Forest Ecology and Management 369 (2016) 10–19

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Biotic and abiotic impacts of Double-crested cormorant breeding colonies on forested islands in the southeastern United States

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ARTICLE INFO

Article history:
Received 2 October 2015
Received in revised form 7 March 2016
Accepted 10 March 2016

Keywords:
Double-crested Cormorant
Forest health
Human–wildlife conflict
Soil chemistry
Waterbirds
Water quality

ABSTRACT

Double-crested Cormorant (*Phalacrocorax auritus*) numbers have increased in North America, and concomitantly cormorants appear to be expanding their nesting range in the southeastern United States. Because colonial nesting waterbirds can impact water quality, soil chemistry and subsequent vegetation succession patterns, our goal was to assess the extent to which cormorant breeding colonies are influencing the biotic and abiotic attributes of forested islands in the southeastern United States. Our objectives were to (1) compare water quality characteristics in near-shore surface waters around forested islands with and without nesting cormorants during the peak-nesting/fledgling period and post-fledgling period, (2) measure soil chemistry parameters for forested islands with and without nesting cormorants, and (3) compare tree health metrics on forested islands with and without nesting cormorants. Our results indicate that cormorant colonies are not significant contributors to general coliforms or *Escherichia coli* levels in waters surrounding southern breeding colonies. Cormorants also do not appear to have significant direct effects on water chemistry. We did find that cormorant colonies are affecting soil chemistry. Soil from within the nesting colony was more acidic and had greater concentrations of phosphorous than soils on reference islands. In addition, we found evidence that cormorants are negatively affecting tree health within nesting colonies as evidenced by a greater number of trees of lower vigor class within the nesting colonies compared to reference sites. While cormorants do cause abiotic and biotic changes, these are part of the natural ecological processes that occur following waterbird colonization. Management to reduce unwanted impacts that nesting cormorants are having on forested island habitats should be considered within a framework that allows for natural ecological processes, including changes in soil chemistry and subsequent vegetation succession.

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1. Introduction

In North America, the Double-crested Cormorant (*Phalacrocorax auritus*; hereafter cormorant) has substantially increased in abundance from relatively low numbers in the early 1970s (Dorr et al., 2012). Cormorants have historically wintered in the southeastern United States, but nesting cormorants in the region were relatively rare compared to their northern breeding regions and occurred primarily along the gulf coast and major rivers (Wires and Cuthbert, 2006; Hanson et al., 2010). More recently cormorants appear to have expanded their southeastern nesting range to include man-made sloughs, lakes, and reservoirs not historically available or reported (Reinhold et al., 1998; Wires and Cuthbert, 2006; Hanson et al., 2010; Dorr et al., 2014). The increased numbers of cormorants throughout their range, while a conservation success story, has also come with increased human–cormorant conflicts (Taylor and Dorr, 2003; Dorr et al., 2012). Conflicts associated with nesting cormorants differ from those associated with wintering cormorants. Issues with wintering cormorants typically are associated with direct predation on aquaculture or recreational fisheries (Taylor and Dorr, 2003), whereas cormorant breeding colonies may have broader impacts due to increased competition with co-nesting species, vegetation damage, and changes in soil and water quality associated with the release of nutrient-rich waste due to guano deposition, regurgitated food,

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http://dx.doi.org/10.1016/j.foreco.2016.03.026
0378-1127/Published by Elsevier B.V.

carcasses and feathers (Jarvie et al., 1999; Shieldcastle and Martin, 1999; Taylor and Dorr, 2003; Ayers et al., 2015; Stewart et al., 2015). Jarvie et al. (1999) found that Black-crowned Night Herons (*Nycticorax nycticorax*) nesting pairs declined with increasing cormorant nesting. Hebert et al. (2005) documented significant damage to trees on forested islands associated with cormorant nesting and that vegetation damage can negatively impact co-nesting avian species that are obligate tree nesters. Fish-eating avian species, such as cormorants, also can affect soil quality (Ishida, 1996; Ligeza and Smal, 2003; Breuning-Madsen et al., 2010; Ayers et al., 2015). Ishida (1996) found that changes in soil nutrients caused by nesting Great Cormorants (*Phalacrocorax carbo*) simplified forest structure and reduced tree species diversity. Breuning-Madsen et al. (2010) found that great cormorant colonies significantly impacted soil nutrient profiles that affected plant community composition by limiting plant diversity to salt-tolerant plants that can grow in extremely nutrient-rich soils.

In addition to the potential terrestrial ecological impacts of nesting cormorant colonies, waterfowl feces may be an important source of fecal contamination in water bodies (Standridge et al., 1979; Makino et al., 2000; Lu et al., 2008). High levels of coliform and *Escherichia coli* bacteria are a concern for many recreational water environments because of the known association between fecal matter and human health risks, and are commonly used as indicator species to measure the quality of recreational and drinking waters (USEPA, 1986, 1999; WHO, 2006). For example, McLellan (2004) found that waterbird feces was an important source of bacterial pollution in some beach areas and contributed to beach closures in efforts to limit potential human health risks. Although research has been conducted on impacts of cormorants on co-nesting species, vegetation, and soil and water quality on their northern breeding grounds (Bédard et al., 1995; Jarvie et al., 1999; Shieldcastle and Martin, 1999; Hebert et al., 2005; Ayers et al., 2015), no research has been conducted on the impact of cormorant breeding colonies in southeastern United States in this regard.

Within the last 10–15 years cormorants began nesting on islands in Guntersville Lake, AL, resulting in concerns regarding impacts to fisheries, vegetation, and soil and water quality (Barras, 2004). Impacts to several islands in Guntersville Lake have been observed including loss of vegetation and possibly increased shoreline erosion (Barras, 2004), presumably due to nesting cormorants. Given the diversity of soil and vegetation types, longer growing season, and generally more eutrophic water-bodies, the ecological impacts of cormorants at southern breeding colony sites may differ substantially from impacts documented at northern colonies. Thus, our goal for this study is to understand if and how cormorant breeding colonies influence biotic and abiotic attributes of forested islands in the southeastern United States. Our objectives were to (1) compare water quality characteristics in near-shore surface waters around forested islands with and without nesting cormorants during the peak-nesting/fledgling period and post-fledgling period, (2) measure soil chemistry parameters for forested islands with and without nesting cormorants, and (3) compare tree health metrics on forested islands with and without nesting cormorants.

2. Methods

2.1. Study site – Guntersville Lake, Alabama, USA

Guntersville Lake (34°32′19.82N, 86°07′05.14W) is the largest lake (27,964 ha) in Alabama, U.S.A. (Fig. 1) and spans 121 km from Nickajack Dam, Tennessee, to Guntersville Dam, Alabama. The reservoir is managed by the Tennessee Valley Authority (TVA) on the Tennessee River in northeastern Alabama and southeastern Tennessee. Cormorants currently nest at three primary locations in Guntersville Lake: Conner's Island (CON), South Sauty Island (SSS), and North Sauty Island (NS); hereafter, these islands will be referred to as colony islands. Reference islands that lacked nesting cormorant colonies were selected based on similar size and proximity (adjacency) to colony islands: southeast of Connor's Island (SEC), north of South Sauty (NSS), west of South Sauty (WSS). When more than one reference island was available, the reference island was selected at random.

