

Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine

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Summary

1. The structure of communities is influenced by the transport of resources across ecosystem boundaries. Seabirds are capable of introducing large amounts of marine-derived nutrients to land, thereby modifying resource availability to terrestrial species.
2. In this study we investigated the hypothesis that variation in nesting densities of great black-backed gulls *Larus marinus* and double-crested cormorants *Phalacrocorax auritus* would modify the effect of these species on soil nutrients and plant species composition on offshore islands in the Gulf of Maine, USA.
3. Our results showed a significant positive correlation between nest density and concentrations of ammonia and nitrate in soils, but no significant relationship between nest density and phosphate. Ammonia and phosphate concentrations were good predictors of plant species composition; there were more annual forbs than perennial grasses in the abandoned cormorant colony compared with the gull colonies. Extremely high concentrations of ammonia in the highest density colony (active cormorant) may have been the main factor inhibiting plant germination at this site. All of the plant species in gull and cormorant colonies showed enriched $\delta^{15}\text{N}$ signatures, indicating substantial input of marine-derived nitrogen from seabirds.
4. Our study demonstrated that gulls and cormorants are effective vectors for the transport of marine nutrients to terrestrial ecosystems. However, transported nutrients occurred in particularly high concentrations in areas with nesting cormorants. Nesting densities and species-specific variation in resource transport should be considered when predicting the effects of seabirds and other biogenic vectors of allochthonous resources.

Key-words: cross-ecosystem, isotopic enrichment, nesting density, seabird, soil ammonia nitrate and phosphate.

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Introduction

Movement of predators, prey, and nutrients across ecosystem boundaries is a widespread phenomenon, and can strongly influence local population dynamics and the structure of communities (Polis, Anderson & Holt 1997). Such exchanges among ecosystems have long been recognized (Summerhayes & Elton 1923; Elton 1927; Likens & Bormann 1975) but a theoretical framework for this process has only recently been generated (DeAngelis 1980; Polis *et al.* 1997; Huxel & McCann 1998; Fagan, Catrell & Cosner 1999; Huxel, McCann & Polis 2002). One of the predictions of this theory is

that nutrients and materials are transported from more to less productive ecosystems. Transport along this productivity gradient depends on either physical factors that connect the adjacent habitats, or on the presence of biotic vectors that actively move across habitat boundaries. The particular mobility, behaviour, and physiology of a biotic vector can strongly influence the rate and type of exchange across habitat boundaries (Nystrom & Pehrsson 1988; Johnston & Bildstein 1990; Fariña *et al.* 2003).

Marine mammals and birds are important biotic links between marine and terrestrial ecosystems along coasts around the world (Gillham 1956, 1961; Sanchez-Piñero & Polis 2000; Fariña *et al.* 2003). Seabirds in particular have attracted much interest because they introduce large amounts of marine-derived nutrients to land, thereby altering resource availability to terrestrial

species (e.g. Anderson & Polis 1999; Mulder & Keall 2001; Vidal, Jouventin & Frenot 2003; Ellis 2005). During the breeding season, seabirds deposit food scraps, egg shells, feathers, and bodies of dead chicks and adults in terrestrial habitats (Heatwole 1971; Sanchez-Piñero & Polis 2000). Also, large amounts of nutrient-rich guano can accumulate in breeding and roosting areas, altering soil and plant nutrient content (Gillham 1956; Anderson & Polis 1999).

A large body of literature indicates that terrestrial plant growth and distribution are limited largely by availability of nitrogen and phosphorus (Chapin 1980; DiTomasso & Aarsen 1989; Koerselman & Mueleman 1996; Aerts & Chapin 2000). Nutrient input by seabirds is expected to increase plant growth and productivity (Burger, Lindeboom & Williams 1978; Smith 1978), but excessive amounts may inhibit growth, change species composition, or even kill certain species of plants (Hogg & Morton 1983). Although there is evidence that seabirds can negatively affect plants (Gillham 1961; Sobey & Kenworthy 1979) many recent studies have tended to emphasize positive effects (Norton *et al.* 1997; Polis *et al.* 1997).

The direction and magnitude of seabird effects on terrestrial systems should be altered by nesting densities and other species-specific characteristics of the birds themselves. For instance, a few descriptive studies indicate that densely nesting species are capable of killing vegetation in nesting areas (e.g. penguins: Smith 1978). Although nesting density is likely to modify the effects of seabirds on terrestrial habitats, there are very few studies that quantitatively compare soil nutrients and plant assemblages across a gradient of nest densities (Ellis 2005). Seabird populations have fluctuated around the world; some species have increased substantially (gulls: Sobey & Kenworthy 1979; Vidal *et al.* 1998, 2000), whereas others have decreased (burrowing petrels: Norton *et al.* 1997). If the density of nesting birds strongly alters their effects on soils and plants, then changes in population sizes of seabirds will have significant consequences for coastal habitats.

