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Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies

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Abstract

Seabirds are chemical and physical engineers that are capable of transforming terrestrial vegetation by altering edaphic conditions, generating physical disturbance, and affecting seed dispersal. Substantial changes in seabird populations are occurring worldwide and are likely to have important consequences for plant community composition on islands and coastal areas. This review focuses on the impact of seabirds on plant biomass, species richness and community composition. A total of 57 publications (42 studies) were selected for review. Of the 42 studies represented in the publications, 55% were descriptive. Most studies took place in Australia, New Zealand, the British Isles, Japan, North America, and sub-Antarctic islands. A few studies showed that aboveground plant biomass in seabird colonies increased with sufficient rainfall and moderate temperatures. The majority of studies on plant species richness showed a decrease in seabird colonies compared to areas unaffected by birds. However, species richness was higher in areas of intermediate seabird disturbance, compared to undisturbed areas. Moreover, the effects of seabirds on species richness varied with respect to island size. Most studies of plant community composition indicated that annuals, 'ruderals", and cosmopolitan species increased in abundance in seabird colonies. Changes in plant communities in seabird colonies appear to result mainly from altered soil nutrient concentrations and pH, increased physical disturbance, and seed dispersal by seabirds and humans. However, few studies have rigorously studied the relative importance of these alterations. Both the direction and magnitude of seabird effects are modified by: (1) density of birds, (2) temperature and precipitation, and (3) proximity to human habitation. A reduction in seabird populations is likely to have negative consequences for native plant species that rely on seabird disturbance for their persistence. However, seed dispersal by nesting seabirds, especially gulls, frequently leads to invasion by cosmopolitan plant species and declines of native species. Further studies that incorporate both quantitative sampling and manipulative experiments would go a long way in improving our understanding of how seabirds affect plant communities.

Introduction

Organisms that modify the availability of soil resources and create physical disturbances can have profound effects on terrestrial ecosystems (e.g. Aho et al. 1998; Reichman and Seabloom 2002). Recently, seabirds have attracted much interest because of their capacity to introduce large amounts of marine-derived nutrients to land, thereby altering resource availability to terrestrial species (e.g. Anderson and Polis 1999; Mulder and Keall 2001; Vidal et al. 2003). The activities of nesting seabirds can change several important factors that impact plants including resource availability, disturbance, and seed dispersal. Through foraging in marine habitats and breeding on land, seabirds deposit prey remains, carcasses, feathers, eggshells, and guano in terrestrial systems (e.g. Burger et al. 1978; Polis and Hurd 1996). Seabirds also generate a considerable amount of physical disturbance through their nesting activities (e.g. Gillham 1956a, 1960a, b; Sobey and Kenworthy 1979). Burrowing as well as activities that directly damage plant tissues (trampling, uprooting and pulling leaves off plants) may play a large role in plant community dynamics in and around colonies. Several studies have shown that seabirds can be important agents of seed dispersal (e.g. Morton and Hogg 1989; Magnusson and Magnusson 2000), thereby influencing plant recruitment.

Seabirds frequently nest on offshore islands where there is a combination of suitable habitat (Ricklefs 1990), and an absence of predators and human disturbance (e.g. Burger and Gochfeld 1993). Seabird populations have fluctuated dramatically worldwide: the introduction of cats and rats to many islands, for example, has led to substantial declines in populations of several species (e.g. Monteiro et al. 1996; Rocamora et al. 2003; Towns and Broome 2003). Conversely, demographic explosions of some seabirds (especially gulls) have also occurred, leading to concern about their detrimental effects on native plant communities and other seabird species (Vidal et al. 2000 Finney et al. 2003). Islands are important sources of endemism (Steadman 1995), and island floras in particular are becoming increasingly homogenized as a consequence of the establishment of nonnative species around the world (Vitousek et al. 1996; Sax et al. 2002). Substantial changes in seabird populations may have important consequences for plant community composition on islands and coastal areas in general.

Seabirds have varying and sometimes opposing effects on plant community structure and ecosystem dynamics. At the community level, they can either dramatically decrease the abundance of native species (e.g. Hogg and Morton 1983; Vidal et al. 1998a, b), or contribute to persistence of rare native species (e.g. Dean et al. 1994; Norton et al. 1997). At the ecosystem level, they can either increase (e.g. Polis et al. 1997; Anderson and Polis 1999) or decrease primary productivity (e.g. Wace 1961). Although numerous studies have noted unique plant communities in seabird colonies, few have quantified these patterns and even fewer have conducted manipulative field experiments to elucidate the underlying mechanisms. The overarching goal of this review is to survey the existing literature in order to assess the magnitude and variability of seabird effects on terrestrial plant biomass, species richness, and community composition. The specific objectives of the review are: (1) to describe the existing literature on the topic, (2) to summarize the results of these studies, (3) identify the major factors that alter the direction and magnitude of seabird impacts on plants, and (4) identify key areas requiring further study.

Methods

Three search techniques were used to locate studies that describe seabird effects in terrestrial systems. First, I searched the Web of Science for articles published between January 1988 and August 2004, using the keyword 'seabird'' and the following search strings: 'seabird AND terrestrial'', 'seabird AND plant'', 'seabird AND nutrient'', 'bird AND guano'', and 'seabird AND disturbance.'' Using the same search strings in JSTOR, I searched the full text of all articles published in American Midland Naturalist (1909–2001), American Naturalist (1867–1999), Annual Review of Ecology and Systematics (1970–1999), Biodiversity Letters (1993–1996), Biotropica (1969–1999), Conservation Biology (1987–2001), Diversity and Distributions (1998–2001), Ecological Applications (1991–2000), Ecological Monographs (1931–2000), Ecology (1920–2000), Evolution (1947–2001), Global Ecology and Biogeography (1999–2001), Global Ecology and Biogeography Letters (1991–1998), Journal of Animal Ecology (1932–2001), Journal of Applied Ecology (1964–2001), Journal of Ecology (1913–2001), Journal of Biogeography (1974–2001), Journal of Tropical Ecology (1905–1999), and Quarterly Review of Biology (1926–2001). Finally, I surveyed the citations of published articles to locate papers not included in the electronic databases. Studies were restricted to those written in English or with English summaries. This should not be considered a complete collection, as mention of plant communities associated with nesting seabirds may occur in studies that were not selected using the keywords and searches employed.