2.2. Study design

2.2.1. Water sampling

Water samples for microbial and chemical analyses were collected at each of the colony islands and the reference islands during the period of peak nesting/fledging of chicks (mid-May) and during the post fledging period when cormorant numbers are at a minimum (mid-August), 2010. Island shorelines were mapped using digital orthoquad imagery ArcGIS ArcMap (ESRI® 9.1, Esri Inc., Redlands, CA, U.S.A.).

For microbial analysis, the largest islands shoreline was divided into 10 equal length sample sections. The beginning of each section represents a shoreline starting point for obtaining water samples. Shoreline sections of smaller islands were sampled in proportion to their length relative to the shoreline of the largest island. If section lengths were less than 100 m, a minimum of four sample points were selected, one in each cardinal direction. Water samples were collected at each shoreline section starting point at intervals of 5 m, 15 m and 25 m from the shoreline. Water samples were placed in sterile Whirl-Pak® bags and placed on ice until all water samples were collected. Samples were plated within 4 h of collection (Vail et al., 2003) on 3M PetrifilmTM *E. coli*/Coliform plates (PetrifilmTM) for enumerating general coliform and *E. coli* bacteria (colony forming units [CFU]). PetrifilmTM count plates are a simple, safe, reliable and low cost method for monitoring environmental water samples in the field (Vail et al., 2003). Prior to plating, water samples were allowed to increase to ambient temperature. Plates were inoculated with 1 mL of water using sterile, disposable pipets and allowed to incubate at 35 ± 1 °C for 24 ± 2 h prior to enumeration. Used plates were disinfected before disposal by soaking in 1% hypochlorite solution for 1-h.

Due to logistic constraints associated with the amount of time to run water chemistry tests on-site, samples were taken only at 5 m from shore and at 4 sample locations, one in each cardinal direction from each study island during both the peak nesting/fledgling period (mid-May) and post fledgling period (mid-August). Four water quality parameters were tested: pH, nitrate (NO_3 mg/L), ammonia (NH_3 mg/L), and phosphate (PO_4 mg/L). A digital meter was used to measure pH (±0.1 pH at 20 °C). A Hach multi-parameter surface water test kit was used to measure water chemistry parameters.

2.2.2. Soil sampling

Soil samples were collected from each of the colony islands and reference islands. To establish sampling plots, each of the six islands was overlain with a 10 m × 10 m (0.10 ha) grid using the most recent digital orthoquad imagery available for the area via ArcGIS ArcMap (ESRI® 9.1, Esri Inc., Redlands, CA, U.S.A.). Sampling of 0.10 ha plots was conducted in proportion to island area by randomly sampling 20% of the total available plots on each island. Soil core samples were collected with a soil auger (9 cm diameter × 20 cm deep) at the center of each plot, excluding surface debris. All soil samples were assigned a treatment level based on location relative to nesting colonies that ranged from 1 to 3 (1 = colony island within a nesting colony; 2 = colony island

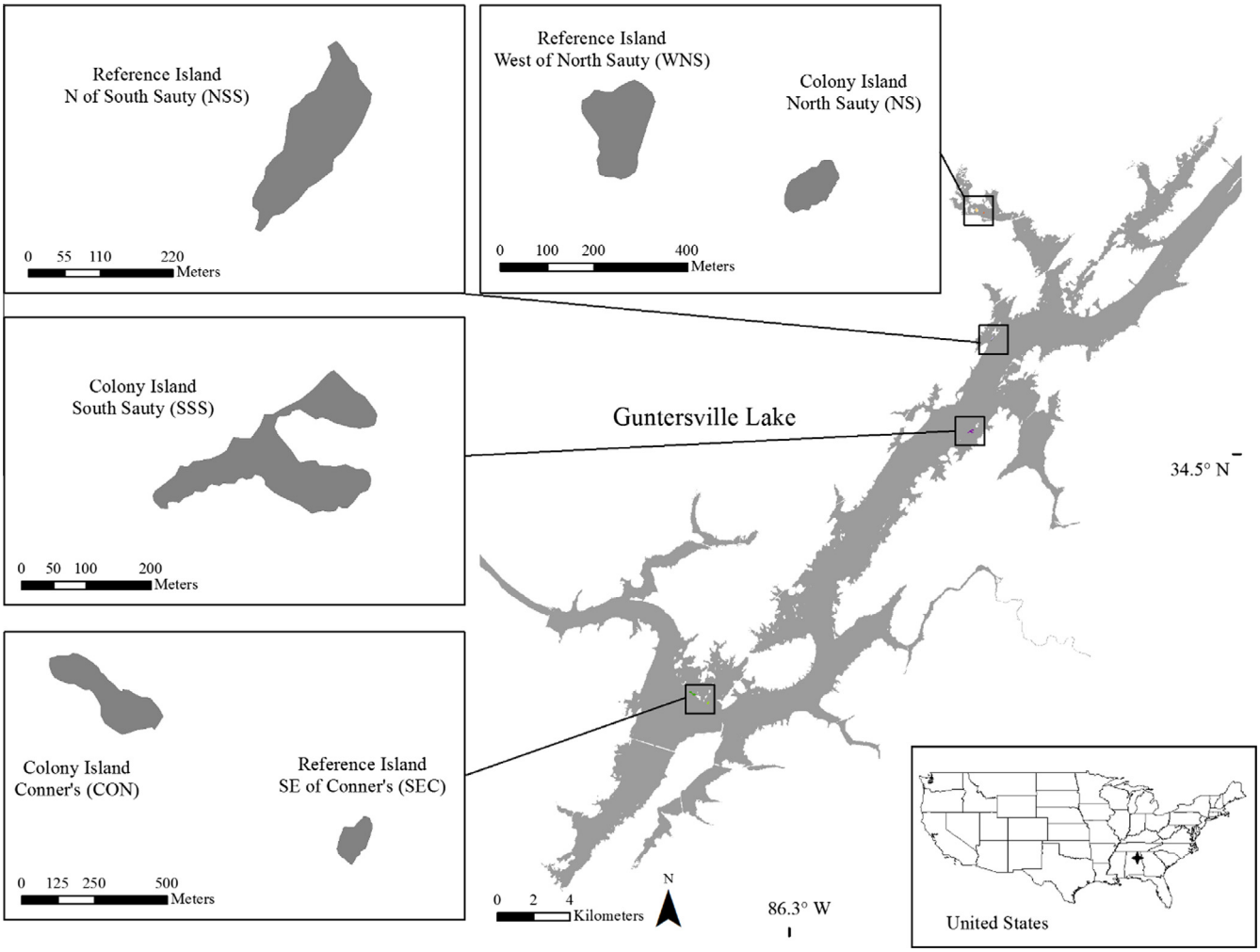

Fig. 1. Study island locations, names and abbreviations (in parentheses) and whether they are reference or colony islands, sampled from mid-May to mid-August, on Guntersville Lake, Alabama, USA. Inset map of the United States of America with a star representing the approximate location of the study area.

outside a nesting colony; 3 = reference island). Soil samples were labeled and placed in ice chests in doubled paper bags for transport to Mississippi State University Extension Service, Soils Testing Laboratory (Mississippi State, MS, U.S.A.) for analyses. Extractable nutrient concentrations (kg/ha), milli-equivalents/100 g, and base saturation were determined for percent organic material (%OM), nitrate (NO_3-N), phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn), sulfur (S), sodium (Na), and soil pH for each sample. Nutrients were selected based on importance in biogeochemical circulation and plant physiology (Ligeza and Smal, 2003; Ishida, 1996; Breuning-Madsen et al., 2010). Soil samples at all locations were collected during the peak cormorant nesting/fledging period (mid-May).