In New England and throughout the North Atlantic, seabird populations have fluctuated dramatically during the 20th century. Several species declined in the late 1800s in response to increased hunting pressure (Kadlec & Drury 1968; Spaans 1971). Legal protection and increases in anthropogenic food subsidies led to substantial increases in great black-backed gulls *Larus marinus* L. and double-crested cormorants *Phalacrocorax auritus* Lesson during the past several decades (Krohn *et al.* 1995; Good 1998). Recent estimates indicate that there are thousands of gulls and cormorants nesting on hundreds of islands in the Gulf of Maine (Maine Department of Inland Fisheries and Wildlife, unpublished data). However, only a handful of published studies have examined the effects of gulls and cormorants on soils and plants.

In this study, we compared soils and plants in gull and cormorant colonies of various densities. Overall, our

working hypothesis was that the density of nesting seabirds would alter the magnitude of exchange across marine and terrestrial habitats. Specifically, we asked the following questions: (1) How do concentrations of soil nutrients (NH_4^+ , NO_3^- , PO_4^{3-}) differ with various densities of nesting gulls and cormorants? (2) What plants occur in the various colonies? (3) What is the relationship between soil nutrient concentrations and plant germination? (4) Do plants vary in assimilation of marine-derived nutrients in colonies with different marine birds and nest densities?

Materials and methods

STUDY SITES AND ORGANISMS

This study took place in the Isles of Shoals, a nine-island archipelago, located *c.* 10 km from the coast of New Hampshire, USA in the Gulf of Maine (Fig. 1). Detailed investigations were conducted on Appledore, Duck, Lunging and Smuttynose Islands (Table 1). The geology of the islands consists mostly of granite, metamorphic rock and diabase dikes (Novak 1971). The soil is composed of decaying organic matter and fine products of weathering (Novak 1971), and glacial till has been found in some depressions on Appledore Island (Boden 1977).

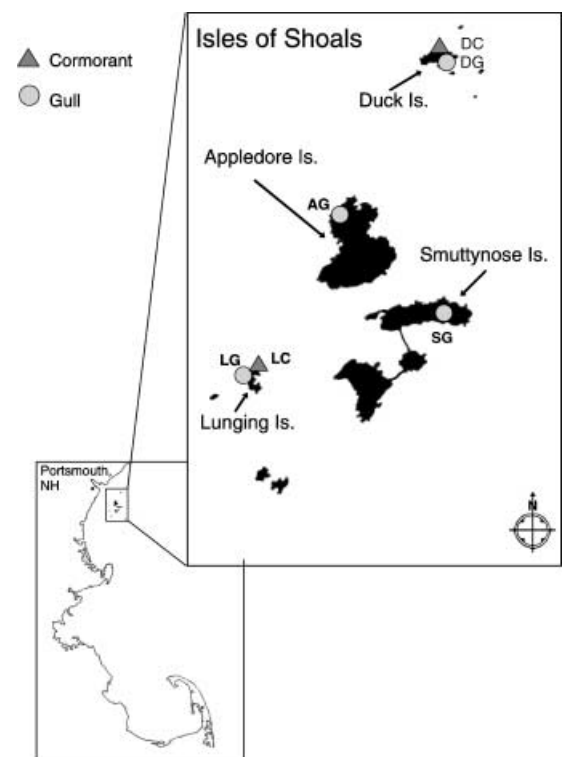


Fig. 1. Map of study sites in the Isles of Shoals. Detailed investigations were conducted on four islands: Smuttynose, Duck, Lunging and Appledore. Lunging and Duck Islands had both gull (LG, DG) and cormorant-affected sites (LC, DC), whereas Smuttynose and Appledore had only gull colonies (SG, AG).

Table 1. Characteristics of the islands and seabird colonies. Islands are located in the Isles of Shoals, NH/ME. Island area estimates are from Borrer & Holmes (1990)

Island	Island area (ha)	Colony	Colony area (m ²)	No. of nests	Nest density (nests m ⁻²)
Appledore	33.6	Gull	3572	15	0.004
Smuttynose	15.4	Gull	2340	21	0.009
Lunging	2.5	Gull	1440	2	0.001
		Old Cormorant	48	0	–
Duck	1.5	Gull	1250	30	0.024
		Cormorant	576	101	0.175

The climate of the archipelago is temperate-oceanic; January and February are the coldest months (*c.* –1.0 to –0.5 °C; NOAA, unpublished data), whereas June through August are the warmest (*c.* 15–20 °C; 1984–2001 monthly averages; NOAA, unpublished data). The islands receive ≥ 1000 mm of precipitation each year (McGill 1977). The major habitat types include: bare rocky margin with little or no vegetation, exposed inland ridges where grasses and herbs dominate, central areas covered with dense shrubs and trees, and areas characterized by human disturbance. Duck Island is the only island of the four we studied that is uninhabited by humans.

