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Predisposing factors' effects on mortality of oak (*Quercus*) and hickory (*Carya*) species in mature forests undergoing mesophication in Appalachian Ohio



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Abstract

Background: Mature oak (*Quercus* spp.) and hickory (*Carya* spp.) trees are gradually being replaced by more shade-tolerant tree species across the eastern U.S., likely due to fire suppression and increased precipitation. Oaks and hickories are highly valuable to wildlife; therefore, studying their mortality patterns can provide information on the longevity of habitat quality for many animal species. Oak mortality has most often been studied following large oak decline events, but background mortality rates in forests with aging oak and hickory canopies warrant equal attention, especially in the context of widespread oak and hickory regeneration failure.

Methods: We studied background mortality rates of five oak and one hickory species over a 23–25 year time period (1993–1995 to 2018), using 82 1/20th hectare permanent plots on the Marietta Unit of the Wayne National Forest in southeastern Ohio. We calculated mortality rates based on remeasurement of individual trees for white oak (*Quercus alba*), chestnut oak (*Quercus montana*), northern red oak (*Quercus rubra*), black oak (*Quercus velutina*), scarlet oak (*Quercus coccinea*), and pignut hickory (*Carya glabra*). For each of these species other than scarlet oak, we also modeled the relationships of mortality probability with a priori topographic, soil, stand structural, and individual tree covariates, using a mixed-effects logistic regression framework.

Results: The species with the highest mortality rate was scarlet oak (61.3%), followed by northern red oak (41.4%), black oak (26.7%), pignut hickory (23.9%), white oak (23.4%), and chestnut oak (19.1%). In our models, northern red oak mortality was associated with more mesic slope positions, shallower solums, more acidic soils, and older stand ages. Pignut hickory and chestnut oak mortality rates were associated with higher basal areas on the plot, while white oak mortality showed the opposite pattern.

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Conclusions: Our data suggest that red oak subgenus trees in mature forests of our area will become increasingly uncommon relative to white oak subgenus trees, as the result of higher mortality rates likely related to the shorter lifespans of these species. Particularly vulnerable areas may include more mesic topographic positions, shallower or more acidic soil, and older stands. Since maintaining oak subgenus diversity is beneficial to wildlife diversity in the eastern U.S., managers in areas with extensive mature mixed-oak forests could choose to favor the red oak subgenus when conducting silvicultural treatments.

Keywords: Mortality, *Quercus*, *Carya*, Mesophication, Wildlife habitat

Introduction

Recent studies have shown that temperate forest canopies currently dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.) are gradually being replaced by shade-tolerant mesophytic tree species, especially maple (*Acer* spp.) (Nowacki and Abrams 2008; Brose et al. 2014). These mesophytic trees slowly change the characteristics of the forest floor, making conditions more favorable for mesophytic regeneration and less favorable for oak regeneration over time (Kreye et al. 2013; Alexander and Arthur 2014). This process has been termed “mesophication” (Nowacki and Abrams 2008). Fire suppression and increased precipitation are the most likely relevant factors, both of which have occurred in the eastern U.S. for roughly a century (McEwan et al. 2011; Nowacki and Abrams 2015; Pederson et al. 2015). Prescribed burning and thinning are the primary management tools for reversing mesophication and promoting oak regeneration. Unfortunately, these measures are rarely effective without multiple treatments (Brose et al. 2013), which may render oak forest restoration too expensive for application to large areas, in the absence of commercial timber markets. Many forests in the eastern U.S. are currently managed with a “hands-off” approach (Widmann 2016), making it seem unlikely that oak forests will be restored across larger landscapes.

Anthropogenic climate change is predicted to favor oaks over their mesic competitors by the year 2100 (Iverson et al. 2008, 2019; Butler et al. 2015). However, it is not certain if or when the effects of climate change will impede mesophytic competitors (Ma et al. 2016). Furthermore, the general pattern of decreasing oak importance (Knott et al. 2019) combined with the sparseness of oak regeneration in mature forests over the past several decades (Jose and Gillespie 1997; Palus et al. 2018; Radcliffe et al. 2020) suggest that even if the changing climate eventually shifts the current competitive balance between oak and maple regeneration, there will likely be a sustained period when mesophytic tree species dominate the canopy of eastern U.S. forests, barring major changes in disturbance regimes. Oak and hickory mortality rates thus have important implications for the short- and mid-term persistence of these species and the ecosystem services they provide.

Oak and hickory benefits to wildlife

Quercus is arguably the most important tree genus for wildlife in the eastern U.S. (McShea et al. 2007). Acorns are a critical food for many common eastern animal species, because they are high in fat, storable through winter, and available in the autumn (Kirkpatrick and Pekins 2002). Oak and hickory leaves are another vital wildlife resource, as they host a high diversity (Tallamy and Shropshire 2009; Narango et al. 2017; Sierzega and Eichholz 2019) and abundance (Butler and Strazanac 2000) of insect taxa (primarily Lepidopteran larvae), relative to maple and beech leaves. Accordingly, the majority of insectivorous songbird species studied prefer oak trees over maple trees for foraging (Graber and Graber 1983; Wood et al. 2012; Narango et al. 2017), and oak forests host a greater abundance of songbirds throughout the year than maple forests (Rodewald and Abrams 2002). Hickory is also often foraged by songbirds at higher rates than its availability (Gabbe et al. 2002; Newell et al. 2014), and pignut hickory bark hosts a relatively high abundance of invertebrates (Zarri et al. 2020).