2.2.3. Tree surveys

Randomly selected 10 m diameter circular plots (e.g. 0.02 ha) were used to survey trees on colony and reference islands. During surveys, species composition, tree diameter at breast height (DBH) in cm, tree health status (e.g., vigor class described below), the number of cormorant nests and the number of nests of other co-nesting waterbird species were recorded. All surveyed trees were assigned a treatment level based on location that ranged from 1 to 3 (1 = colony island within a nesting colony; 2 = colony island outside a nesting colony; 3 = reference island).

Tree health status criteria were adapted from the forest inventory and analysis national core field guide (USFS, 2007). We added 2 categories for standing dead trees to provide a Likert Scale measure (5 categorical values) ranging from healthy to standing dead. Vigor classes are defined as follows: Vigor Class 1 – uncompacted live crown ratio of 35% or higher, <5% dieback, and >80% of the foliage is normal or >50% of each leaf is not damaged or missing. Twigs and branches that are dead because of normal shading are not included. Vigor Class 2 – saplings do not meet Class 1 or 3 criteria. May have uncompact live crown ratio, may or may not have dieback and may have between 21% and 100% of the foliage classified as normal. Vigor Class 3 – saplings may have uncompacted live crown ratio and have 1–20% normal foliage or the percent of foliage missing combined with the percent of leaves that are over 50% damaged or missing equal 80% or more of the live crown. Twigs and branches that are dead because of normal shading are not included. Vigor Class 4 – fresh standing dead tree, limbs almost all present and top pointed or not broken and 90–100% of bark remaining. Vigor Class 5 – old standing dead tree, some or almost all limbs broken and/or top broken, and 10–100% bark slippage (loss).

2.2.4. Cormorant nesting and co-nesting species surveys

Cormorant and co-nesting waterbird species surveys were conducted by an observer using binoculars from a boat that circled the island at <100 m. During this survey, the number of cormorants and co-nesting species nests observed in each tree were documented and the presence or absence of chicks in each nest were

recorded. When nests were observed, the tree species was identified and classified as alive or dead.

2.3. Statistical analyses

2.3.1. General approach

We conducted all statistical analyses in R 3.0.2 (R Development Core Team, 2014). Following Zuur et al. (2009), we began model building by discerning appropriate model distributions (e.g., Poisson). For example, if the data were overdispersed, we examined the application of negative binomial or zero-inflated Poisson models. We also assess the support for random effects and for the inclusion of spatial correlation structures and alternative variance structures when appropriate. We used likelihood ratio tests to test support for the most complex models and for sequentially more parsimonious models until dropping additional covariates did not improve model fits (Zuur et al., 2009). Model validation was conducted following Zuur et al. (2009, 2012). We examined model coefficients with 95% confidence intervals for interpretation of covariate effects if intervals excluded zero.

2.3.2. Water quality

To test for potential effects of nesting cormorants on general coliform and *E. coli* levels in near shore island waters, we used general linear mixed models from the package *nlme* (Pinheiro et al., 2014). We specified treatment (colony or reference island) as a categorical covariate and included distance from shoreline (5 m, 15 m, 25 m) and time (peak nesting/fledgling period [mid-May], post nesting/fledgling period [mid-August]) as fixed effects and we included a treatment × time interaction term when appropriate. In addition, we tested whether the random effect of colony-reference island pairs or the random effect of island alone was warranted. To test for the influence of nesting cormorants on surface water chemistry in near shore water, we used linear models and generalized linear mixed models in the package *lme4* (Bates et al., 2014). Again we specified treatment and time as fixed effects and tested whether inclusion of random effects for colony-reference island pairs or the random effect of island alone improved model fit.

2.3.3. Soil chemistry

We used general linear mixed models and linear models to test for potential effects of nesting cormorants on soil chemistry parameters (%OM, NO_3-N, P, K, Ca, Mg, Zn, S, Na, pH) on the log-scale. We specified treatment as a categorical fixed effects ranging from 1 to 3 (1 = colony island within a nesting colony; 2 = colony island outside a nesting colony, 3 = reference island) and tested whether the random effect of colony-reference island pairs or island alone was warranted, while accounting for spatial correlation and alternative variance structures as needed to improve model fit.

2.3.4. Tree health

To examine the potential effects of nesting cormorants on tree health, we used ordered logistic regression with tree vigor class as the response variable. We included treatment as a categorical fixed effect ranging from 1 to 3 (1 = colony island within a nesting colony; 2 = colony island outside a nesting colony, 3 = reference island). Tree species also was included as a fixed effect, whereas DBH was included as a continuous fixed effects. We also tested whether the random effects of colony-reference island pairs or island alone was warranted.

3. Results

3.1. Water quality

3.1.1. General coliform and E. coli levels

The likelihood ratio test from Poisson distributed models used to explain general coliform levels indicated support for inclusion of a random effect for treatment-reference island pairs ($L = 39.76$, $df = 6$, $P < 0.001$). Inclusion of a treatment × time interaction was not supported ($L = 1.27$, $df = 1$, $P = 0.26$), nor was the inclusion of treatment alone ($L = 3.55$, $df = 1$, $P = 0.06$). Dropping distance ($L = 16.24$, $df = 1$, $P < 0.001$) or time ($L = 791.95$, $df = 1$, $P < 0.001$) effects did not improve model fit. Overall, general coliform levels decreased only slightly with increasing distance from island shorelines ($\beta = -0.009$, SE = 0.002, $P < 0.001$, CI = −0.013 to −0.005) but increased substantially from mid-May to mid-August ($\beta = 1.23$, SE = 0.05, $P < 0.001$, CI = 1.14–1.33) (Fig. 2).