Double-crested cormorants *Phalacrocorax auritus* and great black-backed gulls *Larus marinus* occur in colonies from March through August in the Isles of Shoals. *L. marinus* nest on inland ridges and cobble beaches, and cormorants nest on bare rock ledges and cliffs or along inland ridges (Borrer & Holmes 1990).

COLONY SURVEYS

The study was conducted from June through September of 2002 and 2003. Cormorant and gull colonies occur on the two smaller islands (Lunging and Duck); on the bigger islands (Appledore and Smuttynose) only gull colonies are present. Nesting areas, or subcolonies, are patchily distributed around the islands. We chose to survey a single spatially discrete subcolony on each island rather than sampling the entire island.

We chose subcolonies that represented a gradient of nesting densities. In order of decreasing densities, there was one active cormorant colony, four gull colonies, and one recently abandoned cormorant colony (Table 1). In 2001, a small cormorant colony occurred on the northeast end of Lunging Island (Fig. 1), but by 2002 the colony was abandoned. The effects of seabirds on soils and plants can linger for several years after a colony is deserted (Tatur 1989), therefore we included this site.

We visited the gull colonies several times during the study period. We restricted our visits to the active cormorant colony to late summer because human presence during the breeding season leads to gull predation on cormorant offspring and massive mortality (Kury & Gochfeld 1975). Nest positions were recorded and georeferenced by the use of a handheld GPS (Geographical Position Systems) device (Garmin model 76). In the abandoned cormorant colony, we used the position of

old nests to determine the area of the former colony. We estimated the area of every colony, and the density of active nests for all of the occupied colonies (Table 1).

SOIL NUTRIENTS

Eight soil samples were randomly taken from the first 10 cm of soil in each subcolony. Soils were analysed according to procedures described in Mulder & Keall (2001), which consisted of determining moisture content gravimetrically and using this value to calculate the nutrient (ammonia, nitrate and phosphate) concentration in mg per gram of dry soil. For analysis of ammonia and nitrate, 5 g of sieved (2 mm) soil were extracted in 60 mL 2 M KCl for 24 h. For phosphate, 1 g of sieved soil was extracted in 30 mL of 0.5 M NaHCO₃ for 24 h. All the extracts were filtered through Whatman GF/A glass fibre filters and analysed for each nutrient using a Hach spectrophotometer (model DR 2012, Hach 1997).

PHYTOMETER EXPERIMENT

We conducted a greenhouse experiment in order to determine whether differences in soil nutrient concentrations among subcolonies affected germination rates of plants. Following the methods of Mulder & Keall (2001), *Brassica rapa* L. (Wisconsin Fast Plants, wildtype, Carolina Biological Supply) was used as a 'phytometer' to indicate nutrient availability for plants in soil samples from each colony. Soil samples (*n* = 8) were sieved (2-mm) to remove large roots, twigs and stones. The samples were then randomly allocated to four Styrofoam cells; one *B. rapa* seed was planted in each cell. Standard growth procedures were followed (Wisconsin Fast Plants Manual 1989), but no fertilizer was added. Cells were placed at 20 °C under a 12-h photoperiod from germination to flowering (2 weeks) and germination rates were recorded. As a procedural control, we monitored germination rates of seeds planted in standard potting soil. 'Native' plants germinating from soil seed banks were also recorded in each experimental unit.

ISOTOPIC ANALYSES

To assess the extent of transport of marine-derived nutrients, we determined the isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of plants in each subcolony (Anderson

& Polis 1998). We removed leaves from plants collected in the colonies and transported them to the laboratory where they were oven-dried at 70 °C for 48 h and ground to fine powder. Samples were then submitted to the University of Arkansas Stable Isotope Laboratory for analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The most common plant species occurring in each colony were also recorded during the study period.

STATISTICAL ANALYSES

Data on nesting density in each subcolony were $\log(x + 1)$ transformed and used in three separate linear regressions comparing density with concentrations of ammonia, nitrate and phosphate in the soils. Concentrations of ammonia, nitrate and phosphate were $\log(x)$ transformed.

To assess the relationship between soil nutrient concentrations and plant species composition in each colony, the plant species lists were used to construct a Bray–Curtis similarity matrix (among colonies). This analysis was followed by a Multi-Dimensional Scaling (MDS) ordination on the resultant matrix. The significance level of similarity among the groups from the MDS was estimated using the distribution of Bray–Curtis similarity coefficients, calculated after bootstrapping the plant species composition matrix 1000 times (Clarke 1993).

Data on the proportion of phytometer seeds that germinated in soils from each colony were transformed $[(x + 1)^{0.5}]$ and used in a multiple linear regression to test for the effects of soil ammonia ($\log x$ transformed), nitrate and phosphate on germination.

Results

COLONY AREAS AND NEST DENSITIES

The gull colonies were larger than the cormorant colonies. Gull colonies ranged in area from 3572 m² (Appledore) to 1250 m² (Duck), whereas the cormorant colonies were 48 m² (Lunging) and 576 m² (Table 1). The density of birds in the active cormorant colony was seven times greater than the density of birds in the highest density gull colony (Table 1).