Different oak species and subgenera vary considerably in the services they provide to wildlife. For example, most songbird species studied prefer to nest and had higher nesting success in white oak (*Quercus alba*) compared with northern red oak (*Quercus rubra*) (Newell and Rodewald 2011; Boves et al. 2013), and different studies of acorn production rank different oak species as top producers, depending on locality and other factors (Greenberg and Parresol 2002). Oak species diversity provides a natural buffer against interannual food fluctuations, as masting cycles of the two primary subgenera of oak (white oak subgenus, *Leucobalanus* and red oak subgenus, *Erythrobalanus*) are largely independent of one another. Oak diversity mitigates the negative consequences of spring killing frosts, which result in a lost year of fruiting 1 year after a frost event for white oak subgenus trees and 2 years after a frost event for red oak subgenus trees (Koenig and Knops 2002). Intra-genus food supply buffering is also likely to apply to foliage-gleaning birds, which can change relative foraging preferences within the *Quercus* genus between different years (Gabbe et al. 2002; Wood et al. 2012). Acorns from

red and white oaks can be complementary food sources; white oak is preferred by many animals likely due to lower tannin content (Pekins and Mautz 1987; Kirkpatrick and Pekins 2002), while red oak is preferred for overwinter caching by some animals such as squirrels (*Sciurus* spp.), due to its delaying of germination until spring and greater resistance to pest infection (Fox 1982; Steele et al. 1996). Other attributes of acorns may be critical to some species, for example, blue jays (*Cyanocitta cristata*) preferentially eat small acorns (Scarlett and Smith 1991; Moore and Swihart 2006). These wildlife ecology studies illustrate that a high diversity and abundance of oak species is likely crucial for maintaining healthy, stable, and diverse wildlife populations.

Oak and Hickory mortality

Since oak and hickory are failing to regenerate in many areas (Nowacki and Abrams 2008), understanding oak and hickory mortality is crucial to understanding the rate of habitat quality decline that many animal species are likely to face in upcoming decades. Studying mortality of these tree species may help managers consider how important wildlife resources might change through time, and studying patterns of oak mortality could assist in prioritizing areas for intensive management to regenerate and maintain oak over the landscape.

The mortality rates of oak species differ in relation to many factors. Species in the red oak subgenus consistently show higher mortality rates than those in the white oak subgenus (Starkey and Oak 1989; Kabrick et al. 2008). Scarlet oak (*Quercus coccinea*) in particular is often identified as the oak with the highest mortality rate (Goebel and Hix 1997), followed by northern red or black oak (*Quercus velutina*) (Voelker et al. 2008; Greenberg et al. 2011). This reflects a difference in growth rates and lifespan, as species from the white oak subgenus tend to grow slower and live longer than trees in the red oak subgenus (Shumway et al. 2001; Greenberg et al. 2011). Both within and between tree species, there is a general inverse relationship between growth rates and longevity (Black et al. 2008; Johnson and Abrams 2009; Di Filippo et al. 2015), likely due to tradeoffs between competing for light and defending against insects and pathogens (Loehle 1988).

Oak mortality is often framed as an issue of oak decline (Haavik et al. 2015), even in areas with relatively low mortality rates (Greenberg and Parresol 2002). Oak decline is a disease complex in which many abiotic and biotic factors combined gradually kill trees, and is the most commonly studied cause of oak mortality in the eastern U.S., although it is still poorly understood (Haavik et al. 2015). The decline-spiral concept (Manion 1991) holds that decline-related tree mortality is caused by interactions of predisposing factors, inciting factors,

and contributing factors. Predisposing factors make a tree less resilient to stressors, inciting factors further weaken a tree's natural defenses against damage, and contributing factors take advantage of the tree's weakened state to finish killing it (Manion 1991). Infestations of wood borers, bark beetles, or root rot fungi are often the ultimate cause of oak death, and are generally considered contributing factors. The most commonly cited inciting factor for oak mortality is drought, although mechanical damage from wind and ice storms or defoliation events from pests like gypsy moth (*Lymantria dispar*) can also act as the initial stressor (Haavik et al. 2015; Morin and Liebhold 2016).

Predisposing factors could be most useful in predicting which areas may be subject to future tree mortality events (Oak et al. 1996; Fan et al. 2011). Some general patterns have arisen within the literature about the predisposing factors of oaks. On an individual-tree scale, older age, suppressed crown condition, and slower growth in more recent years are often associated with higher oak mortality, and tree size can have either a positive or negative association with oak mortality depending on species and stand age (Shifley et al. 2006; Fan et al. 2011). On a stand scale, oak mortality is often positively associated with higher basal area of surrounding oaks, higher basal area of other canopy trees, stand age, and shallower soil (Oak et al. 1991; Oak et al. 1996; Wang et al. 2008). On a landscape scale, researchers often identify oaks on drier topographic positions like upper-slope positions and south or west-facing aspects as being more susceptible to mortality, likely because they are exposed to the most severe effects of drought (Oak et al. 1996; Stringer et al. 1989). In contrast to most studies, Bendixsen et al. (2015) found that oak mortality in Oklahoma was higher on more mesic slope aspects and closer to water. They hypothesized that trees on more mesic topographic positions may have less developed root systems, and thus were not as drought-hardy as their xeric counterparts, or that fungal pathogens are more prevalent and lethal on more mesic topographic positions.

Despite the extensive literature on oak mortality, there are few studies of background oak mortality. We define background mortality as occurring at relatively low rates (~0.5%–2% per year (Stephenson and Mantgem 2005)), in areas not experiencing management intervention or severe disturbance events. Understanding background oak (and hickory) mortality rates is crucial, because the majority of vulnerable forests do not experience severe oak decline events at any given time (Oak et al. 1991, 2004). We had the opportunity to study background mortality rates in mature second-growth forests of southeastern Ohio, using a permanent plot network that was established in the 1990s for developing an

ecosystem classification system (Hix and Chech 1993; Hix and Percy 1997). We quantified mortality rates based on individual tree remeasurements for five oak and one hickory species, and modeled the effect of predisposing tree-scale, stand-scale, and landscape-scale factors on mortality rates for five of these species. Our primary research question was whether topographic variables, which are useful for delineation of oak management units in southeastern Ohio (Iverson et al. 1997; Iverson et al. 2018), were predictive of oak and hickory mortality rates in mature second-growth forests. We also sought to compare species-level patterns of background mortality rates with existing studies.

Methods

Study area

Our study area was the Marietta Unit of the Wayne National Forest (hereafter the Wayne) of southeastern Ohio (Fig. 1). Southeastern Ohio is a part of the Allegheny Plateau Province, and has heavily dissected topography (Lessig et al. 1977). The area has a long history of land use and subsequent abandonment by both Native Americans and later Europeans (Kern and Wilson 2014). It has largely proven unfavorable for agriculture, and today is heavily forested (Hutchinson et al. 2003).

