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ABSTRACT

Effects of Double-crested Cormorants (*Phalacrocorax auritus*) on vegetation, soil chemistry and tree health have been documented from their breeding colonies in the northern breeding grounds of Canada and the United States (U.S.) but not for areas within the southeastern United States where breeding activity is relatively novel. We compared vegetation and tree metrics such as structure diversity, and soil chemistry among colony islands, uninhabited islands, and abandoned colony islands within Guntersville Reservoir, a temperate forest ecosystem. Avian diversity and community structure were also quantified on these islands. Concentrations of potassium (K), phosphorus (P) and nitrate (NO_3^-) in soil were negatively related to cormorant use, while tree diversity was lower on historic (tree mean = 4.35 ± 2.46 species) and colony (tree mean = 3.91 ± 3.12 species) islands relative to reference islands (tree mean = 9.11 ± 3.88 species). Canopy cover was less (min: < 20%), and midstories denser on colony and historic islands relative to reference islands. Avian diversity was significantly lower for colony islands (mean = 6 ± 3 species) than both reference (11 ± 7 species) and historic (10 ± 7 species) islands. These effects of cormorant nesting can be seen even after 10 years of colony abandonment supporting that cormorants can have long-term effects on insular habitats in temperate forest ecosystems.

1. Introduction

Double-crested Cormorants (*Phalacrocorax auritus*, cormorant) have the capacity to affect soil properties within their nesting colonies (Rush et al., 2011; Dorr et al., 2014; Lafferty et al., 2016). Changes in soil qualities such as nutrient concentrations and pH can disrupt plant germination and promote invasive vegetation (Cuthbert et al., 2002; Boutin et al., 2011; Ayers et al., 2015). Habitat changes borne through cormorant nesting activities includes simplification of habitat structure by suppressing the presence and growth of sensitive species and the homogenization of species composition, (Ishida, 1996; Hebert et al., 2005; Breuning-Madsen et al., 2010; Boutin et al., 2011).

Changes in soil, plant and animal communities have been recorded in and proximate to cormorant colonies (Ayers et al., 2015; Hobara et al., 2005; Taylor and Dorr, 2003). The effects of excess nutrients on soil chemistry and plant diversity are not constrained to the area immediate to cormorant nest sites (Ayers et al., 2015), as nutrients can leach from the forest floor to areas nearby (Hobara et al., 2005; Breuning-Madsen et al., 2008). Nitrogen (N) and phosphorus (P), as

well as other elements included in cormorant-derived deposition can alter soil properties even after birds are no longer nesting at that location (Rush et al., 2011, 2013). Nesting cormorants can also displace co-nesting species, particularly colonial waterbirds (Taylor and Dorr, 2003; Wyman and Cuthbert, 2015). Black-crowned Night Herons (*Nycticorax nycticorax*) and various gulls (*Larus* sp.) and terns (*Sterns* sp.) have shown displacement and abandonment from encroaching cormorant colonies and destruction of nesting trees, though whether these impacts are directly related to cormorant nesting is debatable (Cuthbert et al., 2002).

The North American Interior population of cormorants has exhibited dramatic growth over the past 40 years (Hatch, 1995). During the past decade, the number of cormorants breeding within the southeastern U.S. has also greatly increased (Barras, 2004). Since 2001, Guntersville Reservoir, a dammed portion of the Tennessee River in Alabama, has had cormorants breeding on islands throughout the reservoir. A study by Lafferty et al. (2016) investigated how breeding cormorants affect these warm temperate moist forest ecosystems (Lugo et al., 1999), and found that cormorants deposit P, potassium (K) and

nitrate (NO_3^-) on their nesting islands while also decreasing pH and damaging tree health (Lafferty et al., 2016). However, Lafferty et al. (2016) did not look at vegetation structure such as midstory height, plant and avian diversity or plant and avian community structure on islands, nor islands abandoned by cormorants over historical time periods. Consideration of abandoned islands can give information on how cormorant colonies recover without direct human intervention.

If cormorants have the capacity to alter vegetation structure and tree composition in temperate forest ecosystems, it begs the question whether they can indirectly affect other avian communities. There is ample evidence that there is a correlation between vegetation structure and avian diversity (Rotenberry, 1978; Erdelen, 1984; Loehle et al., 2005). Cormorant colonies have been shown to alter the structure of the ecological communities of their nest colonies, opening the canopy for growth of woody vegetation. This change may resemble early successional vegetation communities (Ayers et al., 2015), which in turn could influence the structure of the supported avian community. Birds other than colonial waterbirds that use the ecological communities of cormorant colonies would therefore be expected to respond to these changes in predictable ways, predicated on known habitat affinities.

Our objectives with this study were to measure and contrast soil nutrient concentrations, structure and diversity of vegetation and trees and avian diversity on islands where cormorants have nesting colonies (colony), islands where cormorants have no history of nesting (reference), as well as islands that have been abandoned by cormorants after occupation (historic). Soil nutrient concentrations, such as P and NO_3^-, are expected to be higher on colony islands compared to islands where cormorants have no history of nesting (Hebert et al., 2005; Boutin et al., 2011; Lafferty et al., 2016). Additionally, pH values are expected to be lower in soils sampled from colony and historic islands than from reference islands (Lafferty et al., 2016). Diversity of vegetation and trees are expected to be low on colony islands compared to reference islands, with non-native species more prevalent on colony and abandoned islands. Although, historic islands may see more diversity than currently occupied islands, though would still be lower than reference islands.