SOIL NUTRIENTS

The difference in concentration of ammonia in the soil corresponded well with the difference in order of magnitude in bird densities (Fig. 2). There was a highly significant positive correlation between nest density and concentrations of ammonia ($R^2 = 0.790$, $F_{1,47} = 180$, $P < 0.001$); nest density explained nearly 80% of the variation in ammonia. Concentrations of nitrate were also positively correlated with nest densities ($R^2 = 0.443$, $F_{1,47} = 39.2$, $P < 0.001$). There was no significant relationship between nest density and phosphate concentrations ($R^2 = 0.013$, $F_{1,47} = 3.85$, $P = 0.206$); phosphate concentrations were very high in both the active and abandoned cormorant colonies.

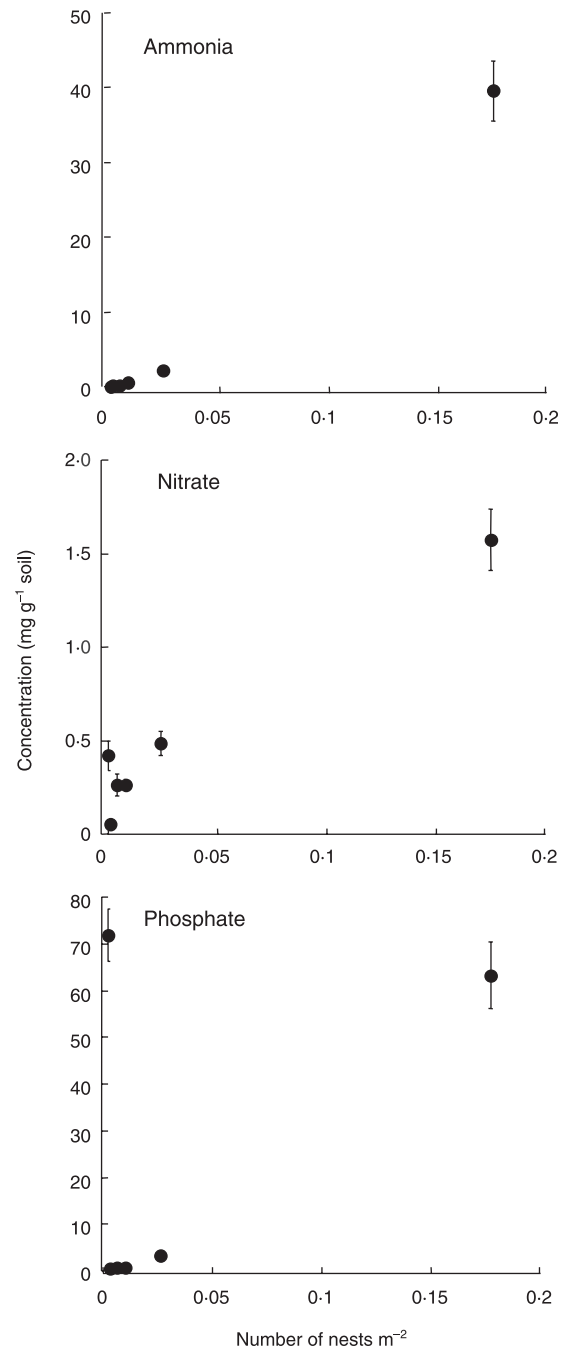


Fig. 2. Soil nutrient concentrations ($\text{mg g}^{-1} \pm 1 \text{ SE}$) of ammonia, nitrate and phosphate in the six colonies. Mean nutrient concentrations in soils from each colony are plotted against the mean density of nests (nests per m²) in each colony. See the text for detailed explanation of statistical analyses.

PLANT COMMUNITIES

Plants were present in all the colonies except the active cormorant colony (Table 2). The ordination analysis indicated that the three gull colonies with the lowest densities of birds formed a single group that was significantly different from the two cormorant colonies and the highest density gull colony (Fig. 3). These groupings corresponded with the ordination of soil ammonia concentrations on the x -axis and phosphate on the y -axis. There was good agreement among ammonia