E. coli data were overdispersed, likely due to the number of zeros in the data (84% of the data were zeros), thus we used a zero-inflated Poisson model. The likelihood ratio test indicated lack of support for inclusion of the random effect for treatment-reference island pairs ($L = 3.16$, $df = 6$, $P = 0.08$) and for the random effect of island alone ($L = 2.75$, $df = 7$, $P = 0.10$). Inclusion of a treatment × time interaction was supported ($L = 6.02$, $df = 2$, $P < 0.001$), although treatment alone had no effect ($\beta = -1.17$, SE = 0.08, $P = 0.14$, CI = −2.75 to 0.40). Distance to shore also had no measurable effect on *E. coli* levels ($\beta = -0.04$, SE = 0.03, $P = 0.11$, CI = −0.10 to 0.01) but dropping the effect of distance ($L = 6.95$, $df = 2$, $P = 0.03$) did not improve model fit. Overall, *E. coli* levels decreased between mid-May and mid-August ($\beta = -3.76$, SE = 0.75, $P < 0.001$, CI = −5.23 to −2.29), although the treatment × time interaction indicated that *E. coli* levels decreased substantially between mid-May and mid-August at islands with nesting cormorants (treatment islands), whereas *E. coli* levels increased slightly between mid-May and mid-August at reference islands without nesting cormorants ($\beta = 4.22$, SE = 1.18, $P < 0.001$, CI = 1.83–6.61) (Fig. 2).

3.1.2. Water chemistry

The likelihood ratio tests from the linear models used to explain variation in surface water pH level 5 m from island shorelines indicated the random effects of treatment-reference island pairs ($L = 0.23$, $df = 6$, $P = 0.63$) and islands alone ($L = 0.30$ $df = 6$, $P = 0.59$) were unwarranted. Inclusion of a treatment × time interaction was supported ($L = 12.38$, $df = 1$, $P < 0.001$) but time alone had no measurable effect on pH levels ($\beta = -0.004$, SE = 0.24, $P = 0.98$, CI = −0.04 to 0.99). Treatment, however, did have an influence on pH levels with higher pH measured in nearshore waters around reference islands ($\beta = 0.78$, SE = 0.22, $P < 0.001$, CI = 0.36–1.21) compared to treatment islands, with treatment × time interaction resulting in lower pH levels in mid-August in nearshore waters around reference islands compared to treatment islands ($\beta = -1.15$, SE = 0.32, $P < 0.001$, CI = −1.77 to −0.52) (Fig. 2).

The likelihood ratio tests from the linear mixed models used to explain variation in ammonia (NH_3) levels in surface water 5 m from island shorelines indicated that the random effect of treatment-reference island pairs ($L = 0.08$, $df = 5$, $P = 0.78$) was unwarranted, however, the random effect of islands alone ($L = 5.54$ $df = 6$, $P = 0.02$) improved model fit. We found no evidence of a treatment × time interaction ($L = 2.12$ $df = 1$, $P = 0.16$) and dropping treatment improved model fit ($L = 27.34$ $df = 1$, $P = 0.98$). Inclusion of time was merited ($L = 29.11$ $df = 1$, $P < 0.001$) and overall, ammonia levels decreased between mid-May and mid-August ($\beta = -0.08$ [mg/L], SE = 0.01, $P < 0.001$, CI = −0.10 to −0.05 [mg/L]) (Fig. 2).

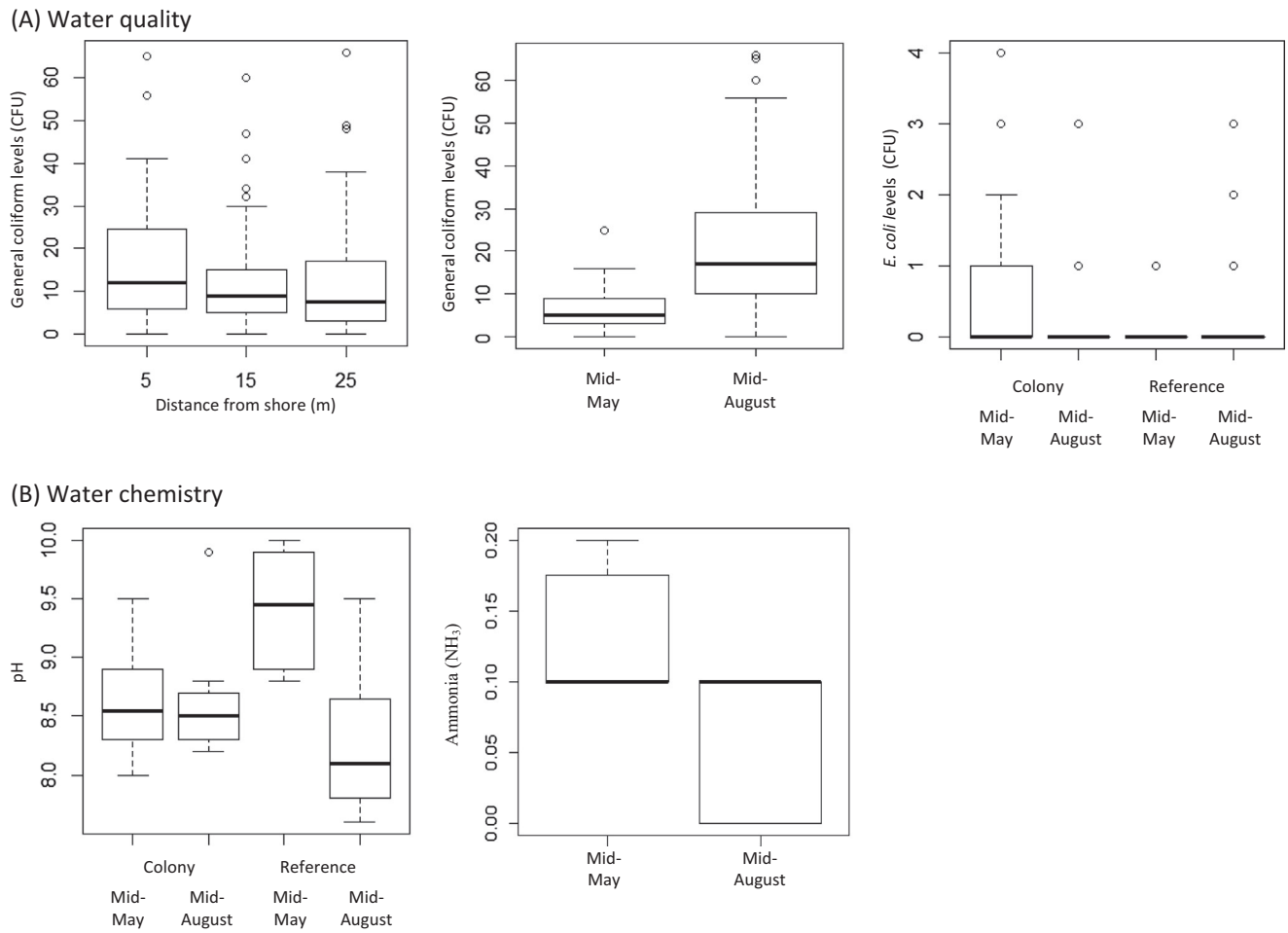

Fig. 2. Panel A, median general coliform levels (CFU) relative to distance from shore (m) and compared between mid-May and mid-August, and median *E. coli* levels (CFU) compared between colony islands (nesting cormorants present) and reference islands (nesting cormorants absent) from mid-May to mid-August. Panel B, median pH levels compared between colony islands and references islands from mid-May to mid-August and differences in ammonia (NH_3) from mid-May to mid-August. For both Panel A and B, only significant results are displayed.