As there is evidence that cormorant colonies can change vegetation structure, we anticipate that avian communities and diversity would also be affected. Early successional habitat from open canopy cover, a hypothetical product of tree death from cormorant nesting, may promote an influx of native pioneer species as well as growth of native hardwoods and shrubs. Conversely, excess soil nutrients may promote a hostile environment for native species not prone to disturbance and over time an overgrowth of shrubs, vines and woody vegetation may decrease diversity of certain avian species on colony and historic islands.

2. Methods

2.1. Study site

This study was conducted on Guntersville Reservoir, located in Marshall and Jackson counties in northeast Alabama, USA. Guntersville Reservoir was created by damming the Tennessee River in 1939 with hydrology controlled by the Guntersville Dam under the Tennessee Valley Authority (TVA). Temperature and climate are temperate, with summers averaging 27 °C and winters around 15 °C (Soil Survey Staff, 2016). Deciduous hardwoods, such as oaks (*Quercus* spp.) and hickories (*Carya* spp.), and coniferous trees such as red cedars (*Juniperus virginiana*) and loblolly pines (*Pinus taeda*) are prevalent (Soil Staff Survey, 2016). Islands are present throughout the reservoir, though fewer are found in the north end of the reservoir.

2.2. Sampling design

Twelve islands were selected for this study and divided into one of

three treatment groups based on cormorant occupancy: colony (islands naturally colonized by breeding cormorants), reference (islands with no history of cormorant occupancy) and historic (islands that were previously colonized and subsequently abandoned). A subset of six islands studied by Lafferty et al. (2016), which were categorized as colony (3) and reference (3), were included in this study. Colony islands for Lafferty et al. (2016) included Connor's Island, South Sauty and North Sauty. An additional three colony islands were included in this study (New Connors 1, 2 and 3) that had been occupied after Lafferty et al. (2016). The three reference islands in both studies were SE Connors, North South Sauty and East North Sauty with an additional reference island of West North Sauty included in our study. One key island type that was included, but not looked at in Lafferty et al. (2016) were historic islands that had been occupied by cormorants and subsequently abandoned and left to recover without any direct management. These three islands were Old Connors, Connors and Old South Sauty.

Our stratified random sampling design was based on island size such that the density of samples per unit of effort was constant across islands of differing area. We randomly sampled each island multiple times (i.e. our plot points) and made inferences relative to whole islands. Most sample locations were determined from previous plots referenced in Lafferty et al. (2016), though some plots from the Lafferty et al. (2016) study were not accessible and/or eroded over time. To replace plots from the Lafferty et al (2016) study that could not be used in the present study, islands were overlaid with a 10 m × 10 m (m) grid and plots were selected by proportionally sampling 20% of the 10 m² grid on each island (Lafferty et al., 2016). This grid was created using ortho-quad imagery of Guntersville Reservoir and ArcMap v.10.1. Plot center was determined by recording the latitude and longitude at the centroid.

2.3. Soil

Soil sampling was completed from June to August 2016. When sampling soil from the center of the 1 m² plot, the surface detritus were brushed away and a soil core was taken to a depth of 22 cm (cm) using a soil auger (9 cm diameter) and homogenized. Samples were kept cool and dry until all soil samples were collected at the end of August 2016 (Lafferty et al., 2016). For processing, nutrient concentrations (kg/ha) and base saturation were extracted from each sample which were used to determine percent concentrations for the following soil characteristics: percent organic material (%OM), pH, phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn), sulfur (S), sodium (Na), hydrogen (H), nitrate (NO_3^-) and ammonium (NH_4^-). These nutrients were selected due to their importance in plant physiology and circulation and to their correlation with excess cormorant guano deposits (Boutin et al., 2011; Rush et al., 2011; Lafferty et al., 2016).

2.4. Community diversity

Habitat characteristics were measured at sample locations on all islands from June to August 2016. A 1 m² quadrat made of PVC pipe was placed at plot center to measure percent plant cover, plant density, and plant diversity for each plot following procedures developed by Ayers et al. (2015). A digital image was taken of the plot before any sampling so that percent cover could be calculated by uploading the images onto a computer and overlaying a grid comprised of 100 equal squares over the image (Ayers et al., 2015). Each box was recorded as covered ($\geq 50\%$ of the box covered by live vegetation) or not covered. Once all 100 boxes were recorded for an image, the number of covered boxes indicated percent, live plant cover for that plot. Plant diversity was recorded by identifying all species in a plot and plant density was recorded by counting each individual of a species in each plot. Any plants that could not be identified in the field were given a unique number and pressed for later identification.