Table 2. List of common plant species occurring in each colony in 2002–03

Islands Colonies	Appledore Gull	Smuttynose Gull	Lunging		Duck Gull
			Gull	Old Cormorant	
Plant species					
<i>Achillea millefolium</i> (P/F)	X		X	X	X
<i>Agropyron repens</i> (P/G)	X		X		X
<i>Ambrosia artemisiifolia</i> (A/F)	X	X	X	X	X*
<i>Aster novi-belgii</i> (P/F)					X
<i>Atriplex patula</i> (A/F)	X		X*	X	X
<i>Bromus tectorum</i> (A/G)	X	X			
<i>Capsella bursa-pastoris</i> (A/F)		X			
<i>Cerastium vulgatum</i> (P/F)			X		
<i>Chenopodium album</i> (A/F)	X		X	X	X*
<i>Elymus virginicus</i> (P/G)	X		X	X	X
<i>Festuca ovina</i> (P/G)	X*	X*	X*		
<i>Lepidium virginicum</i> (A/F)	X				
<i>Poa annua</i> (A/G)	X	X		X	X
<i>Poa palustris</i> (P/G)	X	X	X		
<i>Poa pratensis</i> (P/G)	X	X	X		
<i>Polygonum aviculare</i> (A/F)	X		X*	X*	X
<i>Polygonum persicaria</i> (A-P/F)	X				X
<i>Portulaca oleracea</i> (A/F)	X*	X*	X*		X*
<i>Raphanus raphanistrum</i> (A/F)	X*	X*	X*	X*	X*
<i>Rosa virginiana</i> (P/S)	X*	X*	X		X*
<i>Rubus idaeus</i> (P/S)	X				
<i>Rumex acetosella</i> (P/F)	X*	X*	X*		
<i>Rumex crispus</i> (P/F)			X	X	X
<i>Solanum dulcamara</i> (P/F)	X				
<i>Solanum americanum</i> (A/F)	X		X	X	X
<i>Solidago sempervirens</i> (P/F)				X	X
<i>Spergularia rubra</i> (A/F)	X*	X*		X*	
<i>Stellaria media</i> (A/F)	X	X	X	X*	X
Total number of species	23	13	18	13	17

Letters in parentheses next to species names indicate the life history of the plant – annual (A), perennial (P) – and whether the plant is a forb, grass or shrub (F,G,S). *Denotes a species was present in 2002.

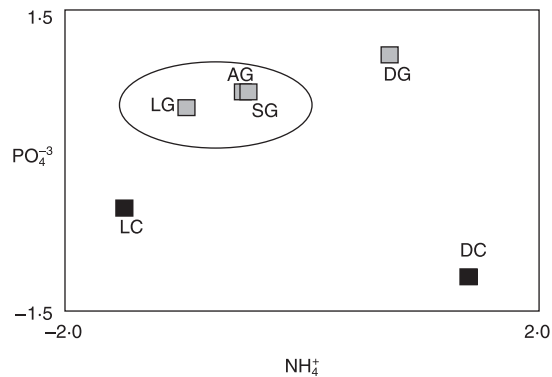


Fig. 3. Results from Multi-Dimensional Scaling (MDS) ordination analysis on a Bray–Curtis similarity matrix using the plant species lists from each colony. The three gull colonies with the lowest densities of birds (AG, SG, LG) formed a single group that was significantly different from the two cormorant colonies and the highest density gull colony (DG). These groupings corresponded with the ordination of soil concentrations of ammonia on the x -axis and phosphate on the y -axis. The cluster of lower-density gull colonies showed 55% similarity. The significance level of similarity among the groups was estimated using the distribution of Bray–Curtis similarity coefficients, calculated after bootstrapping the plant species composition matrix 1000 times.

and phosphate concentrations and plant species composition in the colonies.

The plant species lists showed dramatic differences in the occurrence of perennial grasses and annual forbs among the colonies (Table 2). In the lower-density gull colonies on Smuttynose, Appledore and Lunging islands, 22–28% of the species were perennial grasses and 43–46% were annual forbs. In the high-density gull colony on Duck Island, only 12% of species were perennial grasses and 47% were annual forbs; just one of the plant species was a perennial grass and over 60% were annual forbs in the abandoned cormorant colony. Unlike the gull colonies, there were no shrubs in the abandoned cormorant colony. We found a few species of plants occurring on the edge of the active cormorant colony on Duck Island. These plants were all annual forbs and included *Ambrosia artemisiifolia* L., *Stellaria media* (L.) Vill., *Polygonum aviculare* L., and *Spergularia rubra* (L.) J. & K. Pres *Stellaria media* was common in every colony (except the active cormorant colony) in both years.

PHYTOMETER EXPERIMENT

Germination of *B. rapa* was lower in soils from all colonies when compared with 100% germination rates

in the potting mix. Germination in active cormorant colonies (the highest density colony) was completely inhibited, and was also low in soils from the abandoned cormorant colony. Germination in soils from gull colonies was variable, but not as low as in the cormorant colonies. Overall, there was a significant relationship between rates of germination and soil nutrient concentrations ($R^2 = 0.364$, $F_{3,52} = 11.5$, $P < 0.001$; Fig. 4). The rates of germination were inversely correlated with concentrations of ammonia ($t = -2.87$, $P = 0.006$) and phosphate ($t = -4.32$, $P < 0.001$). In contrast, germination was positively correlated with nitrate concentrations, but the relationship was only marginally significant ($t = 2.02$, $P = 0.049$). Four species of 'native' forbs, *Spergularia rubra*, *Rumex acetosella* L., *Atriplex patula* L. and *Stellaria media* were the only plants that germinated in the experimental units. Following the same pattern observed with the phytometer, these four species appeared in the soils from every gull colony but were absent in soils from the active cormorant colony. In soils from the abandoned cormorant colony only *Atriplex patula* was observed.

