Environmental Management (2012) 50:304–314
DOI 10.1007/s00267-012-9878-6

Double-Crested Cormorant (*Phalacrocorax auritus*) Nesting Effects on Understory Composition and Diversity on Island Ecosystems in Lake Erie

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Received: 22 May 2011 / Accepted: 10 May 2012 / Published online: 30 May 2012

Abstract The context for this study is the management concerns over the severity and extent of the impact of cormorants on island flora in the recent past on Lake Erie islands. Accordingly, this study sought to quantify the nesting colonies' influence on coarse woody litter and how nest densities and litter depth may influence the herbaceous layer, the seed bank composition and viability across the extent of three Lake Erie islands. The data for this study were collected from 2004 to 2008 on East Sister Island and Middle Island using two main strategies. First, herbaceous layer surveys, cormorant nest counts, soil seed bank cores, and litter depth measurements were executed using a plotless-point quarter method to test island-wide impacts from nesting activities (data were also collected on a third island, West Sister Island as a reference for the other two islands). Secondly, a sub-sample of the entire plot set was examined in particularly high nesting density areas for two islands (Middle Island and East Sister Island). Kruskal–Wallis tests indicated that there are subtle changes in the herbaceous diversity (total, native and exotic) and seed bank composition across the islands. The sub sample set of the plots demonstrated that *Phalacrocorax auritus* nest density does influence litter depth, herbaceous species abundance and diversity. Cormorant nesting pressures are restricted to areas of high nesting pressures and competition. However, there remains a risk to the interior herbaceous layer of the island if the effects of nesting pressures at the edges advance inward from this perimeter.

Keywords *Phalacrocorax auritus* · Seed bank · Litter depth · Edge effects · Invasive species · Herbaceous understory

Introduction

Observable changes in island and coastal ecosystems have prompted inquiries into the influences that breeding populations of *Phalacrocorax auritus* Less. [Pelecaniformes: Phalacrocoracidae] hereafter the double-crested cormorant or *P. auritus*, may have on ecological dynamics including changes in canopy structure (Duffe 2006) and changes in nutrient dynamics (Hebert and others 2005; Rush and others 2011). The mandate for protected areas requires land managers like Parks Canada and Ontario Parks to conserve the ecological integrity of lands within their jurisdiction. The situation for ecosystem managers is complicated in the Great Lakes Region. For instance, on the islands in the western basin of Lake Erie the dominant ecosystem is late successional 'Carolinian' forests (and the historical ecosystem will be the seres within that Carolinian succession). There is some concern that the focusing on managing species that are at their northern range limit is superfluous to maintaining the resilience of ecological systems—the common tree species consist of *Gymnocladus dioica* L. K. Koch, *Celtis occidentalis* L., *Fraxinus pennsylvanica* Marsh. and *Ulmus americana* L. However, it is important to remain focused on the question of impacts on the whole ecosystem, including the islands. A core problem faced by managers of protected areas pertains to the fact that ecosystem degradation is cumulative yet also appears to occur, in a sudden dramatic manner (e.g., witness the collapse of fisheries worldwide). In many instances there is difficulty in defining acceptable means for governing protected areas in

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the face of perceived threats (Wilshusen and others 2002) when it is difficult to predict when a critical change in ecosystem dynamics will occur (Scheffer and others 2009).

In this case, determining the appropriate management route requires evaluating the response of these island ecosystems, the native herbaceous communities in particular, to cormorant nesting colonies in order to examine the impacts that individual breeding populations can have on, what are arguably, remnant habitats. This study provides valuable information on the influence of nesting densities on sensitive native flora which can offer insights into other areas inundated by nesting populations of cormorants. Additionally, this study provides insight into the spatial dynamics of cormorant nesting behaviors. Island ecosystems are particularly vulnerable to barriers to population dispersal which can often favor exotic species colonization (Sax and Gaines 2008). Ongoing disturbances interact with habitat fragmentation to influence ecosystem dynamics within remnant habitats (e.g., limitations on species dispersal) and can sometimes result in unpredictable or undesirable outcomes during regeneration (Temperton and Hobbs 2004). Suding and others (2004) argue that feedback loops can affect how systems reassemble after a disturbance. Due to landscape constraints like habitat fragmentation, population isolation, and species dispersal limitations, it may be difficult or impossible for these communities to regenerate after a breeding colony moves to a new nesting location (Suding and Gross 2006).

Context for Management

The increase in the breeding population of the double-crested cormorant on the Great Lakes is well documented (see for instance Weseloh and others 1995; Cuthbert and others 2002; Weseloh and others 2002). Due to nest site fidelity, the birds return to the same islands, possibly even to the same nest or tree each year after hatching (Wires and others 2001). This means properties, like guano, will continue to build season after season (Rush and others 2011). Nesting colonies on Lake Erie islands have been monitored by the Canadian wildlife service (CWS) since 1979 using annual nest counts. The peak year for cormorant nest numbers in total seems to be 2004, with each island included in the census expressing the highest numbers of all the years. The total nests counted in the western basin for 2004 was 17,170 nests. In 2007, the total nest numbers for the western basin was 13,948.