Southeastern Ohio has a continental climate with cold winters and warm, humid summers. It receives precipitation relatively evenly throughout the year, although precipitation is slightly lower in fall and winter than in spring and summer. The average annual precipitation for the weather station in the study area at Marietta Wastewater Treatment Plant was 42.70 in. from 1981 to 2010 (NOAA 2020). The summer average temperature during that time period was 72.6 °F, and the winter average was 32.7 °F (NOAA 2020).

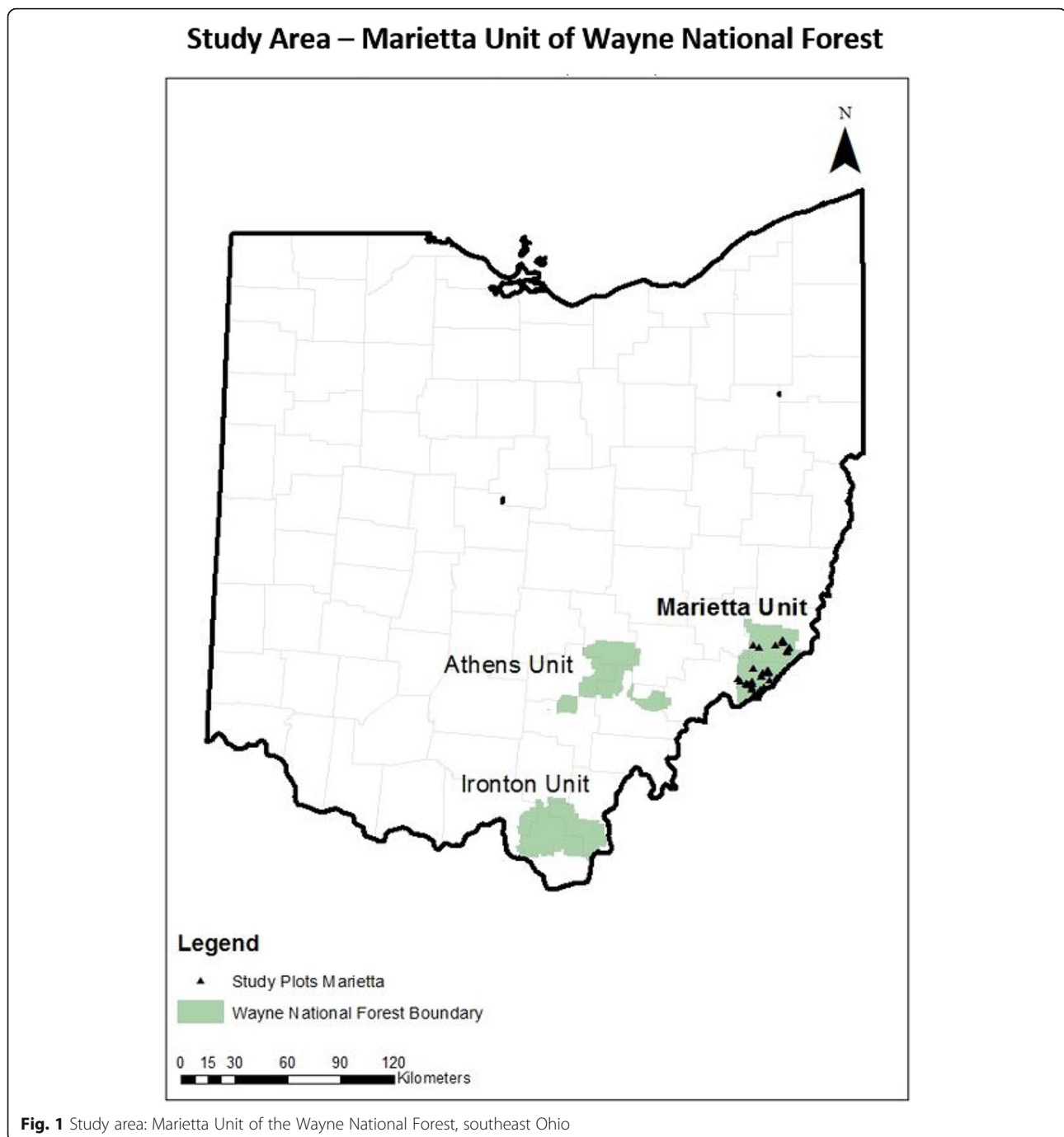
The Marietta Unit is located on the unglaciated Allegheny Plateau Province (Lessig et al. 1977). The main bedrock was formed during the Permian Era of 298–302 million years ago, from sediment accumulation in a prehistoric coastal swamps, with some Pennsylvanian bedrock in modern valleys (Kern and Wilson 2014; Ohio Division of Geological Survey 2017). Common rock types include sandstone, shale, siltstone, limestone, and coal (Lessig et al. 1977). Most soils in the region are udic Alfisols and Ultisols; the udic designation of both suborders indicates a relatively moist climate, adequate for plant growth year round (Brady and Weil 2010). The physiography includes steeply sloping hillslopes and ravines, along with level bottomlands and ridgetops. There are frequently two to three relatively flat structural benches along the length of a hillslope; these are artifacts of the multi-layered nature of the bedrock, and different erosion rates of the rock layers (Hix and Percy 1997). Southeastern Ohio is within the Central Hardwoods

region, Appalachian Mountain section of Fralish (2003), and the (Mixed) Mesophytic forest regions of Braun (1950) and Dyer (2006). It is characterized by a high diversity of primarily deciduous tree species. Today, the most common species by importance value in the Mesophytic forest region (Dyer 2006) are red maple (10.9%) and white oak (5.3%), based on Forest Inventory and Analysis (FIA) data cited in Dyer (2006, page 347). In presettlement land surveys of area, the white oak subgenus comprised 37.0%, the red oak subgenus 12.7%, and hickories 13.9% of witness trees in southeastern Ohio (Dyer and Hutchinson 2019), while red maple, sugar maple, and American beech (*Fagus grandifolia*) combined made up 18.3% of witness trees. In southeastern Ohio areas studied by Hutchinson et al. (2003), the latter three mesophytes were mostly limited to bottomlands. Modern surveys on the Athens Unit of the Wayne National Forest (Palus et al. 2018), and in other areas of southeastern Ohio (Dyer and Hutchinson 2019) found sugar maple, red maple, and American beech to be much greater in abundance and widespread in distribution compared to the presettlement land survey data.