ISOTOPIC ANALYSES

Leaves of most terrestrial plants show nitrogen isotope ratios ranging from about -8‰ to 3‰ (Peterson & Fry 1987). In this study, all the plant species growing in the colonies were enriched with $\delta^{15}\text{N}$ ($\geq 10\text{‰}$) (Fig. 5). Values of $\delta^{15}\text{N}$ were particularly high ($> 16\text{‰}$) in tissues of *Atriplex patula*, *Raphanus raphanistrum* L., *Spergularia rubra*, *Polygonum aviculare*, *Stellaria media*, *Rumex acetosella*, *Ambrosia artemisiifolia* and *Portulaca oleracea* L. All but one (*Rumex acetosella*) of these species are annuals. $\delta^{15}\text{N}$ ratios for the shrub, *Rosa virginiana* Mill., were lower than those of the majority of herbaceous species. Of the three species that occurred in both the gull colonies and the abandoned cormorant colony, *Spergularia rubra*, *Raphanus raphanistrum* and *Polygonum aviculare*, exhibited greater $\delta^{15}\text{N}$ enrichment in the abandoned cormorant colony (23–27‰) than in any of the gull colonies (c. 18–20‰).

The majority of plants exhibited $\delta^{13}\text{C}$ ratios that fall within the range typical for terrestrial C_3 plants (-27.8‰ on average; Peterson & Fry 1987); whereas, *Portulaca oleracea* showed ratios that are representative of C_4 or CAM plants (-13‰ on average). *Polygonum aviculare*, *Spergularia marina*, and to a lesser extent, *Raphanus raphanistrum* exhibited less $\delta^{13}\text{C}$ enrichment in the abandoned cormorant colony relative to the same species in the gull colonies.

Discussion

Our results show that concentrations of ammonia, nitrate and phosphate in soils increased with increasing densities of nests. The exception was the abandoned cormorant colony where nitrate and phosphate remained elevated due to nesting activity during the previous year

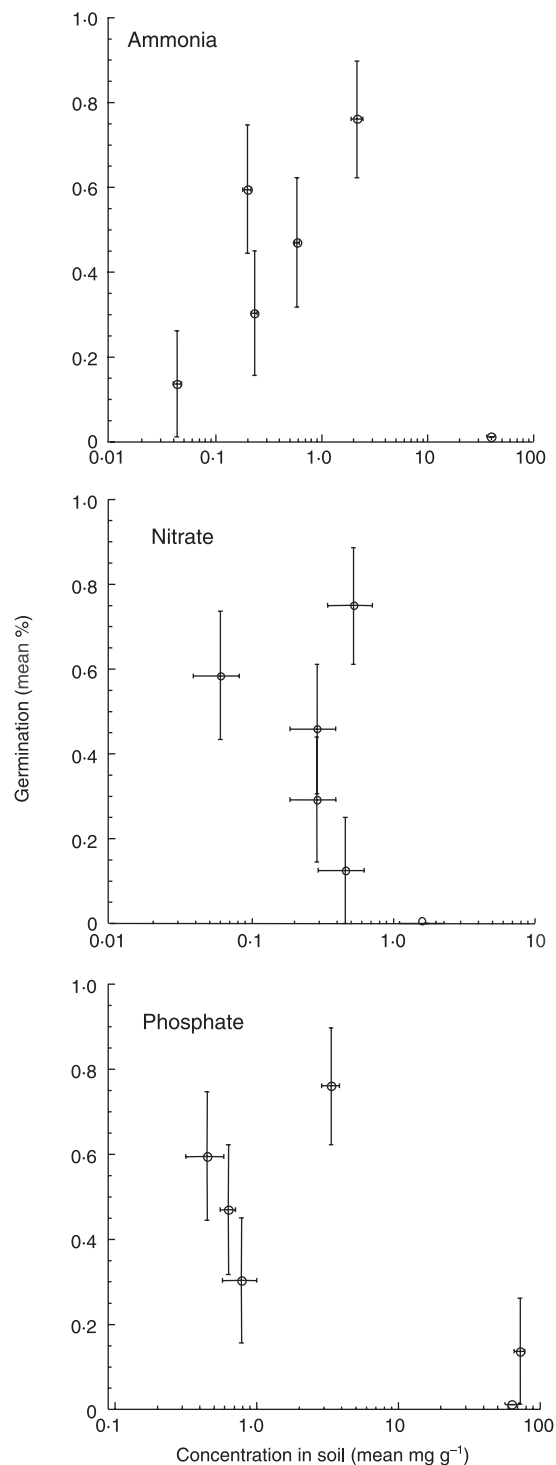


Fig. 4. Results from the phytometer experiment conducted using the annual forb, *Brassica rapa*. Data are the proportion of *B. rapa* seeds (of eight total) that germinated in soils collected from two cormorant and four gull colonies of various nest densities. The mean (± 1 SE) proportions of seeds that germinated in soils from each of the colonies are plotted against the mean concentration of three nutrients (ammonia, nitrate, phosphate) in the soils. See the text for detailed explanation of statistical analyses.