Canopy cover was measured using a spherical densiometer (Lemmon, 1956), with measurements taken in each of the four cardinal

directions at a 5 m radius from plot center. The percent canopy recorded in each direction was used to calculate average canopy cover for sampled plots. A Nudd's board (Nudds, 1977) was used to measure vegetation density of midstory heights, or vertical structure, in two directions with bearings selected randomly at a 15 m radius from plot center. The proportion of each 0.5 m (0–2 m) interval covered by vegetation was recorded as a categorical value between 1 and 5 where: (1) 0–20%, (2) 21–40%, (3) 41–60%, (4) 61–80% and (5) 81–100% cover (Nudds, 1977). Coverage values were averaged from the two samples to obtain a single midstory cover value for each plot.

All tree species in a 10 m radius plot were identified to species, with those that had a diameter at breast height (DBH) of over 8 cm given a unique number and vigor class. The vigor class scale was a metric for how healthy a tree was on a scale of 1 to 5 where: (1) No decay, 100% healthy; (2) Mostly healthy, < 25% decay; (3) Not healthy and/or dying, > 50% decay; (4) Newly dead, 100% decay; and (5) Old snag (Lafferty et al., 2016). If a tree exceeded 8 cm in DBH, it was measured and recorded. Trees less than 8 cm were identified to species and a count of each species recorded. Each plant or tree species was designated as native or non-native using data from the USDA Plant Database (USDA, NRCS, 2018).

Point count surveys of avian species were conducted on all islands sampled. Methods for count data were taken from Ralph et al. (1995) and Hamel et al. (1996). Points were not randomly selected due to the small size of islands and the designation that point plots be at least 200 m away from each other (Hamel et al., 1996). Because all islands except Connors Island were less than 200 m in size, one point was selected as close to the center of each island as possible. For Connors Island, two points were selected that were over 200 m apart from each other and centered in the middle of the island. Once locations for bird survey plots were determined, point counts were started 6 June 2017 and repeated six times at each location, with one week between survey times, before 16 August 2017.

Islands were split by colony complex groups (Connors, South Sauty and North Sauty) and split between two data recording teams. Connors Island complex had six islands total, island groups where split into two groups, Connors Islands and North and South Sauty Islands. The Connors Island complex was further subdivided by reference and historic (e.g., SE Connors, Connors and Old Connors Islands) and current colony islands (e.g., New Connors 1, 2 & 3), with teams alternating surveys every trip. South and North Sauty complexes had three islands each, therefore one group collected data at one complex or the other every visit. Before point counts started, we selected island complexes at random ('Connors' or 'Sautys') and then islands within complexes at random. This was done so all islands were not sampled at the same time each morning to prevent potential sampling bias in point count surveys. After this first survey, teams alternated the starting complex for each subsequent visit. Two days were designated for data collection, unless weather impeded field work. Teams were assigned to island complexes and islands within complexes at random to prevent observer bias. Teams were assigned, at random, to island groups within the complexes for the first visit with teams alternating visits to each island thereafter.

Point count surveys began at dawn, which was established by using the WeatherBug ® Version: 5.3.1.3 application for Google Android. A 10 min count survey was begun, recording all birds heard and seen during the time period…

3. Statistical analysis

3.1. Soil

Generalized linear mixed models (GLMM) were used to analyze all soil characteristics (Lafferty et al., 2016). A model was constructed for each soil characteristic as the response variable, with treatment type (colony, reference or historic) as the fixed dependent variable to test the effects of cormorant occupancy on soil characteristic. As multiple soil

samples were collected per island individual islands surveyed were included as a random effect in all models. Statistical tests and processes were adapted from Zuur et al. (2011) using the packages 'lme4' and 'multcomp' in Program R (R Core Team, 2017). A multiple comparison test, completed using the function 'glht' in Program R and a Tukey's post-hoc test, provided post hoc assessment of differences among treatments types by soil characteristic means.

3.2. Community diversity

We applied separate GLMMs to evaluate the response variables of plant and tree diversity and canopy cover relative to the fixed effect of treatment type and a random effect of individual islands. If significant ($p < 0.05$), post-hoc tests were run on each model to identify differences among treatment types. All analyses were run using 'lme4' and 'multcomp' packages in Program R (R Core Team, 2017).

We used an ordered logistic regression model to examine cormorant impacts on tree health (vigor class), similar to Lafferty et al. (2016), with the response variable being the ordered data of vigor class, and treatment as the categorical fixed effect. Diameter at breast height (DBH) of trees was included as a continuous fixed effect, with individual islands included as a random effect. A step-wise variable selection using Akaike information criterion (AIC) was conducted to find the most suitable model for outputs. Package 'ordinal' was used for all analyses (R Core Team, 2017). Influence of cormorant occupancy on DBH was analyzed using linear mixed models (LME) with DBH as the response variable, treatment as a categorical fixed effect and individual islands as the random effect (package 'lme4', R Core Team, 2017). If the DBH model was significant, we applied Tukey's post-hoc tests for comparison of means among treatment types.

To test for differences in abundance of native vs non-native species on islands we used linear contrast statements in an ANOVA framework. These contrast statements were made between reference-historic islands. Data on native status was evaluated for normality using Q-Q plots and was log-transformed for a normal distribution if a non-normal distribution was indicated. We used a one-tailed post-hoc test (specifying 'less') with $\alpha = 0.05$ to test for statistical significance among treatments.