Studies were restricted to those that examined one or more of the following variables related to plant assemblages: (1) plant cover or biomass, (2) species richness, (3) relative abundance of indigenous and cosmopolitan species, (4) relative abundance of various life histories (e.g. annuals, perennials). I read the full text or summary (if full text was not written in English) of these publications and categorized each study as: (1) qualitative description, (2) quantitative description, (3) natural experiment, and/or (4) manipulative experiment. Qualitative descriptions are studies in which the authors provide descriptions and/or lists of plant species associated with seabirds. In quantitative descriptions, the authors measure some variable associated with plants in seabird colonies (e.g. percentage cover, frequency of occurrence, or plant height). Natural experiments are studies in which the authors choose sites with and without nesting birds, or along a density gradient of nesting birds, and measure the responses of plants to these ‘treatments.’ Field manipulations take place in or around seabird colonies and involve manipulation of an environmental factor for the purpose of investigating the influence of seabirds on plants. Examples of field manipulations include: exclusion of seabirds via cages (Maesako 1999) and planting seeds inside and outside of colonies then recording the proportion that germinated in both areas (Ishida 1997). Greenhouse experiments may involve removing plants from the field and transplanting them to a greenhouse (e.g. Ornduff 1965), or using a single plant species to indicate edaphic conditions of soils from seabird colonies (‘phytometer experiments’ (e.g. Mulder and Keall 2001)).

All studies included in this review involved colonially nesting seabirds, which is the most common mode of breeding in this group of birds (Gill 1995). ‘Seabird” is a catch-all term primarily applied to species in the following orders: Sphenisciformes (penguins), Procellariiformes (albatrosses, petrels, shearwaters, storm-petrels, and diving-petrels), Pelecaniformes (pelicans, boobies, cormorants, frigatebirds, tropic birds, anhingas), Charadriiformes (shorebirds, skuas, gulls, terns, skimmers, auks). I restricted the review to studies of these four orders of birds because: (1) they are the most common groups that breed colonially on coasts and offshore islands, and (2) the vast majority of studies consider these groups.

In order to compare the effects of seabirds on plants, I categorized the results of the studies into the following groups: (1) estimates of aboveground biomass or plant cover, (2) quantification of species richness, and (3) quantification of community composition (including relative abundances of cosmopolitan and indigenous species and life histories). For each group, I restricted the Results to only those studies that used quantitative methods.

Results

A total of 57 publications fit the criteria for review. When publications were grouped by study (more than one publication could be generated from one study site/system) there were a total of 42 studies. Of these, 9 (21.4%) were qualitative descriptions, 14 (33.3%) used quantitative description, 12 (28.6%) were natural experiments, 5 (11.9%) used experimental manipulation in the field, and 3 (7.1%) used greenhouse experiments (Table 1). 55% of all studies were descriptive. The majority of studies focused on description (qualitative or quantitative) of the plant communities associated with seabird colonies. The studies covered a wide spread of geographical locations but most studies took place in Australia, New Zealand, the British Isles, Japan, North America, and islands in the sub-Antarctic.

Aboveground biomass or cover

Although many studies noted dramatic effects of seabirds on growth, cover, or height of plants, I only found three studies that quantified these patterns. Two of them took place on cool, wet, sub-Antarctic islands and demonstrated that aboveground biomass was greater in areas influenced by seabirds compared to areas without birds, except where densities of birds were

Table 1. Studies of terrestrial plants associated with seabird colonies.