(see also Hogg & Morton 1983; Tatur 1989; Erskine *et al.* 1998). Analyses of plant species lists indicated that ammonia and phosphate were particularly important predictors of species composition in the colonies. The

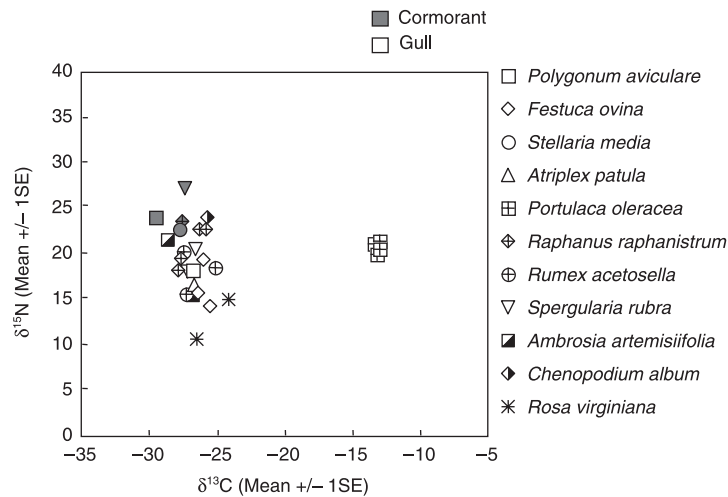


Fig. 5. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios found in leaves collected from plants in cormorant and gull colonies. Values of $\delta^{15}\text{N}$ for all species were higher than 10‰, indicating that plants used nitrogen derived from seabirds. All but one of the $\delta^{13}\text{C}$ values are typical of C_3 plants; one (*Portulaca oleracea*) is typical of C_4 species.

site with the highest density of nests, the active cormorant colony, was completely devoid of plants suggesting that nutrient concentrations at this site were toxic. In fact, the germination experiment showed that high concentrations of soil phosphate and ammonia were negatively correlated with germination of the phytometer, *B. rapa*, and 'native' plants. Some germination occurred in soils from the abandoned cormorant colony, where phosphate concentrations were very high, suggesting that ammonia was the main factor inhibiting plant germination in the active cormorant colony. Clearly, seabird nest density plays a substantial part in determining soil nutrient concentration and plant community composition.

Previous studies have demonstrated that high levels of ammonia in soils can negatively affect plants by inhibiting nitrate uptake (Boxman & Roelofs 1988), reducing cation uptake (VanDijk *et al.* 1989), increasing anion content of tissues (Errebhi & Wilcox 1990), and acidifying soils (Pearson & Stewart 1993). High levels of phosphate can also inhibit germination and growth of plants. In a study similar to this one, Mulder & Keall (2001) found that germination rates of the phytometer, *B. rapa*, were lower in soils taken from sites with high densities of burrowing reptiles and seabirds compared with soils collected from low-density areas. Soil phosphorus was positively related to nesting density and negatively related to phytometer growth. In our study, high concentrations of phosphate inhibited germination in the abandoned cormorant colony; whereas, high concentrations of ammonia appeared to prohibit germination in the active cormorant colony.

We found relatively more annual plant species in the abandoned cormorant colony compared with the gull colonies. Typically, annual and biennial species increase in seabird colonies and perennials decrease, particularly in areas of high nesting density (e.g. Sobey 1976; Smith 1978; Hogg & Morton 1983; Vidal *et al.* 1998; Garcia *et al.* 2002). In our study, densities were not elevated

in the abandoned cormorant colony, but nutrient concentrations were. High nutrient concentrations can be viewed as a form of severe disturbance that maintains plant communities in early successional stages. In fact, many of the species found in the abandoned cormorant colony and gull colonies are characterized as 'arable weeds' (Grime 1977) that are well-suited to persisting in highly productive, disturbed habitats.

The difference in density of nests between the active cormorant colony and the gull colonies was striking. In general, nesting densities of cormorants are much higher than those of the great black-backed gull *Larus marinus*. Distance between nests in *L. marinus* colonies ranges from: 4.7–5.6 m in Maine, USA (Butler & Trivelpiece 1981; McGill-Harelstad 1985; Ellis & Good 2006) to 30.9 m in small colonies in Sweden (Götmark 1982). Inter-nest distances in *Phalacrocorax auritus* are smaller and range from 0.6 to 2.0 m (Hatch & Weseloh 1999); densities can reach $> 1 \text{ nest m}^{-2}$ (Siegel-Causey & Hunt 1981). Our observations from other islands in the Gulf of Maine indicate that cormorants have considerable negative effects on vegetation (J.C.E., personal observation); studies from the Great Lakes have also documented negative effects of cormorants due to excessive guano deposition (Hatch & Weseloh 1999). Although cormorants nested more densely than did gulls in this study, gull colonies covered a much larger area. Therefore, the effects of gulls may be less extreme than those of cormorants, but affect a much larger area.