We assessed differences in vegetation density of midstory heights among treatment types through nonparametric tests. Distributions of vegetation cover data were also evaluated among treatments using nonparametric tests (Kruskal-Wallis tests; package 'stats', R Core Team, 2017). If statistical significance was evident ($p < 0.05$), a Dunn's Multiple Comparison Test (package 'dunn.test', R Core Team, 2017) was used to compare between island treatment types.

We used several methods to measure the diversity of avian communities within each of our island classifications. A conservation concern score was attributed to all species found on each plot point within each island sampled. Conservation scores were obtained from Partners in Flight Avian Conservation Assessment Database (PIF; Panjabi et al., 2017). We conducted a distance-based redundancy analysis (dbRDA) for all avian species by island treatment to identify differences in avian community composition among treatments. Distance-based redundancy analysis is an ordination method that uses non-Euclidean dissimilarity indices (Bray-Curtis distance), but is still considered a linear analysis (Oksanen et al., 2007). Variables in this ordination analysis were simple counts of all species found in a fixed area radius, which were then used to find differences among island types. An ordination plot was then created, with ellipses denoting island treatment type (reference, colony and historic). All analyses were conducted in package 'vegan' in Program R (R Core Team, 2017).

Unadjusted counts were used instead of adjusted due to an inadequate number of detections for some species to provide reliable adjustment factors for distance (Hutto et al., 1986; Thompson, 2002). Additionally, point counts were conducted in one season, (Summer 2017) during the same time of day, (dawn – 9 AM) on similar habitats

on surveyed islands thus making simple counts sufficient for analysis (Raphael, 1987). We used Chao2-type estimators to calculate species richness of all six visits to the 12 islands. Chao2 estimators are non-parametric models that do not include assumptions about distributions of species and give an accurate lower bound richness (Chao et al., 2005). Chao2 estimators were calculated in R-package 'vegan' (R Core Team, 2017). We used a LME to evaluate differences in Chao2 estimators of species richness and PIF scores among treatments. The response variables for each models were Chao2 scores and PIF scores summed for each survey. The fixed categorical effect was island treatment with the random variable of each individual island a nested effect, with six visits for each island. Models were created in package 'nlme' in Program R (R Core Team, 2017). Once modeled, a Tukey's post-hoc test was performed to test for differences in island treatment types for each response variable.

4. Results

4.1. Soils

Generalized linear mixed models testing for differences in K, NO_3^-, and P among treatment types showed significant effects among all treatments (Table 1). Calcium, pH, Mg, Zn, S, Na, %OM and H were not significantly different among treatment types. Colony (K: $z_1 = -3.77$, $p < 0.001$; NO_3^-: $z_1 = -3.02$, $p < 0.01$), and historic (K: $z_1 = 2.7$, $p = 0.02$; NO_3^-: $z_1 = 2.13$, $p < 0.05$) islands soil samples contained greater concentrations of K and NO_3^- than reference islands, but historic and colony islands did not differ (K: $z_1 = -0.84$, $p = 0.68$; NO_3^-: $z_1 = -0.79$, $p = 0.71$) from each other (Table 1).

Results for P were different than other soil characteristics in that historic and reference islands differed significantly from one another ($z_1 = 2.76$, $p < 0.02$), while colony and historic islands ($z_1 = 1.74$, $p = 0.19$) and colony and reference islands ($z_1 = -81.01$, $p = 0.57$) did not differ (Table 1). Though not statistically significant, mean pH was lower on historic islands (4.51 ± 0.6), followed by colony islands (4.66 ± 0.5), and reference islands (5.27 ± 0.6), ($z_1 = -2.12$, $p = 0.08$) (Table 1). With the exception of concentrations of P, where historic islands (mean $\pm$ standard deviation, 990.54 ± 788.17 kg/ha) have significantly more P than colony (488.7 ± 496.84 kg/ha) and reference islands (120.31 ± 172.44 kg/ha), all other soil characteristics showed higher concentrations on colony islands than the other two island types (Table 1).

Table 1
Summary statistics for pH, potassium (K [kg/ha]), phosphorus (P [kg/ha]) and nitrate (NO_3^- [mg/kg in soil]) from samples collected from active cormorant colonies (colony), islands with no history of nesting (reference) and abandoned colony islands (historic). Letters in subscript designate differences in means evaluated by Tukey's post hoc tests.

Island Type	n	pH		K (kg/ha)	
		Mean (SD)	Range	Mean (SD)	Range
Colony	30	4.66 (0.5)$_a$	3.70–6.00	253.20 (139.90)$_b$	97.51–730.80
Reference	32	5.27 (0.6)$_a$	4.30–6.70	100.32 (47.20)$_a$	32.00–196.20
Historic	34	4.51 (0.6)$_a$	3.60–6.10	212.83 (107.10)$_b$	71.73–532.40

Island Type	n	P (kg/ha)		NO_3^- (mg/kg)	
		Mean (SD)	Range	Mean (SD)	Range
Colony	30	488.70 (496.80)$_{ab}$	13.50–1731.70	54.50 (45.60)$_b$	11.50–194.30
Reference	32	120.30 (172.40)$_a$	7.90–840.60	10.10 (18.10)$_a$	0.10–85.80
Historic	34	990.50 (788.20)$_b$	22.40–3299.80	47.40 (61.90)$_b$	0.20–316.30

4.2. Community diversity

Plant diversity did not differ significantly among treatments. Tests for the five midstory cover categories showed differences among treatments at $p < 0.05$ (Fig. 1). Differences in vegetation density varied among colony types and midstory height categories (Fig. 1). The results for plant cover were also significant ($H_{(2)} = 8.02$, $p < 0.01$) between historic islands and the other treatments, with more vegetative cover on historic islands relative to both reference and colony islands (Fig. 1).