List	Location(s)	Response variables	Reference(s)
Qualitative description			
1	Western Australia	*C*	Gillham (1961a)
2	Macquarie Island, subantarctic	*C*	Gillham (1961b)
3	Gulf of Maine, Maine, USA, Bay of Fundy, Canada	*C*	Hodgdon and Pike (1969)
4	Penikese Island, Massachusetts, USA	*C*	Lauermann and Burk (1976)
5	Akpatok Island, Ungava Bay, Quebec, Canada	*C*	Polunin (1935)
6	Jan Mayen Island, Greenland Sea Norway	*C*	Russell and Wellington (1940) Russell et al. (1940)
7	Spitsbergen Archipelago, Norway	*C*	Summerhayes and Elton (1928)
8	Coastal New Zealand	*A*	Norton et al. (1997)
9	Ailsa Craig, Firth of Clyde Scotland	*C*	Vevers (1936)
Quantitative description			
10	Langebaan Islands, South Africa	*C*	Gillham (1963)
11	Chaunskaya lowlands, Russia	*C*, *P*	Zelenskaya (1995)
12	Pembrokeshire Islands, Wales, UK	*C*	Gillham (1953, 1956a, b)
13	New Zealand	*C*	Gillham (1960a, b)
14	South Stack, Isle of Anglesey Wales, UK	*C*	Goldsmith (1973)
15	Shetland Islands, British Isles	*C*	Goldsmith (1975)
16	Carnac Island, western Australia	*C*	Abbott et al. (2000)
17	Iberian Peninsula, Spain	*D*	Calvino-Cancela (2002)
18	Adabra Atoll, Seychelles	*C*	Gillham (1977)
19	'Los Islotes', Canary Islands, Spain	*D*	Nogales et al. (2001)
20	New Zealand	*C*	Gillham (1960a, b)
21	Gough Island, South Atlantic Ocean, Britain	*C*	Wace (1961)
22	Great Barrier Reef, Australia	*D*	Heatwole and Walker (1989)
23	Kent Island Group, New Brunswick, Canada	*C*	McCain (1975)
Natural experiment			
24	Chafarinas Islands, Mediterranean Sea, Spain	*A*	Garcia et al. (2002)
25	Ile de la Possession, Crozet Archipelago South Indian Ocean	*C*	Joly et al. (1987)
26	Great Dog, Little Dog, Little Green Japan	*C*	Kamijo and Hoshino (1995)
27	Gulf of California, Mexico	*P*	Polis et al. (1997) Anderson and Polis (1999) Sanchez-Piñero and Polis (2000)
28	Riou archipelago, Mediterranean Sea, France	*C*	Vidal et al. (1998a, b, 2000)
29	Ile de la Possession, Crozet Archipelago, South Indian Ocean	*C*	Vidal et al. (2003)
30	South Manitou Island, Lake Michigan, USA	*A*	Shugart (1976)
31	Surtsey Island, Iceland	*C*	Magnusson and Magnusson (2000)
32	Georgian Bay and Lake Huron, Great Lakes, Canada	*C*	Hogg and Morton (1983) Morton and Hogg (1989) Hogg et al. (1989)
33	Victoria, Australia	*C*	Gillham (1960a, b)
34	coastal Japan	*C*	Ishizuka (1966)
35	Cape Queen Elizabeth, Tasmania	*C*	Walsh et al. (1997)
Natural experiment and Field Manipulation			
36	Inaccessible and Nightingale Islands, South Atlantic Ocean	*C*	Dean et al. (1994)
37	Unoyama, central Japan	*A*	Ishida (1996, 1997)
Quantitative description and Field Manipulation			
38	Kanmurijima Island, Japan	*C*	Maesako (1985); Maesako (1999)
39	Marion Island, South Atlantic Ocean	*C*, *P*	Smith (1976a, b, 1978) Smith and Steenkamp (2001) Smith et al. (2001)
Natural experiment and Field Manipulation and Greenhouse experiment			
40	Aberdeenshire coast, Isle of May, Firth of Forth, Scotland	*C*	Sobey (1976) Sobey and Kenworthy (1979)

Table 1. Continued.

List	Location(s)	Response variables	Reference(s)
Natural experiment and Greenhouse experiment			
41	Stephens Island, New Zealand	*A*	Mulder and Keall (2001)
Greenhouse experiment only			
42	New Zealand	*G*	Ornduff (1965)

Studies are categorized as either: qualitative description, quantitative description, natural experiment, greenhouse experiment, or field manipulation. See the *Methods* section of the text for definitions of the various types of studies. C = community composition, A = abundance and distribution of certain species, D = dispersal of seeds, G = genetic differentiation, P = estimates of productivity (growth, height, cover, biomass).

extremely high (Smith 1976b; Joly et al. 1987). Studies conducted on arid islands in the Gulf of California, Mexico compared biomass and cover of annual plants on islands with nesting, roosting, or no seabirds (Polis et al. 1997; Anderson and Polis 1999; Sanchez-Piñero and Polis 2000). Results from these studies showed that biomass and cover of annuals increased dramatically on seabird islands in wet years; biomass increased as much as 11.8-fold (Anderson and Polis 1999). However, in dry years, cover of plants was lower on all islands, but even lower on seabird roosting islands than on islands without birds because high rates of soil evaporation combined with large amounts of guano created soil conditions that were toxic to plants (Sanchez-Piñero and Polis 2000).

Species richness

Twelve studies quantified differences in plant species richness between seabird colonies and unaffected control areas (Table 2). Collection and presentation of data on species richness varied substantially among studies. Of the 12 studies, six (50%) of them indicated that the number of plant species was lower in areas affected by seabirds compared to unaffected areas. Of these studies two used statistical comparisons and found significantly fewer species in areas with high densities of nesting birds compared to areas without birds (Kamijo and Hoshino 1995; Ishida 1996). Overall, there were between 5.7 and 146 fewer species in seabird colonies; the median difference was 12.

Two of the 12 total studies found more species of plants in seabird colonies. Species richness in permanent plots on Surtsey Island was higher in a gull (Charadriiformes) colony compared to outside (Magnusson and Magnusson 2000). Surtsey Island is different from most other sites because it is undergoing succession after a volcanic eruption, and areas within gull colonies showed much faster rates of succession due to the introduction of herbaceous plant seeds via gulls, which forage in grasslands and hayfields in coastal areas. Zelenskaya (1995) also found slightly greater species richness on islands in maritime tundra lakes with gull nests compared to surrounding areas without gulls; however, the mechanism promoting this difference was unclear.

Two of the 12 studies indicated that plant species richness was greater at intermediate levels of seabird disturbance (ie. trampling and nutrient input). Hogg and Morton (1983) found that species richness was greater in undisturbed grasslands compared to an active gull colony (Table 2). However, in the second year of the study, there were more plant species in an abandoned gull colony compared to undisturbed grassland. The abandoned colony represented an intermediate level of disturbance where some nutrients were still elevated, but trampling was absent. Similarly, Vidal et al. (2003) found lower species richness near and far from an active penguin (Sphenisciformes) colony, but more species at intermediate distances; this non-linear relationship was statistically significant. At intermediate distances, nutrient levels were elevated, but trampling was much less severe.