Study design

This study is a continuation of the Wayne National Forest Ecological Classification System project, a long-term research project that examines ecosystem structure and dynamics through the development of a hierarchical ecosystem classification framework (Hix and Chech 1993; Hix and Percy 1997). Researchers originally established 128 permanent plots along 58 transects in the Marietta Unit in 1993–1995, primarily in 1994 (Hix and Percy 1997). We resampled 82 of these plots during the summer 2018; the remainder were lost due to access issues, harvesting, or missing covariate values, which disqualified them from the current study. The time between data collection “snapshots” was thus 23–25 years, primarily 24 years.

The original researchers selected these stands to represent mature, relatively undisturbed second-growth forests (at least 70 years old at the original time of sampling, and at least 93 years old at time of first resampling, based on U.S. Forest Service Vegetation Management Information System data and visual inspection). The stands were originally chosen on the basis of five criteria: “(1) no obvious evidence of major anthropogenic disturbance within the past 40 years (e.g., no stumps), (2) no dominance of early successional tree species, (3) no evidence of recent fire, significant windthrow, or unexplainable mortality, (4) stand is ‘fully stocked’ relative to the upland central hardwoods stocking chart (Gingrich 1967) and (5) no extensive (multiple-tree) gaps in the canopy” (Hix and Percy 1997, page 1118–1119). Within a random subset of each stand that met these



criteria, the original researchers established one or two transects running roughly through the center of the stand. Each transect contained two to five circular 500-m² plots randomly placed along the transect, so that the plots were at least 30 m apart from one another. Transects ran parallel with elevational contours.

We relocated plots with GPS coordinates, witness trees, and permanent rebar monuments established by the original field crews. The original crew sampled trees

in clockwise order starting at due north from plot center. We relocated and remeasured individual trees' diameter at breast height (dbh) (tree diameter at 4.5 ft above the ground) and their alive or dead status by sampling in the same order and recording remeasurements on a photocopy of the original data sheets. Because only two witness trees per plot were tagged, this approach could have led to some errors in individual tree reassignment. However we believe that there is low chance of

systematic error rates for our study species, because the original data sheet copy acted as a quality control 'checklist', plots tended to be species diverse, most study species trees were relatively large and thus distinctive, and we focused on a coarse binary metric in analysis (alive or dead). We also recorded any ingrowth that reached the minimum size threshold of 10.1 cm dbh between the two sampling periods.

The first crews to measure the plots in the 1990s recorded the environmental variables that we used as covariates in our models - slope percent, slope aspect, and slope position. Slope percent was measured with a clinometer, and slope aspect was measured with a compass. Slope position was determined by first measuring the slope length from ridgetop to bottomland, in a line that passed through each plot. To calculate the proportion distance to the ridgetop, the distance to the ridgetop above the plot was divided by the total length of the slope. One soil pit per transect was excavated and the following measurements were determined in the field by horizon: texture, pH, depth, and thickness.

Based on our field-derived data, we modelled the mortality rates of five species: white oak, chestnut oak (*Quercus montana*, formerly *Quercus prinus*), northern red oak, black oak, and pignut hickory. We originally planned to model scarlet oak as well, but small sample size ($n = 24$) precluded further investigation. Based on literature review, we chose nine a priori variables, from four types: topographic variables (cosine transformed slope aspect, proportion distance to ridge, the interaction factor of the two, and slope percent), soil variables (acidity of the B horizon, thickness of the solum), stand structure variables (basal area of the plot in the 1990s, stand age), and individual tree variables (basal area of the tree). These variables are summarized in Table 1, along with selected literature citations and further explanation as needed of each chosen metric.

To characterize the effects of these variables on the probability of tree mortality between sampling periods, we used mixed-effects logistic regression models, which model a binary response variable in relationship to the predictor variables. We modelled whether individual trees originally measured in the 1990s period survived to the 2010s period. We set transect as a random variable, to compensate for potential pseudoreplication caused by spatially grouping plots and using one soil pit per transect (Zuur et al. 2009). The models were run in R version 3.5.2, using the "glmer" function in the "lme4" package (Bates et al. 2019). For model evaluation, we kept each a priori variable in the model for each species. We chose this approach because it afforded direct comparison between different species. Variables were pre-screened for covariance, with a threshold of 0.7. Importance of individual covariates was measured with

significance from model outputs with a p -value threshold of 0.1. We chose a higher threshold than 0.05 because of relatively small sample size of species other than white oak and chestnut oak, and to reduce the chance of committing a type 2 error and the potential negative consequences for management (Lieber 1990). The overall predictive ability of each model was assessed using the delta method of calculating r^2 values for mixed-effects models (Nakagawa et al. 2017), using the function "r.squaredGLMM" in the MuMIn package (Barton 2018).

Results

White oak ($n = 130$) and chestnut oak ($n = 169$) trees were more common on our study plots than northern red oak ($n = 66$), black oak ($n = 60$), or scarlet oak ($n = 24$). The mortality rates for both white oak subgenus species were lower than the rates for any of the red oak subgenus species. Over the 23–25 year study period, the overall mortality rate of the white oak subgenus was 22.4% by stem count, while the mortality rate of the red oak subgenus was 40.0% (Table 2). Chestnut oak had the lowest overall mortality rates (19.8% stem mortality), followed by white oak (23.4% stem mortality) (Fig. 2). Scarlet oak had the highest mortality rate (61.3% stem mortality), followed by northern red oak (41.8% stem mortality). Pignut hickory had 23.9% stem mortality, which is approximately 1% stem mortality per year. Scarlet oak, pignut hickory, and chestnut oak had higher mortality rates as proportions of basal area than rates as proportions of stem count, implying that more of the larger trees of those species died, while northern red oak, black oak, and white oak had higher mortality rates by stem count. All study species combined had a mortality rate of 28.3% by stem count.