Seventy-seven species of flora were identified from sampled islands, with colony islands totaling 41 species, reference 36 species and historic having 43 species individually. Pokeweed (*Phytolacca americana*) was the most prevalent species on historic and colony islands (> 3000) and the least prevalent on reference islands, where Virginia dayflower (*Commelina virginica*) was most commonly found. Diversity of native vs. non-native plants did not differ among treatments ($F_{2, 93} = 0.55$, $p > 0.05$), though colony and historic sites did have $\geq 33\%$ more non-native species (33 and 32 plants, respectively) than reference islands (24 total plants).

Tree diversity differed between reference islands and colony islands ($z_1 = 2.23$, $p < 0.05$) though there was no difference between historic and reference ($z_1 = -1.84$, $p = 0.16$), or colony and historic islands ($z_1 = 0.14$, $p = 0.1$, (Fig. 2). Canopy cover was not significantly different among treatments types, though reference islands had a higher mean canopy cover (83.63%) compared to both colony (65.72%), and historic (67.52%) islands. The DBH of trees differed between colony and reference islands ($z_1 = -2.62$, $p < 0.02$), with colony islands populated with trees of smaller DBH relative to reference and historic islands, where DBH was larger overall (Fig. 2). Reference and historic islands did not differ in mean DBH ($z_1 = 0.44$, $p = 0.9$) nor did historic or colony islands ($z_1 = -1.84$, $p = 0.16$). Results for vigor class of trees showed no significance of DBH by treatment type.

The ordination plot of avian species by island type shows a distinction between colony islands and historic and reference islands (Fig. 3). The dissimilarity of reference islands was driven by the presence of four species: Brown-headed Cowbird (*Molothrus ater*), Yellow-throated Warbler (*Setophaga dominica*), and Blue-winged Warbler (*Vermivora cyanoptera*), and to a lesser degree, Pine Warblers (*Setophaga pinus*). Historic and reference islands are relatively similar to each other, though the presence of Prothonotary Warblers (*Protonotaria citrea*) on reference islands differentiated them from historic islands (Fig. 3).

The GLMM for PIF values by treatment types revealed no significant differences in diversity among treatments ($p > 0.05$), though Chao2 diversity estimators were significant among treatment types (Fig. 4). We found higher avian diversity on reference ($z_1 = 3.41$, $p < 0.002$), and historic ($z_1 = 2.64$, $p < 0.02$) islands relative to colony islands. Historic and reference islands were similar in mean avian diversity ($z_1 = -0.46$, $p = 0.89$; Fig. 4).

5. Discussion

Cormorants nesting on islands within Guntersville Reservoir deposited nutrients, reflected in our finding of higher P, K and NO_3^- on colony islands, which in turn affected plant diversity and structure and thus, bird diversity on these occupied islands. Results of this study illustrate that these effects remained evident 10 years after the abandonment of these colonies by cormorants. While other studies have shown soil chemistry changes on active colonies (Ellis et al., 2006; Boutin et al., 2011; Rush et al., 2013; Lafferty et al., 2016), there is not documentation of the long-term effects of soil chemistry changes on abandoned cormorant colonies, and little documentation on impacts to avian diversity, particularly in temperate forest ecosystems.