Species richness also varied with respect to island size. Hogg et al. (1989) found a significantly greater species-area slope on islands with nesting gulls compared to islands with very few or no gulls. Small islands with gulls had fewer plant

Table 2. Studies that quantitatively compared the number of plant species in areas affected by seabirds and unaffected 'controls'.

Reference; type of study	Seabirds	No seabirds	Difference (seabirds − no seabirds)
Gillham (1960a, b), 1,H	166	312	−146
[a]Ishida (1996), 4,W (10 m × 10 m quadrat)	4.5	12	−7.5
	1.69	2.92 (H′)	−1.23 (H′)
Ishizuka (1966), 4,H (2 m × 2 m quadrat)	3.5	9.2	− 5.7
Joly et al. (1987), 5,H	0 to 4 (high density)	> 15 (none)	−15 (high vs. none)
	5–10 (intermediate)		
	11–15 (low)		
Kamijo and Hoshino (1995), 3,H	3 (high density)	36 (none)	−33 (high vs. none)
	10 (intermediate)		
	23 (low)		
Sobey and Kenworthy (1979), 1,H	41	50	−9
[b]Hogg and Morton (1983), 4,H	17 (active colony)	28 (undisturbed)	−9
(15 m × 30 m quadrat)	48 (abandoned 2 yrs)	28 (undisturbed)	+20
[c]Hogg et al. (1988), 2,H,W	184	122	+62 (larger islands)
	63.2	76.1	−12.9 (small islands)
[d]Vidal et al. (1998a, b), 2,H	155 (large islands)	172	−17
	60 (small islands)	49	+11
Vidal et al. (2003), 3,H	1–4 (near colony)	4 (far from colony)	0 to −3
	1–4 (near)	9 (intermediate distance)	−5 to −8
Magnusson and Magnusson (2000), 3,H	15	9	+6
Zelenskaya (1995), 1,H	24	21	+3

Data are the number of plant species occurring in the two types of areas and the difference in number of species between them. Studies presented the following types of data: (1) the total number of species summed across multiple sites of unknown area, (2) the number of species present on each of multiple islands of known area, (3) the total number of species summed across multiple quadrats of known area (4) the total or average number of species per quadrat of known area, or (5) a range of the total number of species occurring in various vegetation types within a site. Each data type is indicated after every reference. For studies that took an average or total number of species per quadrat, the size of the quadrat is given. W = woody species (trees or shrubs), H = herbaceous vegetation.

[a] These data are tree seedlings and saplings; the authors also calculated species diversity (H′).

[b] In this study, three permanent plots were sampled over two years. See Results section for explanation of sampling design.

[c] I took the difference between the average number of species occurring on 'larger' islands (> 10 ha and < 40 ha) with and without nesting gulls to generate the first value. The second value is the difference between the average number of species found on the 'small' (≤10 ha) gull and non-gull islands.

[d] These values are the average number of species on the three 'islets' and the average for the two 'large' islands. The difference is between the same islands before and after a large increase in seabirds.

species than small islands without gulls because they were low in elevation and were often covered by water during storms, so had very little vegetation irrespective of gull disturbance. On larger islands gull colonies created an additional, unique habitat for plants thus increasing habitat heterogeneity. Thus, larger islands with gulls had more plant species than larger islands without gulls. In contrast, Vidal et al. (1998a, 2000) found that plant species richness increased on small islands, but decreased on large ones after a substantial increase in nesting gulls on the islands. This difference was attributed to the fact that small islands are generally more vulnerable to disturbance, and therefore more prone to invasion by additional plant species.

Community composition (abundance of various life histories and cosmopolitan vs. indigenous species)

There were seven studies that quantified the number of native and cosmopolitan plant species associated with nesting seabirds (Table 3). Three of these studies found a greater proportion of cosmopolitan species in or near active colonies compared to undisturbed areas (Hogg and Morton 1983; Hogg et al. 1989; Vidal et al. 2003). Vidal et al. (2003) also found that the proportion of cosmopolitan species further increased in colonies that were near a scientific station. Two of the seven total studies presented the proportion of cosmopolitan species present in seabird colonies, but did not compare them to undisturbed areas (Table 3).

Table 3. Relative abundance of cosmopolitan plant species associated with seabird colonies.

Reference	Seabirds	No seabirds
Hogg and Morton (1983); H	82% (active colony) 75%, 61% (abandoned 1 year; Plots 1 and 2) 73% (abandoned 2 years; Plot 2)	3.6% (undisturbed Plot 3)
Hogg et al. (1989); W,H	24.1% (small gull islands)	9.8% (small non-gull islands)
Vidal et al. (2003); H	58, 46.2 and 41.8% in penguin colonies with increasing distance from a scientific station	NA[a]
Dean et al. (1994); H	3 (albatross nests)	7, 11, 20 (e.g., footpaths, landslides, old settlements)
[b]Kamijo and Hoshino (1995); H	0% (high density) 50% (intermediate) 48% (low)	47% (none)
Gillham (1960a); W	33% (ground-nesting shags) 56% (scrub-nesting shags) 23% (tree-nesting shags) 31.8% (all colonies)	NA
Gillham (1963); H	64.3, 71.4, 76.9, 80, 100% (on guano islands)	NA

Six of the studies presented a proportion (%) of cosmopolitan species out of the total number of species and one study (Dean et al. 1994) presented numbers rather than proportions. W = woody species (trees and shrubs), H = herbaceous vegetation.
[a] In this study, data were presented on the proportion of cosmopolitan species among the three colonies, but not within each colony.
[b] Percentages include both annuals and cosmopolitan species.