Cormorants influence their nesting habitats both vertically (in terms of tree structure) and horizontally (which is manifested in the form of spatial alterations of habitats e.g. increased edge to interior ratios). Studies focusing on the impacts of double-crested cormorants on the canopy layer of island ecosystems on Lake Erie have demonstrated that they decrease canopy cover through nesting activities (Hebert and others 2005; Duffe 2006; Koh and Hudson 2006). One of the components of mature tree mortality, however, that has not been studied in these ecosystems is a by-product of nesting pressures on canopy species. Particularly, the effect that an increase at the base of tall overstory species in coarse woody litter depth may have on the germination of herbaceous species as well as the influence it may have on seed bank composition and viability. Studies on other islands affected by other piscivorous colonial water birds during nesting and roosting, highlight some of these influences; guano coverage and nutrient input, plant clipping to construct nests, fallout from plant clipping activities, as well as increased canopy openness from nest construction, and trampling or “bird induced erosion” (Anderson and Polis 1999; Sanchez-Pinero and Polis 2000; Vidal and others 2000; Wait and others 2005). These problems are apparent on the two Lake Erie islands in the study.

In this paper we examined the severity and extent of the impact of cormorants on island flora. Specifically, our aims were: (1) to study the changes in the composition of native and non-native species in the herbaceous-layer composition as an indicator of the general quality of herbaceous ecosystems on nesting islands, and (2) to study the relationship between nesting impacts on understory ecosystems in terms of seed bank and ground cover (i.e., woody debris). To complement the landscape-level analyses (3) the spatial structure of the understory community was compared between particularly high nesting density areas for two islands (Middle Island and East Sister Island). Ultimately, the question is whether the impact of double-crested cormorants will disrupt the native herbaceous flora on the island ecosystems to an extent that they require a large ecological management effort or if the impacts will remain restricted mainly to the perimeter where smaller scale management, including ecological restoration, may be all that is needed.

Material and Methods

Study Area

Three islands were chosen for this study; Middle Island, East Sister Island and West Sister Island. These three sites are part of the Lake Erie Archipelago located between the Canadian and American shores in the western basin of Lake Erie. The islands are comprised of Devonian Dundee limestone bedrock (Kamstra and others 1995). The shorelines of the islands have characteristic exposed rock ledges with limestone shelves and cobble beaches (Kamstra and others 1995) (Table 1).

Table 1 Nest numbers of *P. auritus* on three Lake Erie Islands [adapted from Canadian Wildlife Service (2008) census]

Year	East Sister Island	Middle Island	West Sister Island	Total nests in the Western Lake Erie basin
1993	2,770	(N/A)	307	3,077
1994	2,998	1,011	580	4,932
2002	4,824	6,635	2,787	14,666
2004	6,028	6,611	3,780	17,170
2007	4,197	4,688	1,967	13,948

The three sites were chosen for this study based on ecological similarity at the time of the study; Middle Island and East Sister Island are both severely impacted by cormorant nesting colonies (Rush and others 2011). The islands are all located in the western basin of Lake Erie. West Sister Island was chosen as a suitable reference site because of the ongoing population control efforts, its similarities in ecological composition and also the regional proximity to both East Sister Island and Middle Island. This assumption is based on personal accounts from Parks Canada, U.S. Fish and Wildlife Service, and the cormorant nest count annual census numbers collected and provided by the Canadian Wildlife Service. Historically, all three islands supported communities; on Middle Island and East Sister Island, Kamstra and others (1995) found 73 and 190 native species respectively. According to Hebert and others (2005) a considerable number of these species are of national and provincial significance. For example, on East Sister Island, in 1995, 22 nationally rare plant species were identified, while on Middle Island, 26 rare plant species had been identified (Kamstra and others 1995). Some of the species of concern on Middle Island and East Sister Island are *Morus rubra* L., *Fraxinus quadrangulata* Michx., as well as herbaceous species like *Camassia scilloides* Raf. and *Phacelia purshii* Buckley.

Experimental Design

Since some of the data collection procedures originated prior to this study, we chose to match those earlier studies for long term comparison (this issue is a common constraint, best illustrated by Price and Weltzin 2003). In order to effectively measure the extent of potential damage from cormorant nesting density across the islands in their entirety, the plotless point centered quarter method (PCQ) as per Mueller-Dombois and Ellenberg (1974) was used. For Middle Island, Parks Canada had established twelve North–South transects for a total of 52 sampling sites along each transect, with each site located at a distance of 50 m apart along the transects. On East Sister Island, in 2004, a total of 11 North-South transects for a total of 29 sampling sites were established, with each site located at a distance of 50 m apart along the transects (information on how the transects were set up can be found in Koh and Hudson 2006). On West Sister Island, 60 plots along pre-existing transects were chosen for sampling with attention paid to representation across the island.