Although not statistically significant, minimum values of pH on historic islands were lower than current colony islands despite historic
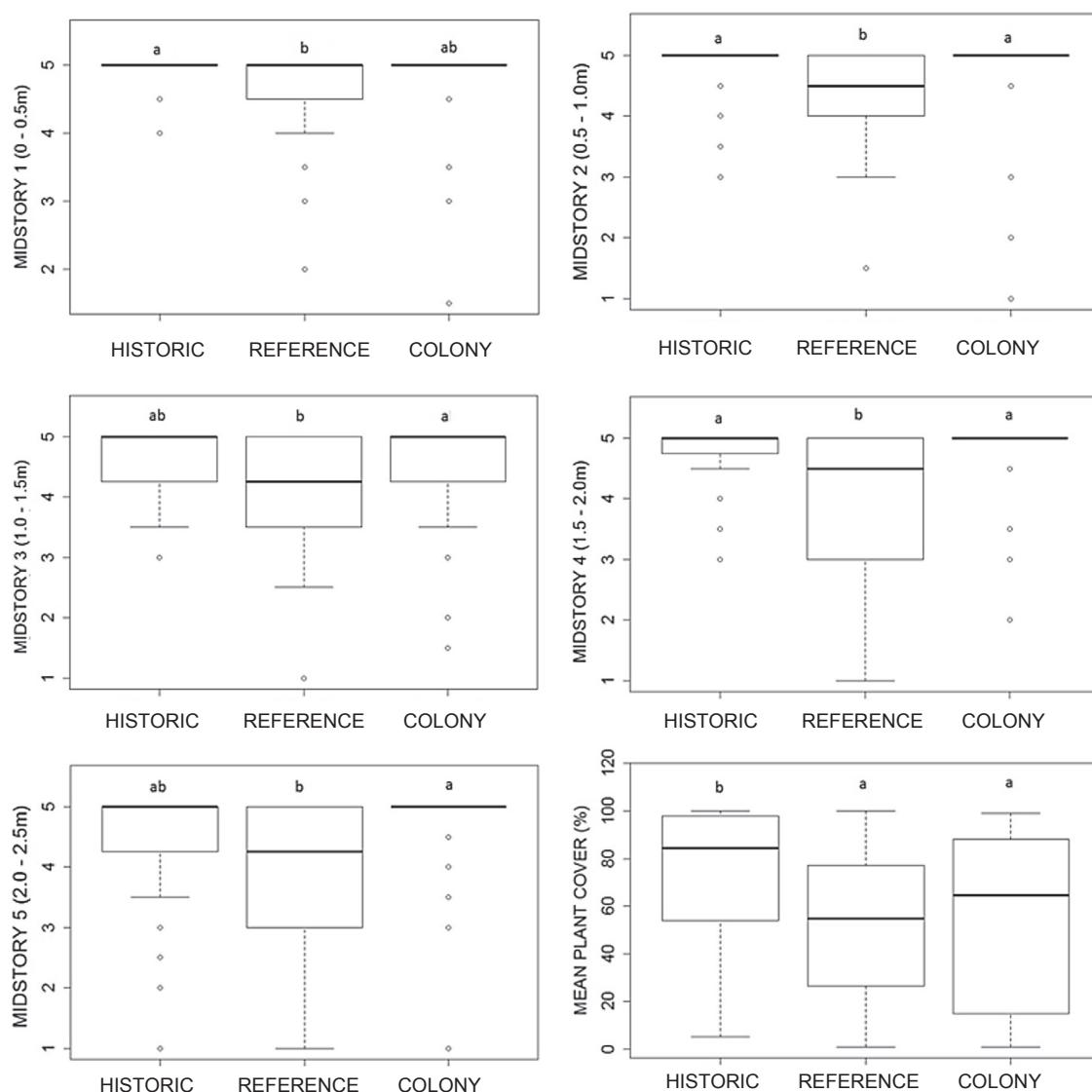
Fig. 1. Comparisons of midstory groups and vegetative cover by treatment types of active cormorant colonies (colony), islands with no history of nesting (reference) and abandoned colony islands (historic). Letters above each boxplot represent results of Dunn tests, with different letters signifying differences in ranked means.

islands being abandoned for 7–13 years minimum and maximum concentrations of P in soils on historic islands were also higher than on colony islands. This could be attributed to the observation that some historic islands, such as Connors Island, were occupied by cormorants for longer periods of time than current colonies that have been just recently occupied (< 5 years old), such as New Connors 2 and 3. Connors Island, once a breeding colony and now abandoned, is a popular roosting spot for cormorants who may deposit additional
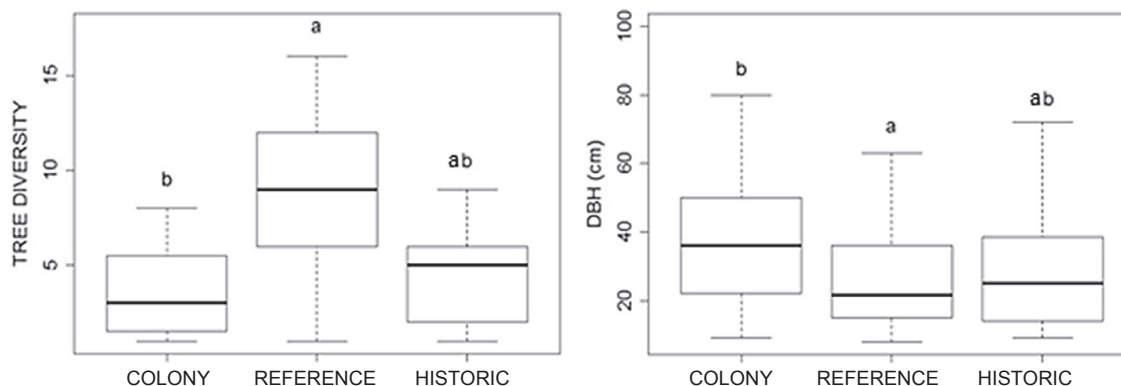