Gillham (1960a; 1963) found that between 23 and 100% of plant species in seabird colonies were cosmopolitan. In scrub-nesting shag colonies, there were relatively more cosmopolitan species because there were gulls in the vicinity that dispersed seeds of these species.

Two of the seven studies found that native species were comparatively more abundant in seabird colonies. (Kamijo and Hoshino 1995) found that the native tussock grass, *Poa labillardieri* was more abundant than cosmopolitan species in areas heavily burrowed by shearwaters (Procellariiformes) because it was one of the only species that could tolerate intense burrowing due to its deep, dense root system that stabilizes it. Similarly, Dean et al. (1994) found more native seedlings on small disturbances created by albatross (Procellariformes) nests compared to larger disturbances. Germination of certain native annuals was dependent on bare patches created by albatross nests; whereas, cosmopolitan annuals rapidly colonized larger disturbances, which tended to occur in lowland areas where there was greater human activity (and thus, a source for cosmopolitan seeds).

Seven studies compared the relative abundance of annual species in seabird colonies (Table 4). Five of these studies (71%) found a greater abundance of annuals in seabird colonies compared to undisturbed areas. Of these studies one used statistical comparisons and found significantly more annuals on islands with gulls compared to islands without them (Hogg et al. 1989). Overall, these studies found between 10 and 96% more annuals in seabird colonies; the median difference was 18%. One of the seven studies found fewer annuals at high densities of seabird burrows compared to intermediate densities (Kamijo and Hoshino 1995); a perennial grass was better at withstanding burrowing than were annual species. Gillham (1963) found between 70 and 100% of all plant species in seabird colonies were annuals; there was no quantitative comparison to the proportion of annuals in undisturbed areas.

In general, numerous descriptive and quantitative studies indicate that the disturbance generated by seabirds maintains plant communities in early stages of succession. Woody species are often damaged or killed in colonies (e.g., Shugart 1976; Maesako 1999) and then replaced by herbaceous ruderals (i.e., fast growing herbs with abundant seed production that often have biennial or annual life cycles (Grime 1977)). For instance, native woody vegetation in arid and semi-arid sites of South Africa, Australia, and Tasmania changes to herbaceous succulents (e.g., *Tetragonia* spp., *Carpobrotus rossii*), xeromorphic grasslands, or in areas of heavy seabird disturbance, halophytic

Table 4. Relative abundance of annual plant species in seabird colonies expressed either as a percentage of the total number of species or as an absolute number.

Reference	Seabirds	No seabirds	Difference (seabirds − no seabirds)
Gillham (1960b)	32.3%	14.4%	+17.9%
Hogg and Morton (1983)[a]	65% (active colony; Plot 1) 59% (abandoned 1 yr; Plot 1) 48–44% (abandoned 1 and 2 yrs; Plot 2)	17.9% (undisturbed area; Plot 3)	+47.1% (active vs. undisturbed)
Hogg et al. (1989)	16% (small gull islands)	6.3% (small non-gull islands)	+9.7
Ishizuka (1966)	10–100%	0–3.7%	+10–96.3%
Sobey and Kenworthy (1979)	11	0	+11
[b]Kamijo and Hoshino (1995)	33% (high density) 50%(intermediate) 39% (low)	33% (none)	0% (high vs. none) + 17% (intermediate vs. none)
Gillham (1963)	70–100%	NA	NA

[a] Includes both annual and biennial species. [b] Percentages include both annuals and cosmopolitan species.

annuals such as *Portulaca oleracea* and *Atriplex hastata* (e.g., Gillham 1960a, b; Kamijo and Hoshinobu 1995; Walsh et al. 1997). Tussock grasslands are also typical of seabird colonies on sub-Antarctic islands, and with heavy disturbance mat and rosette dicots (e.g., *Callitriche antarctica*, *Cotula plumosa*) and annuals are dominant (e.g., Smith 1978; Smith et al. 2001; Vidal et al. 2003). Similarly, at Arctic sites, heaths, sedges, and willows switch to grasses and certain 'nitrophilous' herbs (e.g., Summerhayes and Elton 1928; Russell and Wellington 1940). In Great Britain and North America, vegetation changes from trees, shrubs and perennial grasses (e.g., *Festuca rubra*, *Poa pratensis*) to ruderal perennials and biennials (e.g., *Rumex acetosella*, *Silene maritima*) and halophytic and/or nitrophilous annuals (Gillham 1956a, b, 1975; Hogg and Morton 1983).

Studies of mechanisms underlying vegetation patterns

Several of the studies in this review suggested that seabirds alter vegetation primarily through their effects on soils (e.g. Summerhayes and Elton 1928; Russell and Wellington 1940; Gillham 1961a, b, however only a few studies measured these effects (Table 5). The vast majority of these studies compared edaphic conditions between seabird colonies and control areas, and a handful used field or greenhouse experiments to directly test the effects of edaphic changes on vegetation (Smith 1978; Sobey and Kenworthy 1979; Ishida 1997; Mulder and Keall 2001). Most of the research focused on concentrations of nitrogen, phosphorus, and/or pH (Table 5). Of the 10 studies that compared concentrations of nitrogen (ammonium and nitrate in particular) and/or phosphorus (total phosphorus and phosphate) between seabird colonies and control areas, 100% of them found greater concentrations in seabird colonies. Other nutrients that tended to increase in colonies were potassium, magnesium, and salts.