Study Objectives 1 and 2: Variables Measured

Data collection included the following variables: nest density, vegetation inventories, litter depth, and seed bank cores.

- The number of *P. auritus* nests were counted at each plot for each of the sites in late June and early July of 2008. A 10 m circumference was established around the centre of stake of the plot within nests were counted.
- The vegetation data was collected in a 1 m^2 plot using the PCQ method. The vegetation inventories took place in late June and early July of 2008. Each plant in the plot was identified and density was recorded. Percent cover was estimated using a modified Braun-Blanquet cover scale (viz DeBerry and Perry 2004).
- In late August and early September 2008 seed bank cores were collected in each of the permanent plots at each island. A core sampler was used with a 4.5 cm diameter and 13 cm depth. Five samples were taken at each plot and pooled (Baskin and Baskin 1998). The numbers of subsamples used for seed bank analysis were as follows: 42 from Middle Island, 27 from East Sister Island, 38 from West Sister Island (some cores were insufficient for analysis due to the shallow soil over the bedrock of the islands). The seed bank samples were then cleaned and sieved (see Fenner and Thompson 2005 for particular methods). The samples were identified and counted and viability was tested using the crush-test (viz Borza and others 2007).
- During seed bank sampling in late August and early September, at each plot where a seed bank core was collected a litter depth reading was taken (measured from top of soil to the top of the litter bed). The litter depth was taken at the northern edge of each soil core sample. The five readings were then averaged and the standard deviation was calculated to account for any samples collected that might vary dramatically from the mean due to the variable distribution of litter depths around the sampling points.

Study Objective 3: Analytical Set-up for the Spatial Structure of the Understory Community Comparisons for Particularly High Nesting Density Areas

Parks Canada and Ontario Parks established a set of damage indices on East Sister Island and Middle Island in

2005. The areas were classified as zero, low, medium or high damage. The classifications are related to specific soil plot locations used for soil chemistry tests. Cormorant nest densities were ranked based on aerial photographs as well as expert opinion during the assessment (A. Fisk., personal communication April 3, 2009). This method helps to justify studying more extensively the areas considered to be more highly damaged through cormorant nesting activities.

Analyses

In most ecological studies, it is unrealistic to assume that the data sets will conform to a parametric test because of spatial autocorrelation or skewness (Anderson 2001). That was true in this study as data were non parametric (i.e., failed the Kolmogorov-Smirnov test for normality), hence Kruskal–Wallis tests were used for testing equality of population medians among groups (Vargha and Delaney 1998). This test does not focus on measures of central tendencies like the parametric ANOVA (Ruxton and Beauchamp 2008). The Kruskal–Wallis test is referred to as the ranked equivalent of the ANOVA (Analysis of Variance). Regardless of the shape of the distributions among groups, “if the sample observations across all groups are ranked, and the variances of these ranks are similar for all the groups”, then the Kruskal–Wallis test can be used (Ruxton and Beauchamp 2008).

For study objectives 1 and 2, the data were organized by site (East Sister Island, Middle Island and West Sister Island were included) and year (where appropriate) to examine the interactions between nesting density and the following: native and non-native herbaceous communities, native and non-native seed bank communities, seed bank viability and litter depth. For one test where litter depth was compared with herbaceous species diversity, the Pearson Product Moment test was used (Rodgers and Nicewander 1988) to compare bivariate association or linear dependence between two variables e.g. litter depth against native species diversity.

For study objective 3, the data collected for the herbaceous plots and the seed bank samples was run separately based on the damage indices to determine if there is in fact a significant difference in damage in localized areas across East Sister Island. For example, variables listed in “Study Objectives 1 and 2: Variables Measured” section were categorized based on whether located in an area of zero, low, medium, or high damage. The damage rankings were used as an independent variable to determine if the data collected was stratified along the perceived damage gradient. West Sister Island was not used for this data analysis because the management concerns pertain to East Sister Island and Middle Island exclusively at the point of the study.

Results

Changes in the Composition and Diversity of the Herbaceous Community Island-Wide

Herbaceous data and associated cormorant nesting numbers for the years 2004, 2007, and 2008 demonstrated that *P. auritus* nesting numbers do not affect herbaceous species abundance on East Sister Island or Middle Island. On West Sister Island, the Kruskal–Wallis test found $P < 0.05$ for all species combined for one year of data, 2008. This finding may be subject to the fact that only one year of data was collected and run in the Kruskal–Wallis test. However, in the case of garlic mustard on all of the islands, *P. auritus* was found to be significantly influential in decreasing numbers of this herbaceous species; on East Sister Island $P < 0.01$; on Middle Island $P < 0.01$ and on West Sister Island $P < 0.05$ (Figs. 1, 2).

Relationship between Nesting Impacts and Understory Ecosystems: Seed bank and Woody Debris

Generally, cormorant nest density did not contribute to increased litter depth on the three islands. Neither cormorant nest density nor litter depth caused any significant responses in species using above-ground or seed bank measures (abundance, composition, diversity, seed viability). Cormorant nest numbers decreased the abundance of *Alliaria petiolata* (M. Bieb.) Cavara & Grande on all three islands.