Our greenhouse experiment strongly suggested that excessive nutrients played a major part in killing plants in cormorant colonies. High nest densities could lead to excessive nutrient deposition as could other behavioural attributes of cormorants, including the use of guano to construct nests and excretion of large volumes of guano per bird around territories (Hutchinson 1950). Trampling and collecting plants for nest construction may also influence the magnitude of cormorant effects on plants.

Similarly, gulls can affect vegetation through trampling and plucking up plants in territorial disputes and during nest construction (Sobey & Kenworthy 1979; J.C. Ellis unpublished data). Interspecific variation in these behaviours and the consequences of such variation for vegetation warrant further study.

Plants in both gull and cormorant colonies showed enriched $\delta^{15}\text{N}$ signatures. Previous studies indicate that the $\delta^{15}\text{N}$ values for guano and body parts of gulls and penguins are near 10‰ (Mizutani, Hasegawa & Wada 1986; Mizutani & Wada 1988), but further fractionation occurs in soils resulting in even higher $\delta^{15}\text{N}$ values. Volatilization of ammonia from seabird guano is associated with a very high fractionation rate because the ammonia that is lost is isotopically lighter than that which remains in the soil (Mizutani *et al.* 1986). As a consequence, plants that use enriched nitrogen in the soil also exhibit elevated nitrogen isotope ratios in their tissues. The elevated $\delta^{15}\text{N}$ values in our study indicated that plants in seabird colonies assimilated guano-derived soluble nitrogen from the birds. Plants in the gull colonies in this study had similar $\delta^{15}\text{N}$ values to plants in gull rookeries in Japan: rape *Brassica campestris* had values of 14.4–18.3‰ and values for red fescue *Festuca rubra* were 11.8–21.5‰ (Mizutani & Wada 1988).

The three annual species that occurred in the abandoned cormorant colony and gull colonies (*Spergularia rubra*, *Raphanus raphanistrum*, and *Polygonum aviculare*) showed greater $\delta^{15}\text{N}$ enrichment in the former than in the latter. The abandoned cormorant colony had a thick layer of guano and decayed carcasses of birds from previous years. Such a large contribution of bird bodies and guano may have resulted in greater ammonia input and fractionation, thus increasing $\delta^{15}\text{N}$ enrichment. Also, *Larus marinus* eat marine invertebrates, fish and terrestrial sources of garbage (Good 1998; Rome & Ellis 2004; Ellis *et al.* 2005); whereas, *Phalacrocorax auritus* in the Isles of Shoals prey almost exclusively on fish (Borrer & Holmes 1990). Differences in prey affect the isotopic ratios of seabird tissues (Hobson 1987; Minami, Minagawa & Ogi 1995) and may influence the extent of nitrogen enrichment of plants. If cormorants eat prey that are at a higher trophic level (e.g. fish) than do gulls (e.g. garbage), then plants in abandoned cormorant colonies could show relatively greater $\delta^{15}\text{N}$ enrichment.

The $\delta^{13}\text{C}$ values for the shrub, *Rosa virginiana*, and the perennial grass, *Festuca ovina* L. tended to be larger than those for the annuals. Other studies indicate that long-lived species generally have higher $\delta^{13}\text{C}$ than shorter-lived species (Schuster *et al.* 1992). $\delta^{13}\text{C}$ values for plants in the abandoned cormorant colony were more negative than those for the same species taken from the gull colonies. A more negative $\delta^{13}\text{C}$ value in leaves may indicate lower intrinsic water-use efficiency (WUE) (Ehleringer & Cooper 1988). Water use efficiency is affected by nutrient and water availability; increased water availability decreases WUE. Soil moisture was generally greater in the cormorant colonies compared

with the gull colonies (authors, unpublished data). Variation in water availability among colonies may have contributed to the observed differences in $\delta^{13}\text{C}$ values of plants.

Conclusions

Transport of resources across habitat boundaries can cause significant changes in the structure and composition of communities and ecosystems (Polis *et al.* 1997). Such resources are most likely to benefit ecosystems when added at low to moderate levels, but at high levels can be detrimental (e.g. Sanchez-Piñero & Polis 2000). Our study indicates that nesting densities and potentially the unique characteristics of biotic vectors can determine whether transported resources are beneficial or detrimental to recipient habitats. Thus, effects of nesting density and species-specific variation in resource transport should be considered when predicting the impact of biogenic vectors of allochthonous resources.

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