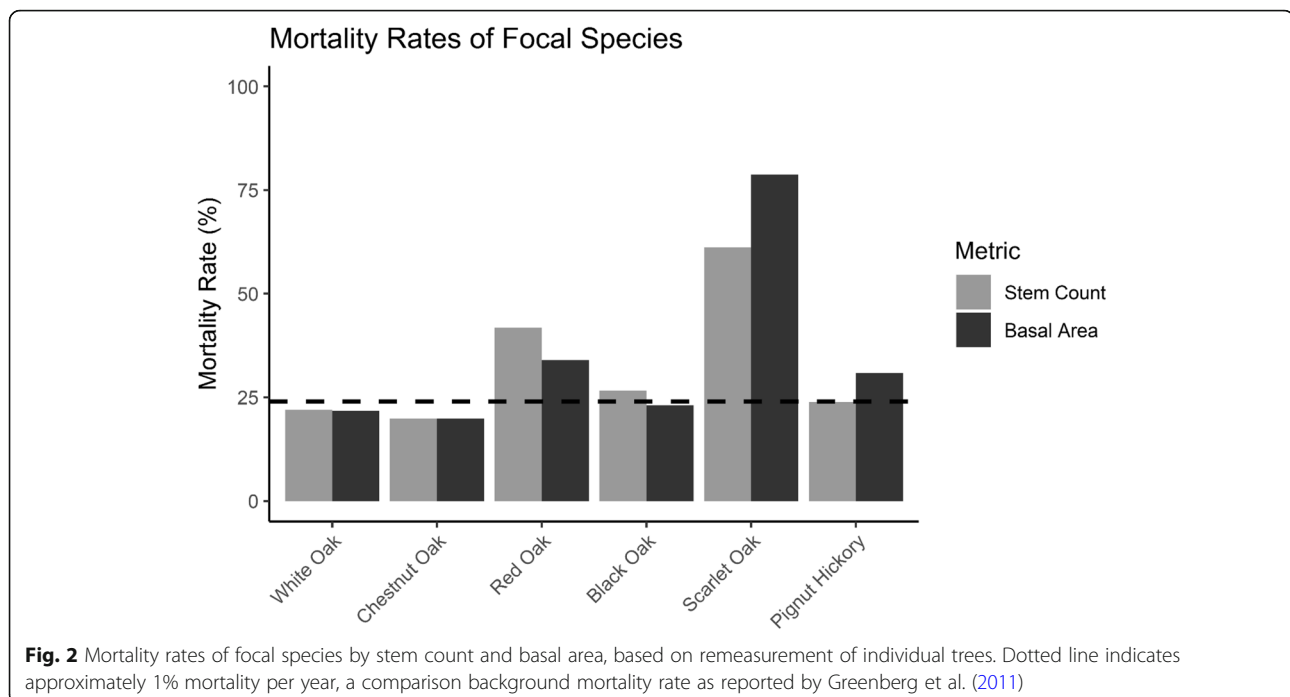
Predictive ability of the mortality models was highest for northern red oak (0.47 conditional r^2), and lowest for white oak (0.12 conditional r^2). Predictive ability was not affected by including the random effect of transect for white oak, northern red oak, or pignut hickory, so the spatial scale of our transects is likely larger than the scale of spatial autocorrelation. However, including random effects improved r^2 estimates for chestnut oak from 0.18 to 0.33 and for black oak from 0.22 to 0.34, indicating including random effects was necessary for appropriately modelling mortality of those species (Table 3). Despite the relatively small sample size, northern red oak mortality had the most sensitivity to the predisposing factors we modeled; northern red oak died at higher rates lower on slopes, on northeasterly aspects, on upper northeasterly and lower southwesterly landscape positions, in older stands, on shallower soils, and on lower pH soil. White oak mortality had a significant negative relationship with basal area of the plot. Chestnut oak had the opposite response; it was significantly more

Table 1 Variables used in mixed logistic regression models of tree mortality, supporting literature, and notes on choice of metric

Variable	Negative correlation with oak mortality	Positive correlation with oak mortality	Notes
Tree basal area (m ² ·ha ⁻¹)	Greenberg et al. 2011 (Erythrobalanus), Voelker et al. 2008 (in low mort areas), Fan et al. 2012 (Leucobalanus), Wood et al. 2018 (white oak), Yaussy et al. 2013 (including managed stands)	Fan et al. 2011 (black and scarlet oaks), Kabrick et al. 2004 (black and scarlet oaks, dominant/codominant crowns)	Basal area of individual tree chosen because it scales more linearly with sapwood area than diameter (Meinzer et al. 2005)
Total basal area of plot (m ² ·ha ⁻¹)		Oak et al. 1991; Wang et al. 2008; Yaussy et al. 2013	Competition of all species chosen rather than competition of <i>Quercus</i> as some other studies have, because of the diversity of our study area and the lack of a major oak decline event
Stand age (years)		Greenberg et al. 2011 (tree age, Leucobalanus), Oak et al. 1991 (tree age, non-linear), Wang et al. 2008	Age is stand age, not individual tree age, and was determined from Forest Service Vegetation Management Information System
Solum depth (centimeters)	Oak et al. 1996, Starkey and Oak 1989		Depth of solum chosen rather than depth of entire soil profile, because some soil pits did not reach the depth to bedrock, and because most fine roots in forest ecosystems are found in upper layers of the soil (Schenk and Jackson 2002)
B horizon acidity (pH)	Demchik and Sharpe 2000 (northern red oak)		B horizon chosen because it had greater significance than A horizon in a study of sugar maple mortality (Bailey et al. 2004), displayed different nutrient concentrations with different levels of oak mortality in (Demchik and Sharpe 2000) and because it is more resistant to erosion over time (Kreznor et al. 1989).
Slope percent	Oak et al. 1996	Wang et al. 2008, Bendixsen et al. 2015	
Slope aspect (cosine transformed [TASP])	Bendixsen et al. 2015, Kabrick et al. 2004 (white oak)		Slope aspect was cosine transformed (cos(45° – aspect) + 1)), to make the metric change continuously in a circular fashion. TASP maximizes at 2 for a 45° aspect, and minimizes at 0 for a 225° aspect (Beers et al. 1966).
Slope position (proportion distance to ridge [PDR])	Oak et al. 1991; Starkey and Oak 1989; Stringer et al. 1989	Bendixsen et al. 2015	Proportion distance to ridge is maximized at the bottom of a slope; positive correlation is higher mortality on lower slopes.
Slope aspect: slope position interaction (TASP:PDR)			High values of the interaction factor indicate upper slopes and northeast facing aspects.