Middle Island has the highest exotic seed bank, $P < 0.001$; West Sister Island has the lowest exotic seed bank for all three islands, $P < 0.01$. The exotic seed bank is significantly higher than the native seed bank on all islands; on East Sister Island $P < 0.01$; on West Sister Island $P < 0.05$; on Middle Island $P < 0.001$. The native seed

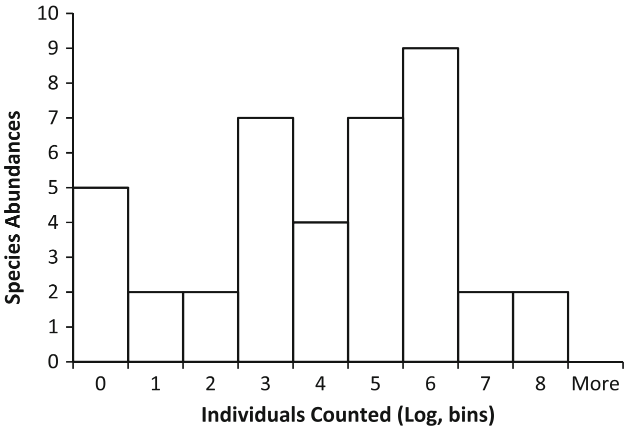

Fig. 1 Relative species abundances of native herbaceous species on Middle Island for 2008

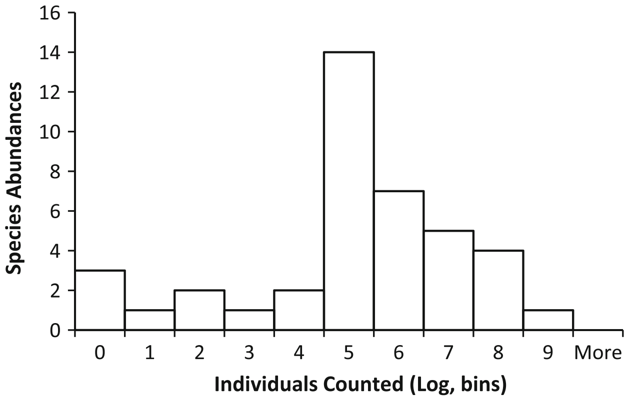

Fig. 2 Relative species abundances of exotic herbaceous species on Middle Island for 2008

bank is the same for all three islands, $P = 0.317$. This suggests that where double-crested cormorants have been culled, there is not a significant difference in the species abundance of native species in the seed bank, namely on the control island, West Sister Island. There is however, a significant difference between West Sister Island and Middle Island and exotic species abundance.

We also compared native seed bank versus native herbaceous vegetation; native seed bank versus non-native herbaceous vegetation; non-native seed bank versus native herbaceous vegetation and non-native seed bank versus non-native herbaceous vegetation. Of the three islands, on Middle Island there are significantly more exotics in the seed bank than native species. Additionally on Middle Island, the exotic species found in the herbaceous count is significantly higher than the native species found in the count; $P < 0.01$. The exotic seed bank is significantly higher than native seed bank on all the islands, and the native seed bank abundance was the same on all of the islands, regardless of pre-existing management efforts of cormorant population density. However, the exotic seed banks are higher on Middle Island and East Sister Island than West Sister Island (Figs. 3, 4, 5, 6, 7, and 8).

Spatial Structure of the Understory Community Comparisons for Particularly High Nesting Density Areas: Middle Island and East Sister Island

The selected plot analysis is a purposive examination of known nesting areas on the islands with high nest site fidelity (high nesting density) in comparison to moderate, low and areas of no known nesting at the time of the study. This comparison revealed that cormorant nest density and litter depth does influence the herbaceous layer abundance and diversity but does not influence seed bank viability or abundance. Table 2 is a summarization of the data from the selected damage indices plots.

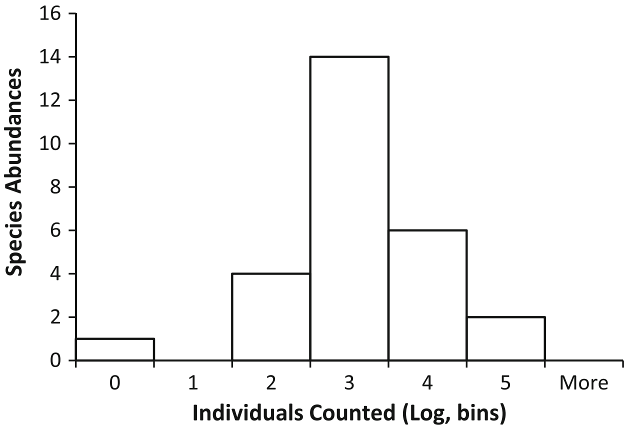

Fig. 3 Relative species abundances of native seed bank species on East Sister Island for 2008

