial, considering that the transect used in this study represented less than one percent of the area of the Oakmulgee District directly impacted by this tornado. Opportunistic surveys of additional portions of the storm track showed similar evidence of anuran breeding, even on the crests of ridgelines > 1 km from any known source of standing water. These data suggest that such large, catastrophic forest disturbances may contribute substantially to the establishment and success of anuran breeding sites across the larger landscape.

More importantly, the creation of breeding habitat across the impacted landscape was not an entirely stochastic process. Instead, scour pools were located more frequently in areas of maximum resistance between wind and terrain vectors than would be expected due to random chance. Mesocyclonic systems such as those impacting the Oakmulgee District are known for producing tornadoes, which in many cases can be intense. As air is pulled into these storm systems, debris is often mobilized and can gouge into topsoil when surface winds drive debris into the ground surface (Karstens et al. 2010). Large, wind-borne objects such as trees and other coarse woody debris are more likely to gouge into topsoil if traveling perpendicular to – rather than parallel with – the aspect of the ground surface. This arrangement of wind and local microtopography would produce higher amounts of force on topsoil and thus increase the probability that debris would gouge an area large and deep enough to retain rainfall during and immediately after the wind disturbance itself.

While large, catastrophic forest disturbances are ultimately stochastic events with respect to when and where they will occur, these data indicate that there may be some predictability in determining where potential breeding habitat may be created within a disturbed area. Using knowledge of local terrain and storm movement, forest managers may be able to pinpoint areas within a storm-damaged region that have a high likelihood of containing newly-created breeding habitat for anurans. Additional factors, such as debris size, soil type, and slope of terrain, may also influence pool formation beyond terrain aspect and wind direction. I did not assess these variables because large machinery would have been required to excavate most debris piles to accurately measure tree type and size. Salvage logging activities in summer 2011 prevented follow-up studies that could have addressed these variables in detail. Future investigation into patterns of pool creation following wind disturbance should take these complicating factors into account, while using the predictive value of terrain aspect and wind direction as a foundation.

To build upon the observations reported here and facilitate pre- and post-disturbance comparisons, there is a need to establish and maintain access to more long-term monitoring sites for anurans in forests prone to wind disturbance and subsequent salvage logging. Moisture availability and temperature in the western Gulf Coastal Plain contribute to this region's status as both one of the most active regions in the world for tornadic wind events and a temperate hotspot of anuran diversity (Buckley and Jetz 2007; Trapp et al. 2007). Legacies of wind disturbance in this region undoubtedly influence local anuran populations, particularly with respect to spatial patterns of breeding activity, but the extent to which storm effects may impact anuran populations is just beginning to be understood. Although salvage logging is commonly used in wind-disturbed areas to remove damaged timber and reduce fire risk, these activities may take place within areas containing newly-created aquatic habitat and breeding anurans. Timber harvesting may either put a developing cohort at risk by eliminating new aquatic habitat or increase habitat availability by expanding pool number and depth, and these impacts should be of interest to future studies of post-disturbance management strategies. Expanding the study of pool creation by storms, not just with discrete tornadic wind events but to other broad-scale wind disturbances initiated by tropical systems throughout the Gulf Coastal Plain region, would greatly improve our knowledge of how wind disturbance affects anurans, how different taxa respond to this form of habitat change, and the role of post-storm forest management.

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Walter H. Smith earned his Ph.D. at the University of Alabama in 2011, during which time he performed research on the impacts of ecological disturbance on herpetofauna within the Longleaf Pine ecosystem of the Gulf Coastal Plain. He is now an Assistant Professor of Biology at the University of Virginia's College at Wise, where his research interests center around the broader implications of habitat disturbance for both wildlife and human populations within the southern Appalachian Mountains. (Photographed by Katie Dunn).