We fit linear mixed models on the log-scale to assess variation in phosphate (PO_4) levels in surface water 5 m from island shorelines. The likelihood ratio tests indicated there was no support for inclusion of the random effect of treatment-reference island pairs ($L = 1.05$, $df = 6$, $P = 0.99$) or little support for islands alone ($L = 3.16$, $df = 6$, $P = 0.06$). Inclusion of a treatment × time interaction also was not supported ($L = 0.66$, $df = 1$, $P = 0.42$) and dropping treatment ($L = 0.64$, $df = 1$, $P = 0.42$) and time ($L = 1.75$, $df = 1$, $P = 0.18$) improved model fit. As such, the null model was the best supported model.

Because only two of the 48 water samples yielded non-zero nitrate (NO_3-N) values, we were unable to assess the effects of treatment and time on nitrate levels (mg/L) in nearshore waters around islands with and without nesting cormorants. Thus, nesting cormorants have no measurable effect on nitrate levels in surface waters near islands that host cormorant nesting colonies.

3.2. Soil chemistry

All data were log-transformed to improve normality of the residuals except pH. With the exception of Na ($L = 3.31$ $df = 5$, $P = 0.06$) and NO_3-N ($L = 2.00$, $df = 5$, $P = 0.16$), likelihood ratio tests indicated that the inclusion of the random effect of island was supported for all other analyses to evaluate the influence of cormorant nesting colonies on soil chemistry parameters. Likelihood ratio tests also indicated the effect of treatment (1 = colony island within a nesting colony; 2 = colony island outside a nesting colony, 3 = reference island) was significant for P ($L = 5.39$, $df = 2$, $P = 0.06$), K ($L = 31.26$, $df = 2$, $P < 0.001$), Mg ($L = 7.52$, $df = 2$, $P = 0.02$) and pH ($L = 5.89$, $df = 2$, $P = 0.05$). Post hoc tests revealed significant differences in P ($P = 0.05$), K ($P = 0.03$) and pH ($P = 0.05$) between soil samples taken from colony islands within a nesting colony (treatment 1) and on reference islands (treatment 3) (Fig. 3). Mg levels were not different within nesting colonies (treatment 1) and on reference islands (treatment 3) although Mg levels were higher on colony islands outside the nesting colony (treatment 2) compared to the other treatments ($P = 0.02$) (Fig. 3).

3.3. Tree health

Although we documented differences in the number of tree species identified during tree surveys across the six study islands (Table 1), tree species was not an important factor in regards to tree vigor class. However, variation in tree vigor class was influenced by a combination of DBH and treatment (1 = colony island within a nesting colony; 2 = colony island outside a nesting colony, 3 = reference island) (Fig. 4a). For a unit increase in DBH the odds of a tree being categorized as vigor class 1 versus vigor class 2, 3, 4 or 5 was multiplied by 0.98 (CI = 0.97–1.00) (Fig. 4). In addition, the odds of a tree being classified as vigor class 1 versus vigor class

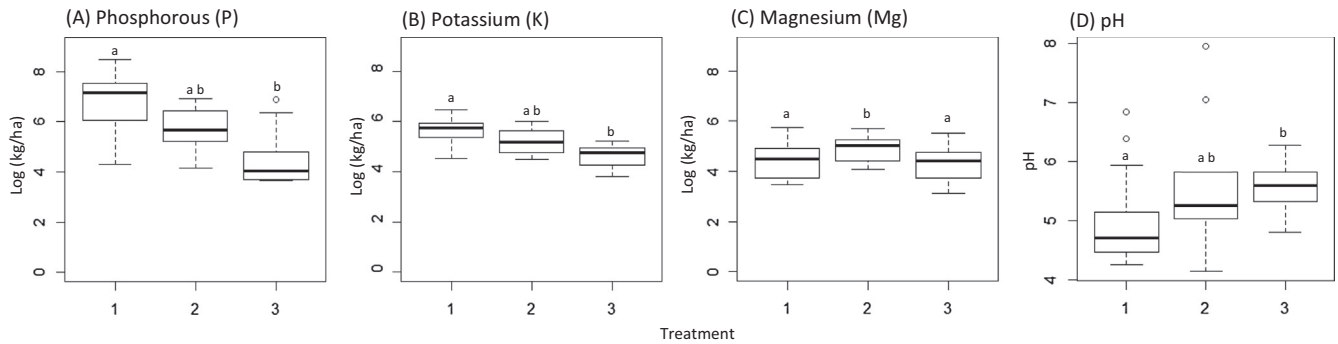

Fig. 3. Median differences in soil chemistry values among treatments: (A) phosphorous, (B) potassium, (C) magnesium and (D) pH. Differences between treatments are represented by different letters above the quantile values. Treatment is based on location relative to cormorant nesting colonies ranging from 1 to 3: 1 = colony island within a nesting colony, 2 = colony island outside a nesting colony and 3 = reference island. Only significant results are displayed.

Table 1
Summary of tree species documented at random tree survey plots on three islands with nesting cormorants (CON, SSS, NS) and reference islands (SEC, WNS, NSS) that lack nesting cormorant on Guntersville Lake, AL, U.S.A., represented by the percentage of the total number of trees recorded in all survey plots per island, rounded to the nearest whole number.

Common name	Scientific name	Colony islands			Reference islands		
		CON	SSS	NS	SEC	WNS	NSS
American Elm	*Ulmus americana*		4	1		5	1
Bald Cypress	*Taxodium distichum*		4				
Black Cherry	*Prunus serotina*	8				1	9
Black Locust	*Robinia pseudoacacia*	1	1		3		6
Box Elder	*Acer negundo*		3				
Carolina Buckthorn	*Frangula caroliniana*	4					
Chinese Privet	*Ligustrum sinense*		4				
Devil's Walking Stick	*Aralia spinosa*	1					
Eastern Red Cedar	*Juniperus virginiana*			1			33
Flowering Dogwood	*Cornus florida*	2		4		1	5
Hackberry	*Celtis occidentalis*	2	6		40		8
Ironwood	*Ostrya virginiana*		1			3	
Loblolly Pine	*Pinus taeda*	60	29		48		8
Maple spp.	*Acer* spp.	1		3		1	
Oak spp.	*Quercus* spp.	1				1	
Persimmon	*Diospyros virginiana*			3	5	12	4
Pine spp.	*Pinus* spp.	1					
Red Maple	*Acer rubrum*	3	4	19		20	8
Sassafras	*Sassafras albidum*				3		
Shortleaf Pine	*Pinus echinata*						1
Silver Maple	*Acer saccharinum*	1	22	47		23	1
Southern Red Oak	*Quercus falcata*	1				1	1
Swamp Chestnut Oak	*Quercus michauxii*						1
Sweetgum	*Liquidambar styraciflua*	2	4			25	4
Sycamore	*Plantus occidentalis*		1				3
Water Oak	*Quercus nigra*	1		6	3	1	4
White Oak	*Quercus alba*			3			
Willow Oak	*Quercus phellos*			6			
Yellow Poplar	*Liriodendron tulipifera*	7	2	6		2	6
Unknown genus		5	10	1			9