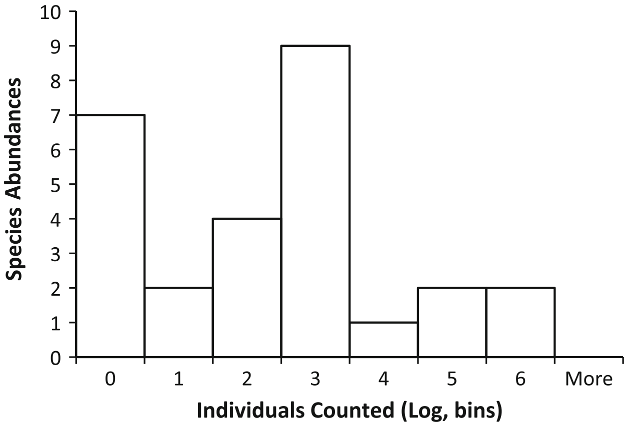

Fig. 4 Relative species abundances of exotic seed bank species on East Sister Island for 2008

Discussion

Changes in the Composition and Diversity of Species in the Herbaceous-layer are an Indicator of the general Quality of Herbaceous Ecosystem on Nesting Islands

Due to the concerns of changes in biodiversity by ecosystem managers of these protected island ecosystems, this study was concerned with the potential turnover of native species and the colonization of exotic species. We acknowledge that the effect of cormorants on the vegetation structure can be manifested in the transformation of the dominance structure within the group of native plant species and not necessarily in an increase in the numbers of exotic invasive species. However, one major concern pertaining to island ecosystems, particularly those that are experiencing stresses (i.e., by high nesting densities of water birds), is that ecological communities will become more permeable to exotic herbaceous species invasions which formed the basis of one of our study objectives. That

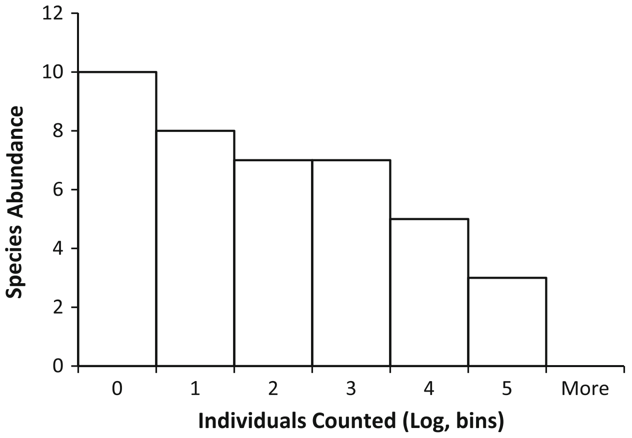

Fig. 5 Relative species abundances of native seed bank species on Middle Island for 2008

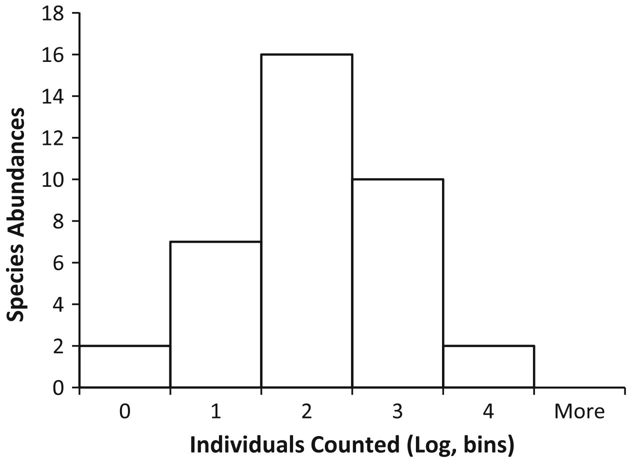

Fig. 7 Relative species abundances of native seed bank species on West Sister Island for 2008

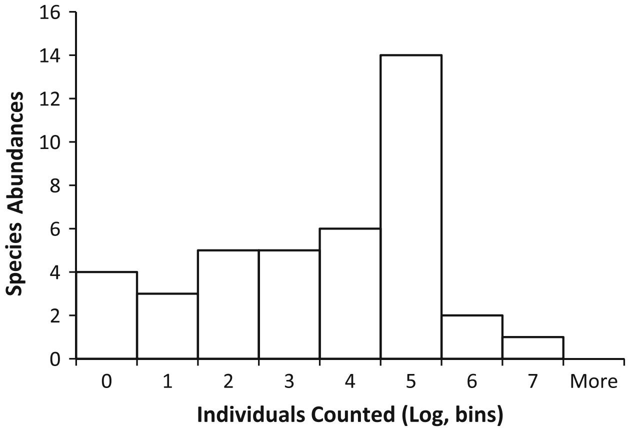

Fig. 6 Relative species abundances of exotic seed bank species on Middle Island for 2008