Fig. 2. Tree diversity and DBH (cm) measurements collected from active cormorant colonies (colony), islands with no history of nesting (reference) and abandoned colony islands (historic). Letters above each boxplot represent results of post-hoc tests, with different letters signifying a difference in means.
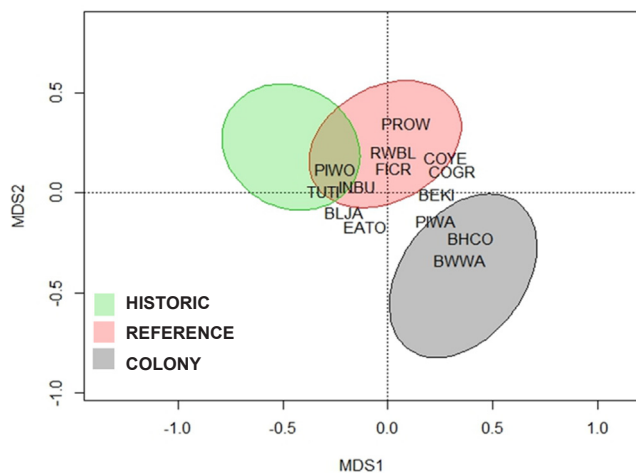
Fig. 3. Ordination plot of all avian species found on active cormorant colonies (colony), islands with no history of nesting (reference) and abandoned colony islands (historic) on Guntersville Reservoir. Colored ellipses represent the three island types. The four letter ALPHA codes in black are species that have the most influence on variables in the CCA and differentiate island types (ellipses) from each other.

concentrations of guano over time. Historic islands, though still showing lingering effects of occupancy, did show a trend of lower amounts of most soil nutrients. Lack of significance of lowered pH on colony islands could be attributed to some colony islands only being occupied for 5 years or less (New Connors islands) where effects on soil pH would not be as apparent. It is important to note that slight variations in acidity in the soil can affect vegetation (Kidd and Proctor, 2001). Maximum values of pH on colony and historic islands was 6 while on reference islands maximum values were close to 7. Biologically, this can make a difference in what could grow on more acidic soils versus more neutral soils as seen on reference islands.

Vegetation diversity showed a negative trend among islands types, with plant and tree diversity lower on colony and historic islands compared to reference islands. Results in this study are substantiated by previous studies that found similar numbers of plant and tree species on breeding grounds in the Great Lakes (Hebert et al., 2005; Boutin et al., 2011). Most notably, studies in the Great Lakes found that growth and

development of native species was suppressed while pioneer species and annuals proliferated under cormorant impacted conditions. This pattern of habitat degradation is seen on Guntersville Reservoir where the understory vegetation on colony islands lacked the diversity found on unoccupied islands. Pioneer species such as pokeweed, privet and various *Rubus* sp. were in high numbers on colony and historic islands compared to reference islands, where native species and species sensitive to disturbance had higher numbers, such as violets (*Viola* sp.), and dayflowers (*Commelina* sp.). Canopy cover was also affected, with greater percent overstory cover on reference islands than on colony and historic islands. This is apparent when looking at minimum values of overstory on islands, with reference islands having a minimum 67.6% overstory compared to 12.9% and 8.0% on colony and historic islands. Thick understories of early successional plant species and higher soil nutrient concentrations were also found on islands where cormorants had, and currently are, nesting.

Plant and midstory cover were also affected on islands in Guntersville Reservoir. Midstory cover (within 2.5 m of ground) was denser on historic and colony treatments than on reference islands (Fig. 1). Reference islands had less midstory cover on all levels, but especially between 0.5 and 1.0 m and 1.5–2.0 m. Additionally, reference islands had less plant cover on the forest floor. Mature trees and greater canopy cover limit understory growth and reduce plant cover on reference islands while a more open canopy resulted in a dense understory on colony and historic islands.

Tree diversity also differed significantly within cormorant colonies. Thirty three tree species were present on reference islands, compared with 27 species on colony, and 18 species in historic treatments. These differences among treatments may be due to differences inherent among islands as some islands have been occupied for longer periods, such as South Sauty (> 10 years). Tree species found on island types were also of note as they follow the same trend in successional characteristics as flora species. Pioneer species such as black locust, devil's walking stick and common persimmon are typically found in areas that have been disturbed (reference and historic islands) whereas species that proliferate in later successional habitats, such as oaks, sweetgum and American hornbeam, are found on reference islands. Past studies corroborate these findings, in that some unique plant communities that are susceptible to disturbance tend to do poorly after cormorant occupation (Boutin et al., 2011). Lastly, loblolly pine was found almost exclusively on colony and historic islands. Lafferty et al., (2016), found
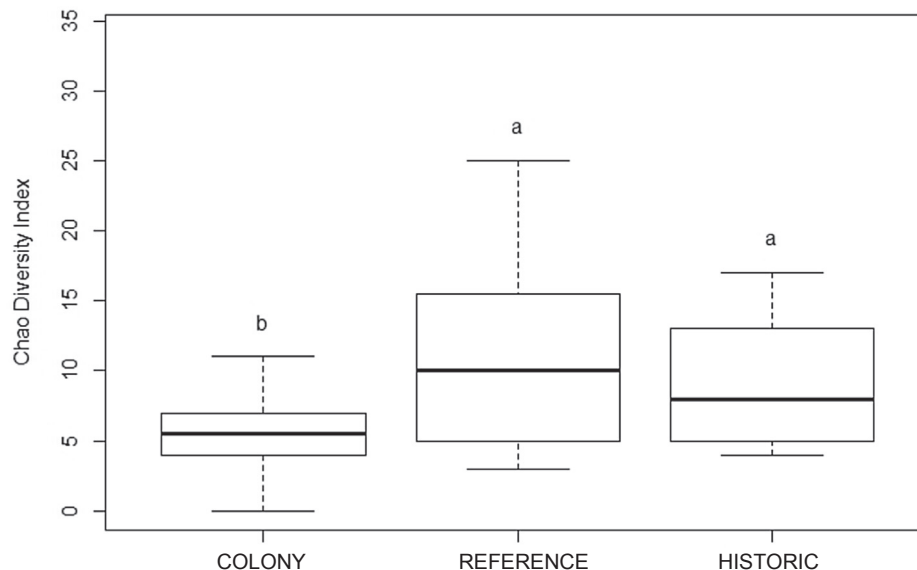