2, 3, 4 or 5 was 0.51 times greater (CI = 0.28–0.93) in treatment 2 compared to treatment 1, whereas the odds of a tree being classified in vigor class 1 versus vigor class 2, 3, 4 or 5 was 0.30 times greater (CI = 0.09–1.00) in treatment 3 versus treatment 1. We also found a more even distribution of tree vigor classes inside cormorant nesting colonies than outside nesting colonies or on reference islands (Fig. 4b). Tukey post hoc tests confirmed significant differences in tree vigor class between all pairwise treatment combinations (2–1: $P < 0.001$; 3–1: $P < 0.001$; 3–2: $P = 0.021$) (Fig. 4b), with the greatest difference observed between treatments 1 and 2.

3.4. Cormorant and co-nesting species

During nesting surveys, we documented 308 cormorant nests and 92 Great Blue Heron (*Ardea herodias*) nests on colony islands as well as 16 Great Blue Heron nests on one reference island (Table 2). Cormorant chicks were present in 100% of cormorants nests documented during nesting surveys and >90% of Great Blue Heron nests contained chicks (Table 2). Of the cormorant nests documented during nesting surveys, 90% occurred in Loblolly Pine (*Pinus taeda*), while only 6% occurred in Yellow Poplar (*Liriodendron tulipifera*), 3% in Bald Cypress (*Taxodium distichum*) and 1% in Sycamore (*Plantus occidentalis*). The status (i.e., live/dead) of cormorant nesting trees varied across islands with approximately 50% of cormorant nesting trees were identified as dead (Table 3). Although not included in nest surveys, during tree surveys, additional cormorant nests were observed in Sweetgum (*Liquidambar styraciflua*; $n = 6$) and Silver Maple (*Acer saccharinum*; $n = 1$) on each island (Section 2.2.3 above). Of the Great Blue Heron nests documented during nesting surveys, 67% occurred in Loblolly Pine, 32% in

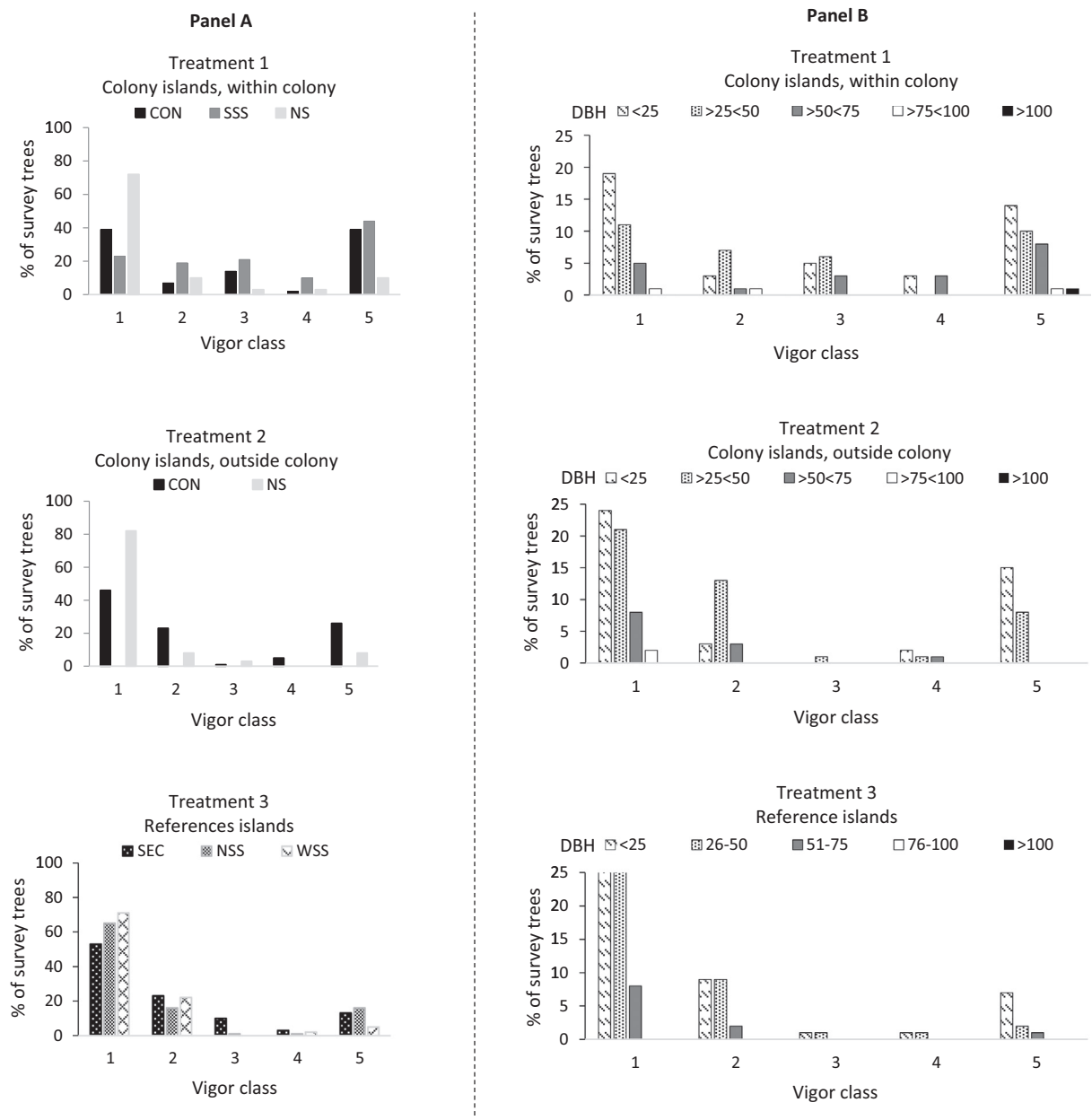

Fig. 4. Panel A: Tree vigor classes across colony an reference islands relative to treatment; represented as the percentage of total trees surveyed in each treatment by island. Panel B: Tree vigor classes across five categories of tree diameter at breast height (DBH) in centimeters (<25 cm, >25 < 50 cm, >50 < 75 cm, >75 < 100 cm, >100 cm) in each treatment; represented as the percentage of total trees surveyed of each size class by treatment. Tree vigor classes range from 1 = healthy to 5 = standing dead (see methods for full description). Treatment is based on location relative to cormorant nesting colonies ranging from 1 to 3: 1 = colony island within a nesting colony, 2 = colony island outside a nesting colony and 3 = reference island.