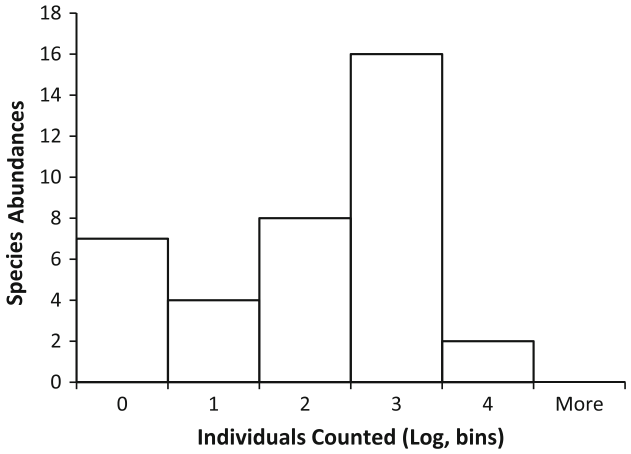

Fig. 8 Relative species abundances of exotic seed bank species on West Sister Island for 2008

being said, the immediate impacts on understory herbaceous species were not yet measurable for the duration of this study except on Middle Island. This is likely a result of the filtering effect the canopy layer provides in terms of nesting fallout. As the canopy becomes more damaged the negative effects on the understory layer will be measurable. Hebert and others (2005) found that cormorant nest density was negatively correlated with tree cover on both East Sister Island and Middle Island. Koh and Hudson (2006) also found that trees in which cormorants are nesting become increasingly damaged until they are killed, and when they are too decayed and little nesting material is left for construction, they abandon the tree. This corroborates our findings, indicating that the direct impacts are on the canopy and supercanopy (Koh and Hudson 2006) and the impacts on the herbaceous layer are more indirect and perhaps take longer to become apparent.

Although East Sister Island does not have as many exotic species and has the most natives in both the seed bank and the herbaceous count; in general East Sister Island has less overall vegetation cover than Middle Island. Duffe (2006) found that East Sister Island expressed increasing percentages of bare soil from 2001 to 2003. In 2001, only 2 % of the ground was considered bare, and by 2003, 15 % of the ground was considered bare, or 1.5 ha in total (Duffe 2006). East Sister Island has less overall herbaceous cover than Middle Island, which may suggest that all herbaceous species, including native species, have low survivorship.

One main significant result was that higher densities of cormorant nests decrease the abundance of garlic mustard. While it may seem counterintuitive that disturbance impedes garlic mustard, this is consistent with the literature. Garlic mustard colonizes unoccupied or sparsely occupied habitats—though it also will invade any disturbed habitat with higher initial densities of invasives (Anderson and others 1996). However, garlic mustard is also sensitive

Table 2 Effects of nest density (as the dependent variable) on all other independent variables measured

Tests	ESI		MI	
	P value	Progression of significance	*P* Value	Progression of significance
a. Cormorant nest density vs. litter depth	<0.001	High > medium > low = zero	<0.001	High > medium > low = zero
b. Cormorant nest density vs. native herbaceous species abundance	<0.001	High > medium = low = zero	<0.001	High > medium = low = zero
c. Cormorant nest density vs. exotic herbaceous species abundance	<0.001	High > medium = low = zero	<0.001	High > medium = low = zero
d. Cormorant nest density vs. total diversity of herbaceous species.	<0.05	High > medium = low = zero	<0.05	High > medium = low = zero
e. Cormorant nest density vs. diversity of native herbaceous species.	<0.05	High > medium = low = zero	<0.05	High > medium = low = zero
f. Cormorant nest density vs. diversity of exotic herbaceous species.	<0.05	High > medium = low = zero	<0.05	High > medium = Low = Zero

"Progression of significance" refers to the relative influence that nesting density has on the island of interest and the measured variable of interest. Interactions that were not significant are not reported below (non-significant at $P = 0.05$)

to litterfall (more often in the form of mulched leaves but nest litterfall may suffice) and it is possible that garlic mustard is more sensitive to even small litterfall changes, and changes in the pH which may not be affecting the other herbaceous species. Bartuszevige (2007) found that garlic mustard survival and seedling establishment was significantly diminished by increasing litter amounts. In this study where different litter treatments were used to test garlic mustard establishment and survival, the findings demonstrated that garlic mustard responds well to increased light and nutrient influxes, but adding litter to the plots decreased establishment and survival.