Table 2 Mortality rates by stem count and basal area for focal species and major groupings, based on remeasurements of individual trees

Group	Species	Sample size	Stem count mortality (%)	Basal area mortality (%)
White oak subgenus	White oak	130	23.4	21.7
	Chestnut Oak	169	19.8	19.8
	Total	299	22.4	20.8
Red oak subgenus	Northern red oak	66	41.8	34.0
	Black oak	60	26.7	23.0
	Scarlet oak	24	61.3	78.8
	Total	150	41.3	40.0
Oak genus	Total oaks	449	28.7	28.7
Hickory genus	Pignut hickory	52	23.9	30.9
All trees	Total trees	501	28.3	28.7



likely to die with higher basal area on the plot, as was pignut hickory. Black oak mortality did not show any significant relationships with the covariates (Table 4). Plot-level summary statistics are shown in Table 5, and diameter distributions, showing temporal shifts to fewer and larger trees for all study species, are shown in Fig. 3.

Discussion

Red oak subgenus, white oak subgenus, and hickory trees provide different and complementary benefits to wildlife (i.e. Steele et al. 1996; Kirkpatrick and Pekins 2002; Newell and Rodewald 2011), therefore studying species-specific tree patterns is critical to understanding habitat quality (Adams and Matthews 2019) in mature forests lacking self-replacement of oaks and hickories (Palus et al. 2018; Radcliffe et al. 2020). The high rates of red oak subgenus mortality (Fig. 2) combined with greater initial white oak subgenus dominance indicate a loss of oak diversity on the subgenus level. Our relative

Table 3 r^2 values for mixed effects logistic regression model, delta method. Values from `r.squaredGLMM` {MuMIn}, R version 3.5.2

Species	Marginal r^2	Conditional r^2
White oak	0.12	0.12
Chestnut oak	0.18	0.33
Northern red oak	0.47	0.47
Black oak	0.22	0.34
Pignut hickory	0.29	0.29

mortality rates were consistent with a study of background mortality for the same five oak species in similarly mature forests of the southern Appalachians: scarlet oak had the highest, followed by northern red oak, black oak, white oak, and chestnut oak, respectively (Greenberg et al. 2011). However, Yaussy et al. (2013) found different relative rankings among the same oak species in a multi-state study that included many thinned stands. Thus, oak mortality in managed forests may be driven by different factors than those affecting background oak mortality, perhaps due to thinning capturing mortality and thereby decreasing competition (Yaussy et al. 2013). The mortality rate for pignut hickory was intermediate between the white oak subgenus and the red oak subgenus rates, which contrasted with other studies that gave a background mortality rate for a grouping of hickory species, finding them to have the same or higher mortality as northern red oak (Shifley and Smith 1982; Smith and Shifley 1984; Widmann et al. 2014). This could suggest pignut hickory has a lower mortality rate than other hickory species, a regional difference exists in hickory mortality relative to oak mortality, or our hickory mortality results are specific to mature forests.

Northern red oak's high mortality rate and apparent sensitivity to multiple predisposing factors likely reflects the timing of our study relative to the ages of the stand (mean 135 years, Table 5); many northern red oaks are likely approaching their natural lifespans (Johnson and Abrams 2009; Greenberg et al. 2011). One unexpected result was that northern red oak was more likely to die

Table 4 Mixed effects logistic regression model coefficients (standard error in parentheses), raw output from glmer (lme4), R version 3.5.2. *P* values denoted with asterisks (** < 0.01, * < 0.05, . < 0.1), alpha level 0.10

Variable	White Oak	Chestnut Oak	Northern Red Oak	Black Oak	Pignut Hickory
Intercept	-1.128 (±3.995)	-0.844 (5.761)	-17.087 (±6.142)**	-12.183 (±18.762)	2.420 (±6.837)
Basal area of tree 1990s (m ² ·ha ⁻¹)	-0.148 (±0.124)	-0.171 (±0.188)	-0.264 (±0.160)	-0.386 (±0.295)	0.802 (±0.502)
Basal area of plot 1990s (m ² ·ha ⁻¹)	-0.087 (±0.048)	0.087 (±0.046)	0.045 (±0.048)	-0.127 (±0.110)	0.141 (±0.077)
Age (years)	0.015 (±0.020)	0.000 (±0.021)	0.055 (±0.025)*	0.022 (±0.038)	-0.034 (±0.029)
Depth of solum (centimeters)	-0.014 (±0.011)	0.020 (±0.024)	-0.058 (±0.023)*	-0.027 (±0.025)	0.019 (±0.013)
B horizon acidity (pH)	0.368 (±0.492)	-0.610 (±0.723)	0.958 (±0.576)	3.241 (±3.387)	-1.272 (±0.907)
Slope percent	0.018 (±0.019)	-0.026 (±0.026)	0.025 (±0.025)	-0.016 (±0.029)	-0.011 (±0.027)
Slope aspect (cosine-transformed, TASP)	-0.067 (±0.850)	0.223 (±0.889)	4.515 (±1.720)**	0.086 (±1.652)	0.891 (±1.256)
Slope position (prop. distance to ridge, PDR)	0.493 (±1.973)	-2.641 (±3.408)	12.750 (±4.524)**	-1.609 (±3.434)	-1.404 (±2.769)
TASP:PDR	-1.807 (±1.684)	0.820 (±2.25)	-8.266 (±3.266)*	-0.344 (±3.353)	2.638 (±2.740)