Effects of seabirds on soil pH were variable (Table 5). Five studies found a decrease in pH in seabird colonies (see also Ward 1961; Blakemore and Gibbs 1968), two showed no change in pH, and one found that pH increased with guano deposition but only in the absence of sea spray. Although guano is typically alkaline (e.g. Gillham 1956b; Blakemore and Gibbs 1968), the process of guano decomposition in the soil often results in increased soil acidity (Ward 1961; Blakemore and Gibbs 1968). However, Gillham (1956b) suggested the sea spray may confound this effect, and the combination of guano and sea spray can increase soil pH, mainly due to the effects of sea spray.

A few studies measured soil moisture and water-retention capacity; results from these studies were

Table 5. Mechanisms that were investigated in studies of seabird effects on vegetation.

Mechanisms	Quantitative studies	Increased	Decreased	No to very little change
Altered soil characteristics				
pH	1,2,5,6,7,9,12,15	5[a]	1,2,9,12,15	6,7
Nitrogen	1,2,5,7,8,9,11,12,18	1,2,5,7,8,9,11,18		12[b]
Phosphorus	2,5,7,8,9,11,12,16,18	2,5,7,8,9,11,12,16,18		
Potassium	2,7,8,9	2,7,8,9		
Magnesium	2,7,8,9	2,8,9		7
Calcium	2,5,7,8,9	2,7,8	9	5
Carbon (organic and/or total)	1,8,9	1,8	9	
Heavy metals (Zn, Fe, Mn, Cu)	8	8		
Total salts	2,7,8,9,17	2,7,8,9,17		
Water retaining capacity	5,8,15	8	5,15	
Soil moisture	6,7,9,12,16	6	9,16	7,12
Soil depth/litter accumulation	6,7,12	6,12		7
Organic matter	7,8	8		7
Other mechanisms				
Adhesion of guano to seedlings	6			
Seed dispersal	2,3,4,5			
Trampling; nest building	7,10,13,14			

Each mechanism is listed along with the studies that quantified it. The direction (increase, decrease, no to little change) of edaphic changes caused by seabirds are also indicated.

[1] Magnusson and Magnusson (2000), [2] Hogg and Morton (1983), Morton and Hogg (1989), [3] Nogales et al. (2001), [4] Calvino-Cancela (2002), [5] Gillham (1956b), [6] Ishida (1997), [7] Sobey and Kenworthy (1979), [8] Garcia et al. (2002), [9] Smith (1976a, b, 1978, 2003); Smith et al. (2001), [10] Vidal et al. (2003), [11] Anderson and Polis (1999), Piñero and Polis (2000), [12] Mulder and Keall (2001), [13] Dean et al. (1994), [14] Maesako (1999), [15] McCain (1975), [16] Walsh et al. (1997), [17] Goldsmith (1973), [18] Ishizuka (1966).

[a] Only when guano deposition was independent of sea salt input.

[b] In this study, N content of the soils was high, but was not correlated with guano deposition or burrow density.

also highly variable. Ishida (1997) and McCain (1975) found higher soil moisture in gull colonies, but did not give a mechanistic explanation for the increase. Walsh et al. (1997) and Smith (1976a, b) found relatively low soil moisture in areas heavily burrowed by seabirds, however, it is unclear whether the burrowing dried the soils, or whether birds prefer to burrow in dry soils. Garcia et al. (2002) found greater water-retention capacity in soils from gull colonies due to greater amounts of soil organic matter (from the birds) present in colonies. In contrast, Gillham (1956b) found that soils in seabird colonies had lower water retaining capacity and inferred that the organic matter from guano was less effective in retaining water compared to organic matter derived from plants. Mulder and Keall (2001) and Sobey and Kenworthy (1979) found no difference in soil moisture in colonies of burrowing procellarids and gulls, respectively.

A handful of studies demonstrated that factors other than edaphic ones contribute to changes in vegetation of seabird colonies. Four studies showed that gulls are effective agents of seed dispersal; these studies found viable seeds in pellets and feces of gulls (Gillham 1956b; Morton and Hogg 1989; Nogales et al. 2001; Calvino-Cancela 2002). Two studies simulated trampling by using either herbicide or cutting aboveground vegetation and found that physical disturbance played a substantial role in vegetation dynamics in colonies (Sobey and Kenworthy 1979; Dean et al. 1994). Maesako (1999) was the only study that used an exclusion experiment to test for effects of trampling on tree seedlings; trampling resulted in increased damage and mortality of seedlings. Vidal et al. (2003) estimated the degree of trampling, guano deposition and distance from the edge of the colony in a multivariate analysis and found that all three factors were important determinants of plant community composition. Finally, Ishida (1997) inferred from a field experiment that adhesion of guano to plant leaves inhibits photosynthesis and thus reduces growth and survival of tree seedlings and saplings.

Discussion

The evidence provided by the studies in this review indicates that nesting seabirds can have substantial effects on aboveground biomass of plants, species richness, and community composition. Although there are relatively few quantitative studies of seabird impacts on plant biomass, the results demonstrate a considerable effect on vegetation in arid and sub-Antarctic sites. Plant species richness typically declined within colonies, but also varied with the degree of seabird disturbance and with island size. Although seabirds influenced patterns of species richness, their effects on community composition may be even greater; some studies showed that the relative abundance of annual and cosmopolitan species was much greater in colonies compared to undisturbed areas.

What are the major factors that alter the direction and magnitude of seabird impacts on plants?