Changes in the soil chemistry may also be a factor in the relationship of garlic mustard and cormorant nest densities. Ornithogenic soils are found to be extremely high in phosphate, nitrate and ammonium as well as exhibiting generally low pH values over long periods of time (Wait and others 2005). While this evidence may seem contradictory is important to keep in mind that studies on seabird effects on islands in arid climates in salt water ecosystems may yield different results from the islands on Lake Erie; additionally compressing the time scale from such a study would also yield contradictory results in soil chemistry composition. Duffe (2006) found a significant negative relationship between cormorant nests in 2003 and pH; conversely he also found a significant positive relationship between cormorant nests and soil ammonia and nests and nitrate concentrations. Rush and others (2011) found that both Middle Island and East Sister Island have decreased soil pH and P concentrations with increased with nest density. Rush and others (2011) also discovered that soil nitrate concentrations increased with cormorant nest density on Middle Island. Wait and others (2005) also found that soils inundated by guano deposition can inhibit some herbaceous species while facilitating the growth of other species. Ishida (1996) also found that in cormorant nesting colonies seedling survival is greatly influenced by both direct and indirect nesting impacts. Long term guano deposition is associated with a decrease in soil pH (Wait and others 2005) which ultimately could inhibit the survivorship of garlic mustard. Vidal and others (2000) found that species turnover is positively correlated to gull nesting density and also that seabird activities tend to select and facilitate some adapted plant species at the expense of others, including native indigenous flora as well as other exotic flora species. Hobara and others (2001) found that excreted nitrogen (N) was quickly mineralized and taken up and cycled throughout the ecosystem. Hobara and others (2001) also found that plant carbon: nitrogen ratios and leaf litter carbon: nitrogen ratios decrease with an advanced stage of bird colonization. What our findings indicate, however, is that there is not any major change in the nutrient cycling because the plant compositions remain relatively the same island-wide. Garlic mustard may be more sensitive to these changes than other herbaceous species.

Relationship between Nesting Impacts on Understory Ecosystems: Seed Bank and Woody Debris

The analysis reveals that cormorants influence herbaceous ecosystem dynamics (at least initially) in a targeted way and may be predicted based on indicators of suitable nesting locations (e.g., canopy age, canopy species composition, distance to foraging areas etc.) As a result, herbaceous species abundance and diversity (total, native or exotic), seed bank composition, and seed viability were not significantly affected by either cormorant nest numbers or large-diameter litter-fall from cormorant nesting activities in a significant way across the islands in their entirety.

Hobara and others (2001) found that in cormorant nesting activities may lead to increased litter fall as a result of nest construction debris. We did not find that litter depth had a consistent or even significant impact on herbaceous species diversity, abundance, seed bank composition or viability in terms of dispersal of impacts across the islands. There was no significant correlation between *P .auritus* nest density and increased litter depth in the herbaceous species plot. Based on the findings from the damage indices section, we predict that more localized testing would provide a better indication of influences from cormorant nesting on increased coarse woody litter. Observable increases in litter depth around mature tree deaths corroborate the damage indices findings (D. McGrath pers. ob.), suggesting that cormorants may increase the litter depth on the islands, but not in a significantly damaging way for the herbaceous species across the entire island ecosystem at this time.

On Middle Island the exotic seed bank is increasing (2004–2008) as a result of the presence of exotic herbaceous species on the island; however, this is not unique to the archipelagos. For example, Sax and Gaines (2008) argue that naturalization of exotic species on islands is not a new phenomenon and has been evident for over two centuries. They also found that the number of naturalized plant species has increased linearly over time (Sax and Gaines 2008). On islands invaded by exotic species, the exotics tend to be widely distributed across the island (Blackburn and others 1997; Kotze and others 2003; Gillespie and others 2008). Changing numbers of plant richness, specifically, exotic species, on these islands is not unique to Lake Erie, nor is it uniquely characteristic of the cormorant nesting colonies. Increasing amounts of exotic species becoming naturalized on islands all over the world, both continental and oceanic, are predicted with varying magnitudes of native plant extinction in future years (Sax and Gaines 2008). Seed abundances of native species may be reduced by declines or absence of plants in proximity to the islands (few species can send seeds via the water or via longer-distance dispersal on wind or animals). Native and invasive species could potentially be transported to the islands via the cormorants, and they may be an important vector for seed source input within the island archipelagos (see also Laurence 2008).

Spatially Distributed Impacts on the Understory Community Resultant from High Nesting Density Areas on Middle Island and East Sister Island

After analyzing the damage indices data on the specific plots on Middle Island and East Sister Island, based on nesting preferences (determined by nesting density and damage rankings) we determined that higher nesting densities results in decreased herbaceous abundance (native and exotic); decreased herbaceous species diversity (total, native and exotic) and increased litter depth. The analysis also revealed that a difference in the damage gradient between areas with zero or low damage (e.g., the interior) compared to the highly degraded areas where the cormorants primarily nest would help to determine the rate of collapse of the perimeter of the islands. Modification of edge areas have been found to influence biogeochemical nutrient transport (Kitchell and others 1979) and can also influence the outcomes of species interactions (Kareiva 1987; Roland 1993). Additionally, island size and shape may determine the amount of damage cormorants may exert on a system. As mentioned, cormorants, on island ecosystems, are primarily edge nesters (Quinn and others 1995; Wires and others 2001). Edge effects can very easily impact species dynamics by facilitating the colonization or regeneration of some species while inhibiting the abundance of other species (Malcolm 1994) and also expose new areas adjacent to disturbances causing alterations to the interior of the habitat (Harris 1984; Chen and others 1992; Collinge 1996). This can lead to a whole host of changes such as changes in temperature, light, moisture and wind (Collinge 1996). Matlack (1993) found edge effects altered humidity and litter moisture up to 50 m into the interior of the forest. These types of changes can affect the herbaceous communities in proximity to the disturbed areas (Collinge 1996); suggesting that further research on the islands should be focused on these areas.