on more mesic slope positions and aspects. Researchers have often found the opposite: that red oak subgenus trees have higher mortality rates in oak decline events on more xeric sites. Trees on xeric landscape position are often assumed to be more susceptible to drought, a leading predisposing factor in oak decline (Starkey and Oak 1989; Oak et al. 1991). Bendixsen et al. (2015) did find that oak decline in a xeric area of Oklahoma was more likely on lower slope positions, but the dominant species in that study was post oak (*Quercus stellata*), which is part of the white oak subgenus. Growth-longevity tradeoffs are a likely explanation; trees in more mesic positions will likely grow faster, which may inherently cause them to die younger (Loehle 1988; Black et al. 2008; Johnson and Abrams 2009; Di Filippo et al. 2015). Additionally, the significant positive association of northern red oak mortality with stand age suggests our study forests are at an age sensitive to growth-longevity tradeoffs in northern red oaks. Northern red oaks commonly grow in more mesic plant associations than other oaks (Adams et al. 2019), perhaps increasing the importance of growth-longevity tradeoffs for this species. Other possible explanations for the higher northern red oak mortality on more mesic aspects include increased competition from mesophytes on more mesic landscape positions, conditions being suitable for fungal pathogens

on more mesic aspects, or trees on mesic aspects allocating relatively fewer carbohydrates to their root systems, thus rendering them less adapted to drought conditions (Canadell et al. 1999; Bendixsen et al. 2015).

More generally, the difference between our results and those found in many Ozark oak decline events suggest that different drivers may be predominately responsible for oak mortality in different regions. Drought stress is more acute for oaks in the Ozark region, while competition and associated growth-longevity tradeoffs may exert more relative influence on our relatively xerophytic study species (Abrams 1996) in our relatively mesic study area (Hanberry and Nowacki 2016). However, higher mortality was associated with shallower soils, similar to associations reported in Oak et al. (1996) and Starkey and Oak (1989), and more acidic soils, similar to results from southwestern Pennsylvania (Demchik and Sharpe 2000). It is thus probable that northern red oak mortality is driven by different factors in different parts of our study area, some dying due to stressful conditions, others due to favorable conditions. Again, these results are important to interpret in relation to the age of our stands and the lifespan of northern red oak.

Our other modelled study species showed fewer significant relationships of tested variables with mortality, likely because our study forests have not yet reached the age of these species' lifespans, reflected in lower mortality rates than northern red oak. For example, we found no significant relationships of tested variables with black oak mortality. Black oak responds conservatively to stress; Keyser and Brown (2016) found that black oak slowed its relative growth rate more than red oak, white oak, or chestnut oak in the two years following drought. Black oak often has lower absolute growth rates than northern red oak, a strategy likely to confer more longevity (Loehle 1988; Johnson and Abrams 2009).

Consistent with the literature, both our focal species from the white oak subgenus, white oak and chestnut oak, died at relatively low rates and were relatively

Table 5 Summary statistics of plot-level covariates

Covariate	Mean	Median	Standard error
Transformed aspect	1.08	1.16	0.08
Proportion distance to ridge	0.53	0.56	0.03
Percent slope	31.62	33.00	1.95
Basal area plot (m ² ·ha ⁻¹)	33.38	30.68	1.46
Age (years)	135.3	130.0	1.93
Solum depth (cm)	73.90	74.00	3.33
pH of B horizon	5.08	5.00	0.06

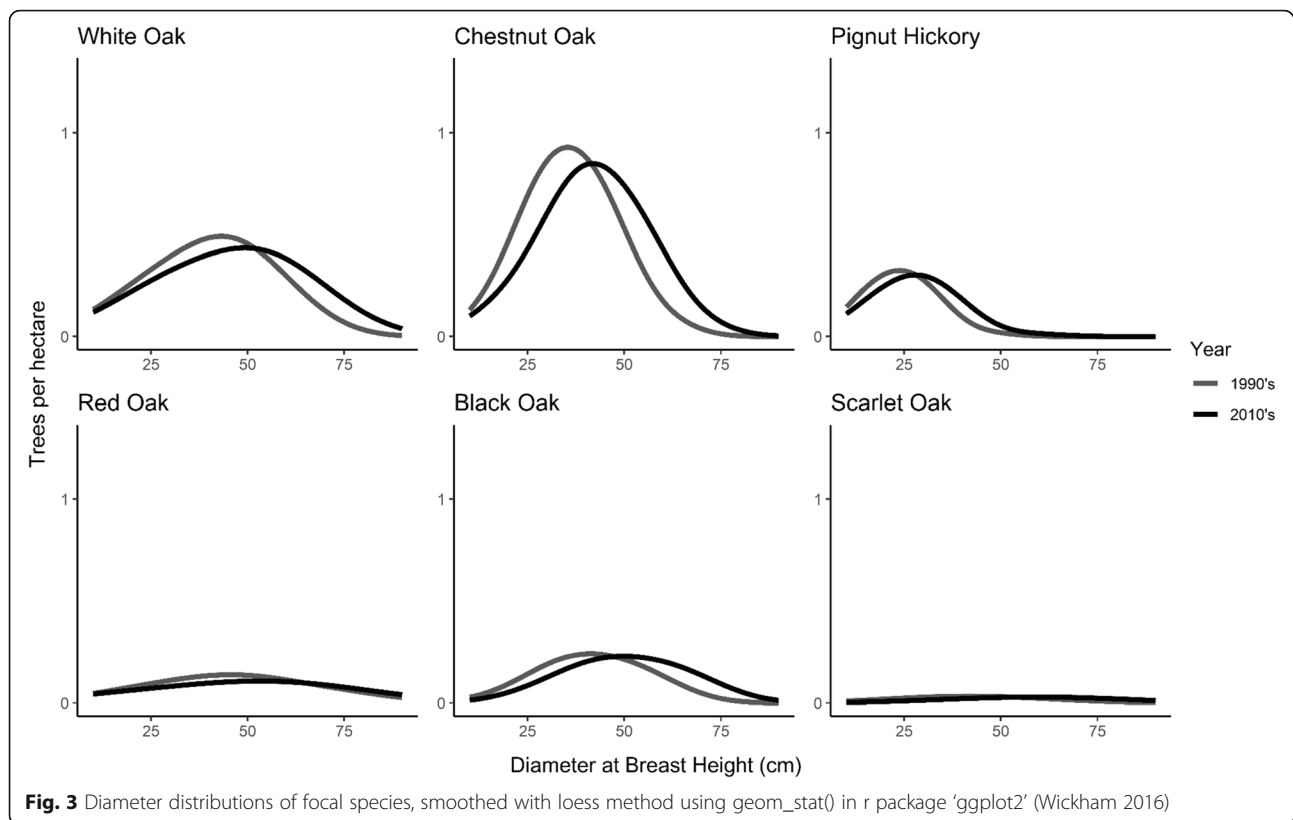


Fig. 3 Diameter distributions of focal species, smoothed with loess method using `geom_stat()` in r package 'ggplot2' (Wickham 2016)