Table 2
Study islands on Guntersville Lake, Alabama, U.S.A.

Colony island	Island size (ha)	Cormorant Nests (% with chicks)	Other nests (% with chicks)	Reference island	Island size (ha)	Cormorants nests (% with chicks)	Other nests[a] (% with chicks)
CON	4.69	101 (100)	26 (100)	SEC	1.36	0 (0)	16 (100)
SSS	2.80	272 (100)	22 (91)	NSS	2.21	0 (0)	0 (0)
NS	0.76	7 (100)	28 (96)	WNS	2.20	0 (0)	0 (0)

[a] Co-nesting species were exclusively Great Blue Heron (*Ardea herodias*) with the exception of a single Osprey (*Pandion haliaetus*) nest on South Sauty Island with no chick (s) observed.

Yellow Poplar, and <1% in Sycamore, with approximately 50% of Great Blue Heron nesting trees identified as dead (Table 3). Again, although not included in nest surveys, additional Great Blue Heron nests were observed in Sweetgum ($n = 1$), Silver Maple ($n = 1$), Persimmon (*Diospyros virginiana*; $n = 1$) and Willow Oak (*Quercus phellos*; $n = 1$) during tree surveys (Section 2.2.3 above).

Table 3
Percentage of Double-crested Cormorant and Great Blue Heron nesting trees identified as alive or dead during nesting surveys conducted on Guntersville Lake, Alabama, U.S.A.

Island	Cormorant nesting trees			Great Blue Heron nesting trees		
	N	% alive	% dead	*N*	% alive	% dead
CON (colony)	34	69	31	20	50	50
SSS (colony)	49	100	0	18	92	8
NS (colony)	4	35	65	12	0	100
SEC (reference)	0	N/A	N/A	9	100	0

4. Discussion

We found significant differences in general coliform and *E. coli* levels, with general coliform levels increasing substantially from mid-May to mid-August and to a lesser degree with proximity to island shorelines regardless of presence of cormorant colonies. *E. coli* levels had the opposite trend compared to general coliforms, decreasing between mid-May and mid-August with a greater declines occurring on islands with nesting cormorants compared to reference islands. Our results also indicated few differences in water chemistry between islands with and without cormorant colonies. Treatment, however, did have an influence on pH levels with higher pH measured in near shore waters around reference islands compared to treatment islands, and lower pH levels in mid-August in near shore waters around reference islands compared to treatment islands. We also found significant differences in pH, P and K between soil samples taken from colony islands within a nesting colony and on reference islands. Differences in Mg were only significant between samples taken from colony islands within a nesting colony and colony islands outside a nesting colony (Fig. 3).

Loblolly pine and maple spp. were the most common tree types on most islands (Table 1) although the majority of cormorants (90%) nested in loblolly pine, suggesting a preference for this species. Similar to soil chemistry data we found tree vigor class was influenced by the presence of cormorant colonies and interestingly tree DBH. For each unit increase in DBH, the odds of a tree being categorized as vigor class 1 versus a higher vigor class increased by a factor of 0.98, which suggests that cormorants are selecting larger trees. In addition, the odds of a tree being classified as vigor class 1 versus higher vigor classes was 0.51 times greater outside of a colony versus within a colony and 0.30 times greater to have a vigor class 1 on reference islands versus colony islands, which suggests that cormorants are affecting tree health as indexed by vigor class regardless of differences among tree species.

Despite some spatial and temporal difference in water parameters, the patterns we observed suggested that water quality and chemistry of near shore waters surrounding cormorant colonies may have been influenced to a greater degree by factors other than the presence of cormorant colonies. For example, if cormorants were a significant contributor to *E. coli* levels in near shore waters, we expected to see an increase in *E. coli* levels from mid-May to mid-August, yet we observed a slight decrease in *E. coli* over this timeframe. However, observed decrease in *E. coli* levels from mid-May to mid-August may simply reflect a reduction in *E. coli* levels following a rapid decrease in cormorant numbers during the post fledging period. As expected, general coliform levels increased from mid-May to mid-August in near shore waters, although this may have been a consequence of increasing water temperature from mid-May to mid-August. We also found no measurable differences in nitrate levels in surface waters around colony and reference islands. Further, despite slightly lower pH levels in surface waters surrounding colony islands relative to references islands, pH levels were still alkaline, thus showing no evidence of water acidification. Although cormorant colonies may be a source of bacterial and chemical pollution on islands and in near shore waters (Stewart et al., 2015), cumulatively our data suggest nesting cormorants had little effect on water quality and chemistry in Guntersville Lake.

Our results provide an interesting contrast to other studies that have found that waterbirds such as gulls (*Larus* sp.), Canada Geese (*Branta canadensis*) and Great Cormorants occurring at high densities can be drivers of changes in water quality. For instance, several studies have demonstrated that waterbirds can be a significant source of bacterial contamination in inland water bodies (Hussong et al., 1979; Benton et al., 1983; Lévesque et al., 2000; Kirschner et al., 2004; Meerburg et al., 2011; Klimaszyk and Rzymski, 2013). Additionally, guano inputs to surface waters can accelerate the process of eutrophication (Niewolak, 1999; Nakamura et al., 2010; Klimaszyk and Rzymski, 2013) and lead to hyper-eutrophic and polluted systems (Stewart et al., 2015). However, factors including the density and diversity of waterbirds, their diet and feeding habits as well as the size of the waterbody all influence the level of bacterial contamination in the water (Hussong et al., 1979). For instance, the highest density of cormorant nests recorded on any of our study islands (South Sauty Island [SSS]) was 97.1 cormorants/ha^2, whereas cormorant nest densities during the same sampling year (i.e., 2010) in the Great Lakes region on some islands was substantially higher (e.g., >500 cormorants/ha^2), although islands in the Great Lakes also host large populations of other waterbird species (Ayers et al., 2015; Stewart et al., 2015). In addition, the movement of water, variable nutrient inputs and the suspension of inorganic and organic matter in the water column also may influence the density of general coliforms and *E. coli* in near shore waters thereby affecting water quality (Gwiazda et al., 2014). Thus, although we did not find evidence that cormorants were having a direct effect on water quality or chemistry, cormorants may have indirect effects due to interactions among nutrient flow, aquatic plant growth and slight differences in pH associated with cormorant colonies.