Invasion and dispersal of species can be influenced by the patch size or shape of an ecosystem (Forman 1995). One predicted outcome of cormorant nesting on the islands is a modification of patch size and shape of the habitable parts of the islands. Modification of the shape of the patches can influence the colonization of exotic species. Certain shapes, such as rounded patches, can be more effective for conserving internal resources in an ecosystem through the minimization of the exposed perimeters to outside effects (Forman 1995). Patch creation or modification is linked to disturbance agents (Peters and others 2006) such as the cormorants. Cormorant nesting behavior indicates that nest creation and maintenance will be close to the shoreline and foraging locations (Quinn and others 1995; Wires and others 2001; Hebert and others 2005; Duffe 2006; Koh and Hudson 2006). Cormorants stress the edge of the island ecosystems with nesting activities and may be modifying the perimeter of the island ecosystems through these pressures. Smaller islands with a smaller interior and therefore a larger edge to interior ratio, may suffer more impacts to the interior due to sheer nesting density on the edges (Malcolm 1994). Our findings, therefore, will be most relevant for managers dealing with islands of similar size (e.g., 15–36 ha in size, in respect to the size of the islands included in this study).

There seems to be a consensus among those who have long studied these islands that a focus on the perimeter nesting areas has yielded sufficient data for determining impacts on the canopy layer (Quinn and others 1995; Hebert and others 2005; Duffe 2006). For instance, Quinn and others (1995) studied and characterized cormorant nesting behavior in order to facilitate nesting on a constructed island in Hamilton harbour. They found that cormorants build their nests in open and highly visible trees most commonly those trees found along the shoreline. Additionally they also nest along the shore close to their foraging areas and are also believed to have intense nest site fidelity to colony sites (Wires and others 2001). Young cormorants are often found to gravitate to their natal colonies, and initiate their first breeding season at that site (Wires and others 2001). As a result, an information gap exists because there has been more attention given to impacts on trees where nests exist and on the guano that builds near the shoreline where there was inherently little understory growth (because of exposure to winds and waves on porous beach soil). We tested as much of this as possible in the perimeter areas, with the constraint that we also had to study the entire islands. This meant that while we could draw some limited and yet important conclusions, more extensive comparisons of the perimeter and interior areas will be needed.

Conclusions

In conclusion the perceptible changes in the forest understory composition suggests that further changes in biodiversity are likely on these island ecosystems. The island ecosystems are being fragmented by cormorant nesting densities and will most likely make these habitats more permeable to exotic species invasions. Management of island ecosystems that support nesting double-crested cormorants will require a dynamic approach that integrates biodiversity conservation and protection with the restoration of understory species in areas that are no longer suitable for nesting. Particular areas suitable for restoration on the islands can be found in places that have been abandoned because the mature nesting trees have been killed. Although conservation of native flora is paramount for protected area management, particular attention should be paid to the potential benefit of nurse guilds of native species (e.g., dominance and competition sensu Murphy 2005) and should be guided by ecosystem assembly rules. The major challenge will be to examine the nutrient and light availability in those areas because the canopy is greatly reduced and the nutrients are presumably increased (see Rush and others 2011) in order to determine which sequence(s) for ecological restoration will prove to be most successful.

This research is important because it provides evidence to managers of areas subject to cormorant nesting pressures (particularly managers of protected areas) of the levels of disturbance that can be expected in the initial colonization period (i.e., approximately 10 years of increasing nesting pressures). Future studies on these islands should try to determine at what rate the cormorant nesting areas are expanding. As a result of this study, we now have a synthesis of the data collected on each island and some baseline findings about the herbaceous layer and the seed bank that are integral for the design of a management plan for ecosystems influenced by high density nesting pressures from breeding waterbird colonies.

Acknowledgments In kind support for this project was provided by Ontario Parks, Parks Canada, the U.S. Fish and Wildlife Service and Ohio Wildlife Service. This project would not have happened without the generous supply of data from both Parks Canada and Ontario Parks. The richness of the data collected and available to us for this project was only possible through the hard work of the Parks Canada staff, Tammy Dobbie, Josh Keitel and Rachel Thorndyke and the Ontario Parks staff, Sandy Dobbyn and Jennifer Hoare. The authors would also like to thank Ohio Wildlife Services staff, especially Dave Sherman and Doug Brewer from U.S. Fish and Wildlife Service for transportation and all their and guidance on this project. The authors would also like to acknowledge the work by Dr. Saewan Koh which helped to shape the basis of the data collection for this project.

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