insensitive to landscape-scale variables (Greenberg et al. 1997; Keyser and Brown 2016). These two species, however, showed opposite relationships to basal area of the plot, likely reflecting different abilities to survive under competitive stress. Alternatively, the observed relationship could be confounded with site productivity, and white oak could be favored on more productive sites, although the other covariates in our model such as slope position, aspect, pH, and depth of solum likely represented a large portion of the productivity gradient. Relatively long-lived white oak (Johnson and Abrams 2009) is likely not as vulnerable as northern red oak to growth-longevity tradeoffs at the age of our study stands. In contrast to white oak, chestnut oak showed less resilience to competition, despite it having similar shade tolerance and growth rates compared with white oak (Burns and Honkala 1990). It is likely that the association of chestnut oak with drier landscape positions (Nowacki and Abrams 1992) renders it more sensitive to competition for water during drought. Other studies have found positive relationships of white oak mortality (Kabrick et al. 2004) or white oak subgenus mortality (Bendixsen et al. 2015) with mesic aspects, but our data did not show this association.

We did not find studies modeling species-level hickory mortality rates in relationship to predisposing factors, although (Yaussy et al. 2013) modeled the association of

genus-level hickory mortality with competition, and found a positive correlation. Our pignut hickory model corroborated these results, showing higher mortality with more competition.

Conclusion

Our data on oak and hickory mortality rates in mature forests, in combination with the documented importance of oak diversity for wildlife, suggest that forest managers prioritizing wildlife management in mature forests similar to our study area should consider focusing management efforts towards favoring red oak subgenus species. Similar to patterns found in many studies, scarlet oak, black oak, and northern red oak are dying at higher rates than white oak and chestnut oak, and they are less common in our second-growth study forests averaging 135 years old. Our literature review indicated a mix of white oak subgenus and red oak subgenus tree species is beneficial if not essential for many wildlife species; land managers and wildlife ecologists should be aware of the higher red oak subgenus background mortality quantified in this study. Foresters may act by harvesting white oak subgenus trees preferentially to red oak subgenus trees, thinning to promote individual red oak tree vigor (Yaussy et al. 2013), or designing regeneration treatments specifically for red oak subgenus species (Crow 1988). Some caveats are necessary, however, before

focusing too specifically on red oaks. First, red oak subgenus trees are currently more common than white oak subgenus trees across the state of Ohio (Widmann 2016), and the eastern U.S. (Abrams 2009); therefore, our observed patterns of greater numbers of white oak subgenus trees likely apply only to mature, second growth forests. White oaks have been harvested at high rates in recent years to support a rapidly growing bourbon industry (Peters and Rebbeck 2017), which is likely reflected in rising white oak stumpage prices (Luppold 2019). Finally, given that white oak was more common than red oak subgenus trees in pre-settlement Ohio (Dyer and Hutchinson 2019), our results could be interpreted as forests of the Marietta Unit returning to a more 'natural' state following widespread nineteenth century forest clearing for agriculture and industry (Abrams 2009; Iverson et al. 2018). However, the current dominance of mesophytic species and the lack of oak and hickory in the regeneration layer of our study area (Radcliffe et al. 2020) suggest a change to an alternative stable state (Beisner et al. 2003; Nowacki and Abrams 2008). Our points above illustrate that while red oak conservation efforts will become increasingly worthy of consideration in forests of our study area, local context determines which oak groups are under the most pressure.

Our results are based on an observational study design, so any causal explanations we offer should be taken as suggestive and require experimental testing to corroborate. Our models suggest that competition is the only tested predisposing factor that significantly predicts mortality rates for any of our focal species other than northern red oak, as it was significant for chestnut oak, white oak, and pignut hickory. In topographically complex landscapes, designing thinning treatments to increase drought resilience (D'Amato et al. 2013) may mitigate overall oak and hickory mortality. Additionally, our finding of a negative relationship between white oak mortality rate and competition warrants further consideration and study. Northern red oak, however, was more likely to die on more mesic landscape positions and in older stands, possibly due to growth longevity-tradeoffs (Loehle 1988), which northern red oak may be vulnerable to at the age of our study stands (Johnson and Abrams 2009). These mesic areas could thus be relatively low in protection priority on properties where northern red oak is a species of concern. Black oak appears to be relatively resilient to the predisposing factors we studied.

Overall, there is relatively little research into patterns of background oak and hickory mortality in mature forests east of the Ozark Highlands, especially in relation to scales larger than individual tree growth and competition. Hickory in particular is relatively understudied,

especially on the species level, and we believe it merits more attention from ecologists, considering its high benefits to wildlife (Fralish 2004; Sierzega and Eichholz 2019; Zarri et al. 2020). Future research should investigate drivers of oak and hickory mortality outside of major decline-affected areas, in both managed and unmanaged stands in multiple successional stages.

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Authors' contributions

Hix contributed to original study design in the 1990s, all authors contributed to resampling design. Radcliffe led field resampling, data analysis, and writing. All authors contributed to data analysis and commented on drafts of the paper. All authors read and approved the final draft of the paper.

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Availability of data and materials

Datasets used and model results are available from corresponding author upon reasonable request. Data is not publicly available because of ongoing work with the dataset.

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare no conflicts of interest.

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