Although several studies show large effects of seabirds, they also indicate that the following factors may alter the magnitude of these effects: (1) density of birds, (2) temperature and precipitation, and (3) proximity to human habitation. Seabird nesting density plays an important role in determining the severity of the disturbance they generate. For instance, several studies that described plant growth or productivity indicated that areas where birds nested very densely had very few or even no plant species in them (e.g. Wace 1961; Smith 1978; Sanchez-Piñero and Polis 2000). In contrast, intermediate levels of disturbance by birds can increase plant species richness relative to control areas (e.g. Hogg and Morton 1983; Vidal et al. 2003). Abandoned seabird colonies or those with low densities of nesting birds may represent an intermediate level of disturbance in which the heterogeneous environment created by bird disturbance allows a greater total number of species to persist (Huston 1979; Connell and Slatyer 1977). Hutchinson (1950) suggested that birds with the following characteristics may have particularly large effects on their nesting areas: (1) highly social (densely nesting), (2) breed in large colonies, (3) use a minimum of material other than guano in nest construction, and (4) deposit an appreciable fraction of excreta at the nest. In particular, several species of penguins (Spheniscidae), boobies (Sulidae) and cormorants (Phalacrocoracidae) excrete substantial amounts of guano around their colonies, and are considered some of the most important 'guano birds.''

Precipitation and temperature appear to strongly influence the magnitude of seabird effects. In systems where nitrogen levels are naturally low, relatively small increases in nitrogen may cause especially large changes in plant productivity and communities because the ratio of increased nitrogen to plant biomass is higher compared to ecosystems with higher plant productivity (e.g. Aber et al. 1989). Therefore, seabird effects may be particularly large where nutrient availability to plants is limited either by lack of precipitation as in arid regions (e.g. Sanchez-Piñero and Polis 2000), or by low temperatures that severely reduce bacterial decomposition and nitrification rates, such as in the Arctic (e.g. Summerhayes and Elton 1928). Moreover, in hot, dry climates nutrients from guano are either unavailable to plants, or at high deposition rates become highly concentrated and toxic to plants much more quickly than in temperate zones where higher rates of precipitation dilute high concentrations of guano (e.g. Hutchinson 1950; Gillham 1961a, b, 1963).

Several studies also suggest that where anthropogenic sources of seeds from cosmopolitan plant species are combined with fertilization and disturbance by birds, plant communities are often dominated by these species. If breeding sites are far from anthropogenic sources, such as scientific stations (Vidal et al. 2003), gulls may facilitate the transport of seeds by foraging in mainland areas and transporting seeds back to breeding sites (e.g. Gillham 1956b; Heatwole and Walker 1989; Morton and Hogg 1989; Abbott et al. 2000; Magnusson and Magnusson 2000; Nogales et al. 2001; Calvino-Cancela 2002). In fact, commenting on the vegetation of islands off Australia, New Zealand, and South Africa (Gillham (1970) as quoted by Hogg and Morton (1983)) stated that, 'a tour of gull colonies can in fact be a tour of the oases of British weed species which are insinuating themselves irrevocably around the temperate coasts of both Southern and Northern hemispheres.''

What specific aspects of seabird disturbance drive changes in plant communities?

Although changes in vegetation associated with seabirds have been widely demonstrated, the relative contribution of raised nutrient levels, soil drought, or trampling have yet to be established. The results thus far, indicate that seabird guano increases certain soil nutrients (especially N, P, and K; see also Blakemore and Gibbs 1968; Cocks et al. 1998; Erskine et al.1998; Hawke and Powell 1995; Otero and Fernandez-Sanjurjo 1999; Figure 1). However, there is less known about the effects of other soil nutrients including metals, some of which may change substantially in the presence of seabirds (Zn, Fe: Garcia et al. 2002, Al: Hawke and Powell 1995). Soil pH generally decreases in seabird colonies, but may vary in response to other factors such as soil type and presence of sea spray. Changes in organic matter and soil water retention were quite variable among studies, making it difficult to generalize. However, changes in soil water retention may have considerable effects on vegetation, especially in arid regions (Garcia et al. 2002). A few studies demonstrated that physical disturbance is also an important determinant of plant community dynamics in seabird colonies by damaging adult plants and inhibiting germination and establishment of seedlings (e.g., Maesako 1999). Establishment of cosmopolitan species with 'ruderal' strategies is also facilitated by seed dispersal by seabirds. Overall, increased soil nutrients, physical disturbance, and/or dispersal of seeds promote the expansion of herbaceous, ruderal species that often have biennial or annual life cycles.

Characteristics of current studies and future key directions

Although dramatic effects of seabirds on the vegetation of their colonies have been noted since the early 1900's (e.g. Summerhayes and Elton 1928), surprisingly few studies have rigorously investigated the mechanistic causes and variations in seabird effects. Moreover, relatively few studies have used statistical analyses and manipulative experiments to estimate the magnitude of seabird effects. Of the 57 publications selected for review, seven used field manipulations or greenhouse experiments (Table 1). I found only one published