Further, we found that soils within cormorant nesting colonies had lower pH and higher accumulations of P and K compared to soils on references islands. In addition, soils on islands with cormorant colonies but outside the spatial extent of the colonies exhibited intermediate pH levels and intermediate concentrations of P and K, thus showing a stepwise pattern of pH levels and P and K concentrations across the three natural treatments (Fig. 3). Several studies have reported significant changes in soil chemistry associated with colonial nesting birds (e.g., Mun, 1997; Ligeza and Smal, 2003; Hobara et al., 2005; Ayers et al., 2015; Borkowska et al., 2015). Specifically, soils tend to be more acidic within nesting colonies compared to reference sites, suggesting that deposition of avian guano results in soil acidification (Ishida, 1996; Cuthbert et al., 2002; Breuning-Madsen et al., 2010; Ayers et al., 2015). Soil acidification can result in some nutrients (e.g., Al) becoming noxious and potentially toxic to plants depending on the nutrients' reactivity at low pH, whereas other nutrients (e.g., Ca, K, Mg) may be depleted or become unavailable for uptake by plants in acidic soils (Ashman and Puri, 2013). Further, high concentrations of P can be toxic and limit plant uptake of some macronutrients (e.g., iron, zinc), thereby effecting plant growth (Pitt and Provin, 2008), whereas high concentrations of K are neither noxious nor toxic but may influence osmotic pressure caused by the number of K ions in the soil thereby affecting synergistic action with other soil nutrients (Ligeza and Smal, 2003). In addition, avian guano, regurgitation, carcasses and feather deposits and subsequent changes in soil chemistry also can lead to loss of native vegetation, diminished plant diversity and facilitation of nutrient-tolerant exotic species (Ishida, 1997; Mun, 1997; Rippey, 2002; Weseloh et al., 2002; Ayers et al., 2015). However,

the negative effects of cormorants and other avian species on biotic and abiotic environments are conditioned by the number of waterbirds contributing to the system, which, compared to northern ecosystem, cormorant inputs in Guntersville Lake is relatively limited.

Although the general pattern of differences in soil chemistry parameters across the three treatments in our study area were similar to what has been documented in northern ecosystems, our results were less dramatic likely because our study system has substantially fewer nesting cormorants. In northern ecosystems the impacts of cormorants and other colonial nesting birds on soil chemistry includes significant differences in additional nutrients (e.g., NO_3-N, Zn) that extends well-beyond the spatial extent of the nesting colony, thereby impacting adjacent soils and vegetation (e.g., Ayers et al., 2015). Greater spatial extent of the impact of colonial nesting birds on soils in northern ecosystems may be a due to multiple factors. For example, in northern ecosystems the additive effects of high numbers of co-nesting species (e.g., gulls [*Larus* spp.], American White Pelicans [*Pelecanus erythrorhynchos*]) that only nest on the ground may result in more direct guano inputs to the soil (Ayers et al., 2015), whereas in our southeastern study area, we observed high numbers of cormorants but relatively few co-nesting species and no ground nesting species. Moreover, the density of nesting cormorants in northern systems is substantially greater that what we observed in our study system (see Ayers et al., 2015; Stewart et al., 2015).

Northern and southeastern ecosystems also have different precipitation regimes, microsite characteristics, soil properties (e.g., texture, substrate [sand, clay loam]), different plant assemblages and subsequent differences in nutrient uptake by different plant species, all of which could affect soil chemistry. Further, differences in spatio-temporal patterns of cormorant colonization, subsequent population increases as well as differences in nest densities may account for some of the observed differences in the magnitude of soil chemistry parameters among samples within colonies, adjacent to colonies and on reference islands in northern and southeastern ecosystems.

Our result also indicated that tree vigor class was negatively affected by nesting cormorant colonies, although impacts were mainly to loblolly pine due to an apparent preference of this tree species by cormorants. The greatest impacts were found within the spatial extent of the nesting colonies relative to trees on reference islands, which is a similar stepwise pattern to what we observe in the soil data across the three treatments. Previous studies have reported substantial tree damage and tree cover loss on islands with nesting cormorant colonies (Bédard, 1988; Chapdelaine and Bédard, 1995; Rippey, 2002; Boutin et al., 2011). Cormorants can cause physical damage to trees by removing foliage for nesting material and by breaking branches (Lemmon et al., 1994; Aderman and Hill, 1995; Hobara et al., 2001; Hebert et al., 2005). In addition, as trees die, branches become less stable for nesting and cormorants often abandon unstable trees in favor of nearby sturdier trees with remaining foliage (Rippey, 2002; Hebert et al., 2005). As such, it is not surprising that tree damage caused by cormorants often expands across islands habitats as dead and dying trees are abandoned and new trees are selected as nesting sites (Hebert et al., 2005). Interestingly, we also found that trees with smaller DBH appeared to be more affected by nesting cormorants. This result may be a consequence of multiple interacting factors. For instance, large increases in tree debris (i.e., litterfall) resultant from cormorant damage has been reported (Hobara et al., 2001) and this debris may negatively affect smaller trees via physical damage as well as changing microsite conditions. Also, elevated ammonium levels in the soil under cormorant colonies due to guano can result in toxicity to many plants, particularly in areas where soil pH is low (Britto and Kronzucker, 2002). Thus, cormorant guano may have a more immediate impact on understory vegetation that includes smaller trees within the colony compared to larger, well-established trees. However, the impacts of nesting cormorants on large healthy trees in our study area was apparent, although the effects may be more evident in subsequent years as trees die and are subsequently abandoned by nesting cormorants in favor of healthier trees with remaining foliage (Rippey, 2002; Hebert et al., 2005).

5. Management and research implications

Our study indicates that cormorants are having an effect on forested island habitats in Guntersville Lake, AL, USA, particularly changes in soil characteristics and damage to tree health. Due to a possible preference for loblolly pine for nesting, if restoration of island trees is a management goal, use of non-pine species may reduce attractiveness of these islands to cormorants. Overall, the biotic and abiotic impacts of cormorants nesting in this watershed appears to be less dramatic than findings in northern ecosystems. For example, we found little evidence that cormorants are impacting water quality and chemistry at current cormorant nesting densities. However, large numbers of waterfowl do not always affect water quality (Brierley et al., 1975). As such, it is likely that the impacts of nesting cormorants on water quality/chemistry and forest structure and composition may be uncoupled. Despite quantifiable impacts, colonization and subsequent succession of forested islands following waterbird colonization is a natural process (Wires and Cuthbert, 2006). Stewart et al. (2015) used paleoecological techniques to evaluate spatial and temporal patterns of colonial nesting waterbirds use of islands over relatively long time scales (100–150 years) in the Great Lakes region, providing greater historical ecological context for current patterns of cormorant and other waterbird use of island habitats. Thus, any consideration of management action to reduce unwanted abiotic and biotic impacts that nesting cormorants are having on forested island habitats for socio-economic reasons should be considered within a framework that allows for natural ecological processes, including vegetation succession following cormorant colonization.

Author contributions

BD and KCHD conceived of the idea; BD, KCHD and AMP conducted fieldwork; DJRL conducted statistical analyses; DJRL, wrote the manuscript; BD, KCHD, AMP reviewed the manuscript and provided editorial advice.

Acknowledgements

This research was funded by the United States Department of Agriculture, Wildlife Services, National Wildlife Research Center. We thank Robert Ritchey and Jerry Feist of Unites States Department of Agriculture, Wildlife Services and Paul Fioranelli with the National Wildlife Research Center for logistical and field support. We thank Keith Crouse of Mississippi State University Extension Service Soil Testing Laboratory for conducting soil nutrient analyses and Tara Conkling for advice regarding statistical analysis.

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