Fig. 4. Chao2 diversity indices from avian point count surveys recorded from active cormorant colonies (colony), islands with no history of nesting (reference) and abandoned colony islands (historic). Letters above the boxplot represent result of the post-hoc test, with different letters signifying a difference in means.

that nesting cormorants primarily nested on loblolly pine. No pine regeneration was found on historic islands and native hardwoods such as tulip poplars (*Liriodendron tulipifera*), maples (*Acer* spp.) and sugarberry (*Celtis laevigata*) were found to be proliferating.

Although tree diversity can be affected by cormorants, tree health was not seen to be adversely affected by cormorant occupation. Unlike Lafferty et al. (2016), we found no significance in vigor class by island type, though inclusion of abandoned colonies and a confounding variable of years occupied may have influenced this result. Occupancy did not alter results, though a histogram of vigor class and occupancy does show a pattern of healthier trees (vigor class 1 and 2) on reference islands and more dead or dying trees (Vigor class 3 and 5) on colony islands, increasing with years occupied. Because trees do not die immediately after occupancy, it makes sense that vigor class would not be affected on colony islands that have only been occupied ≤5 years. Also, historic islands had nearly equal distributions of healthy trees (vigor class 1) and dead trees (vigor class 5). Given cormorants abandoned these islands due to tree die-off (blown down by inclement weather or similar factors), a lack of nesting habitat would be prevalent on historic islands. Because cormorants have stopped nesting on historic islands, saplings and secondary successional habitat would be present, accounting for the influx of saplings and healthier trees. Vigor class 1 trees also had the smallest DBH (< 25 cm) compared to other vigor classes, while those in vigor class 5 dominate the upper DBH class (> 25 cm). Historic islands indicated effects of cormorant occupancy even after ~10 years of abandonment, though regeneration of native tree species is apparent. Analyses of DBH by treatment type supports these conclusions in that mean DBH on colony islands differ significantly from reference islands.

There is a clear distinction between colony islands and reference/historic islands for avian diversity. Many warbler species and those species that prefer shrubby understory, were found on colony islands, some of which were species of conservation concern. Loss of overstory tree canopy, decreased shading and increases in early successional ground cover and midstory vegetation may support some of these early successional species. These changes in vegetation structure are likely borne out through cormorant nesting activity including nutrient deposition (Boutin et al., 2011).

Overall, colony islands had a lower Chao2 diversity index than reference and historic islands (Fig. 4). Red-headed Woodpecker were more likely encountered in the historic islands, especially Connors, likely due to the presence of snags from cormorant abandonment seven years earlier. Prothonotary Warbler were also found more frequently on historic islands than the other two island types. Prothonotary Warblers favor wooded areas that are flat and shaded with standing dead trees, inhabited by woodpecker species and Carolina Chickadees (*Poecile carolinensis*), all seen on historic islands on Guntersville Reservoir (Petit, 1999). After cormorant abandonment, avian diversity and community structure seemed to increase and proliferate, suggesting that these islands could stabilize over time, although it may take more than a decade to occur. Further research would provide insight into how quickly these communities change and what subsequent avian community structure develops.

Our findings highlight that breeding cormorants have long-term impacts to soil, vegetation structure, tree density and health and bird diversity even after a decade or more of colony abandonment. Although similar impacts on soil, vegetation, tree density and tree health have been recorded for cormorants colonies in North America, Europe and Asia (Ishida, 1996; Breuning-Madsen et al., 2010; Kolb et al., 2010; Boutin et al., 2011), long-term impacts of nesting cormorants to insular habitats in warm temperate moist forest ecosystems have not been documented. Furthermore, this research links direct cormorant impacts on vegetation, which indirectly changes avian diversity and use on colony and abandoned islands.

6. Conclusion

Materials deposited by cormorants can significantly affect soil chemistry, structure of vegetation, and bird diversity in southeastern insular habitats. Early detection and action can be a useful tool to decrease effects of cormorants in these systems. If management action to curtail colony formation within these systems can be employed early in the colony formation process, then long-term effects of cormorants on nesting islands may be reduced.

More research is needed to fully understand the indirect effects of cormorant occupancy on bird communities, such as a decrease in avian diversity. This research should include yearly point count surveys and nest counts of birds breeding on islands used in this study. Additionally, focus can include small mammal and amphibian communities, and how they may be impacted by cormorant borne changes.

Future studies are needed to understand cormorant behavior in this system and others, including why cormorants may choose certain islands over others for nesting. Because cormorants on this reservoir are observed to abandon one island and move on to another, these impacts will likely increase throughout the reservoir, while abandoned colonies will sustain impacts for decades to come. This is a key difference in southeastern breeding colonies from northern breeding grounds in North America where cormorants will often ground nest after tree die-off and movement to additional islands is not as evident.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117588.

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