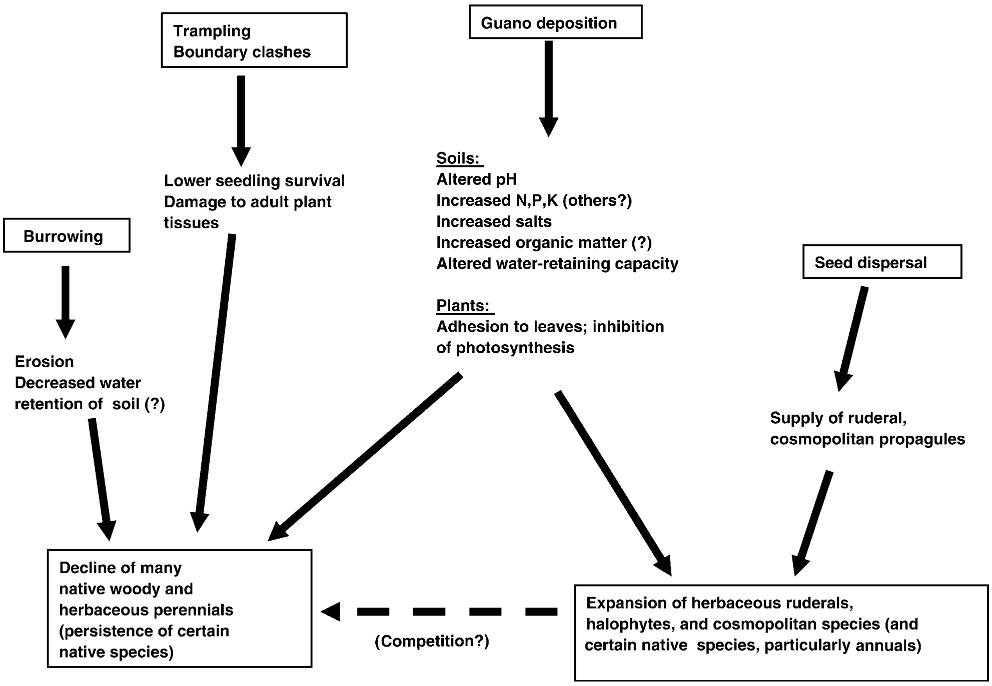

Figure 1. Various mechanisms through which seabirds affect vegetation.

study (Maesako 1999) that used exclusion cages in the field to investigate the impact of seabirds on plants. Therefore, although there is extensive documentation that particular species of plants are associated with seabirds, we have yet to fully understand why. For instance, a few studies suggest that interactions among plant species may play a large role in determining which species are dominant in colonies (e.g. Sobey and Kenworthy 1979; Maesako 1999), however, there are *no* field studies that specifically test the relative importance of interspecific interactions among plants. Further, there are no studies that use field manipulations to compare the relative role of biotic factors (e.g. competition) and abiotic factors (e.g. soil nutrient concentration) in determining distribution and abundance of plants in colonies. In addition, most published studies of plant biomass in seabird colonies focused on the aboveground component of biomass; only a few have examined belowground biomass (e.g. Smith 1976a). The limited number of manipulative field experiments may result in part from difficulties conducting such studies in seabird colonies, many of which are legally protected from human disturbance.

Several studies suggest that seabird impacts on plant communities vary with climate gradients. Toxicity effects of guano may be more common on islands in hyperarid regions, but trampling effects may be more common on islands in wetter areas (Hutchinson 1950; Gillham 1956a). However, no studies have compared seabird effects on plants across climate gradients. The ability to generalize about the effects of seabirds on vegetation would be greatly enhanced by conducting similar quantitative studies across numerous island systems that span climate gradients and include islands or areas that exhibit gradients of seabird usage.

Most of the studies in this review considered effects of seabirds at relatively small spatial scales (i.e. within a colony or in an adjacent area). However, a few studies (e.g. Hogg et al. 1988) suggest that examining larger scales (i.e. whole island) may reveal very different patterns. For instance, seabird disturbance may substantially reduce plant diversity within seabird colonies, but diversity may increase at the whole-island scale due to increased habitat heterogeneity created by the colonies (Wright et al. 2002). In addition, it is likely that the effects of nutrient input from seabirds may operate on much larger spatial scales than physical disturbance. Because ammonia can be volatilized into the atmosphere from seabird colonies and deposited to sites far away from colonies, guano deposition can have far-reaching effects (Lindeboom 1984; Erskine et al. 1998). In contrast, physical disturbances such as trampling and uprooting plants are likely to have only local impacts. Therefore, issues of spatial extent of seabird effects should be considered in future investigations.

Conservation implications of seabird effects

A reduction in seabird populations is likely to have negative consequences for native plant species that rely on seabirds for their persistence. For instance, avian populations on Tristan da Cunha and in coastal New Zealand for example, have been greatly reduced by humans and introduction of rats (Atkinson 1985). These declines have implications for vegetation since indigenous herbs may depend on open microsites created by seabirds (Dean et al. 1994; Norton et al. 1997). Similarly, on Marion Island, tussock grasslands, which are associated with burrowing petrels and prions have shrunk over time due to cat predation on the birds Smith et al. 2001; Smith and Steenkamp 2001). Conversely, disturbance by nesting seabirds (especially gulls) frequently leads to invasion by cosmopolitan plant species and declines of native species (e.g. Vidal et al. 2000). Studies in other systems have also shown that disturbance can facilitate invasions and establishment of alien plants, especially annuals, which may in turn respond to increased levels of soil nitrogen (e.g. Wedin and Tilman 1996; Vitousek et al. 1997; Kolb et al. 2002; Brooks 2003). Therefore, an important goal for future studies is to gain greater understanding of the conditions in which seabird disturbance either increases or decreases abundance of native plant species.

Finally, although plant species richness may be lower within seabird colonies (i.e. at the patch scale), primary and secondary productivity and consumer populations may be much greater in areas associated with birds (e.g. Polis et al. 1997). For instance, in New Zealand, seabirds appear to function as keystone species that support high biological diversity by enriching the soil thus giving rise to an abundant invertebrate community that supports populations of seven species of lizard, one species of frog and at least 50,000 tuatara (Daugherty et al. 1990). On some more depauperate islands, the majority of insects and other arthropods are associated with seabirds (Summerhayes and Elton 1928; Heatwole 1971; Edwards and Lubbock 1983). Therefore, both seabird preservation and control programs should consider whether the goals of management are: (1) promoting plant species richness, (2) conservation of native plant species, or (3) increased primary and secondary productivity.

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