

other five CPS loci did not manifest significant differences in their expression during growth in vitro versus in vivo, nor with diet manipulation. These findings suggest that *B. thetaiotaomicron* is able to change its surface carbohydrates in response to the nutrient glycan environment that it is accessing and perhaps also for evading a host immune response (17).

A schematic overview of how *B. thetaiotaomicron* might scavenge for carbohydrates in the distal intestine is shown in fig. S10. Bacterial attachment to food particles, shed mucus, and exfoliated epithelial cells is directed by glycan-specific outer-membrane binding proteins (exemplified by SusC/SusD paralogs) (20). *B. thetaiotaomicron* contributes to diversity and stability within the gut by adaptively directing its glycan-foraging behavior to the mucus when polysaccharide availability from the diet is reduced. Hence, host genotype and diet intersect to regulate the stability of the microbiota. Co-evolution of glycan structural diversity in the host, together with an elaborate repertoire of nutrient-regulated glycoside hydrolase genes in gut symbionts, endows the system with flexibility in adapting to changes in diet. Although our study has focused on the glycan-foraging behavior of *B. thetaiotaomicron* in monoassociated germ-free mice, similar analyses can

now be used to assess the impact of other members of the gut microbiota on *B. thetaiotaomicron* and on one another. The results should help to define the molecular correlates of behaviors that underlie the assembly and maintenance of microbial communities in dynamic nutrient environments. They should also provide a framework for developing effective ways to manipulate these communities to promote health or treat various diseases.

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Materials and Methods

Figs. S1 to S10

Tables S1 to S4

References

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Introduced Predators Transform Subarctic Islands from Grassland to Tundra

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Top predators often have powerful direct effects on prey populations, but whether these direct effects propagate to the base of terrestrial food webs is debated. There are few examples of trophic cascades strong enough to alter the abundance and composition of entire plant communities. We show that the introduction of arctic foxes (*Alopex lagopus*) to the Aleutian archipelago induced strong shifts in plant productivity and community structure via a previously unknown pathway. By preying on seabirds, foxes reduced nutrient transport from ocean to land, affecting soil fertility and transforming grasslands to dwarf shrub/forb-dominated ecosystems.

Nearly half a century ago, Hairston *et al.* (1) proposed that plant productivity and composition were influenced by apex predators through cascading trophic interactions. According to their "Green World" view, the direct effects of predators on herbivore populations transcend

multiple trophic levels indirectly to enhance plant community productivity and biomass. Despite great progress in food web ecology, the indirect effects of top predators on vegetation dynamics in terrestrial systems remain unresolved and actively debated (2–6). Compelling demonstrations of multitrophic predator impacts on entire plant communities are scarce, in part because the spatial and temporal scales necessary to perform the appropriate community-wide experiments are daunting.

The introduction of predators to islands provides an opportunity to explore the indirect effects of predators on vegetation. Introduced predators commonly have devastating direct

effects on their prey (7). The histories of these introductions are often well known, and the relative simplicity and isolation of insular systems facilitate the study of whole-community responses. Here we investigate how the introduction of arctic foxes (*Alopex lagopus*) to the Aleutian archipelago affected terrestrial ecosystems across this 1900-km island chain.

The Aleutian archipelago is a remote series of physically similar volcanic islands extending westward from the Alaska Peninsula (Fig. 1). The archipelago currently supports 29 species of breeding seabirds, together numbering >10 million individuals (8). Seabirds deliver nutrient-rich guano from productive ocean waters (9) to the nutrient-limited plant communities (10, 11). Historically, seabirds inhabited most islands along the Aleutian chain. Following the collapse of the maritime fur trade in the late 19th and early 20th centuries, foxes were introduced to >400 Alaskan islands as an additional fur source (12). The introduced foxes severely reduced local avifaunas, especially seabirds (13). However, several islands remained fox free, either because introductions failed or were not undertaken (12–14). Hence, a large-scale natural experiment to evaluate the effects of exotic predators on insular ecosystems was unwittingly initiated more than a century ago. We use this experiment to show how differing seabird densities on islands with and without foxes affect soil and plant nutrients; plant abundance, composition, and productivity; and nutrient flow to higher trophic levels. These determinations

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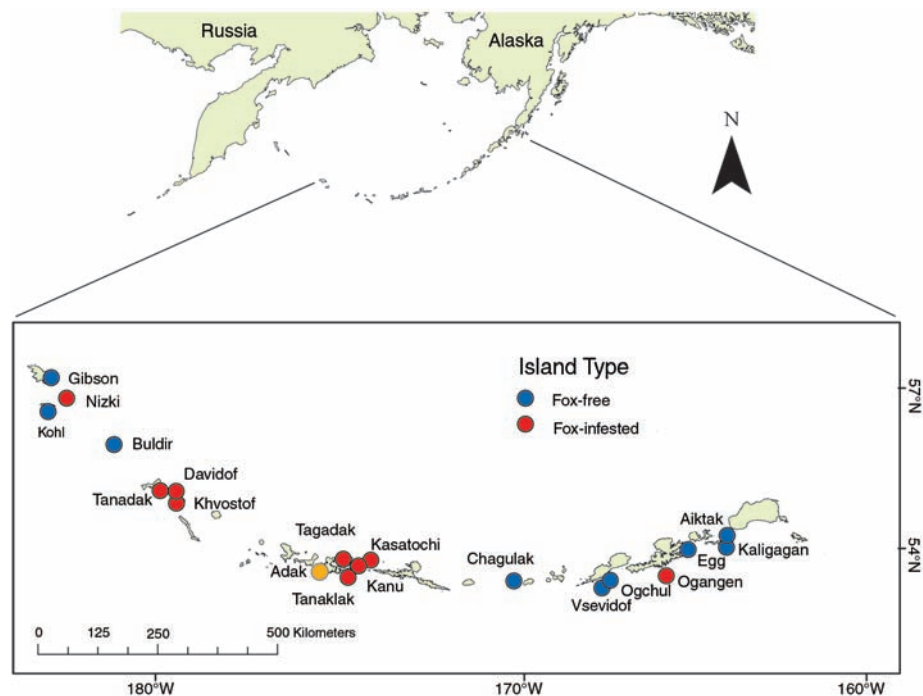
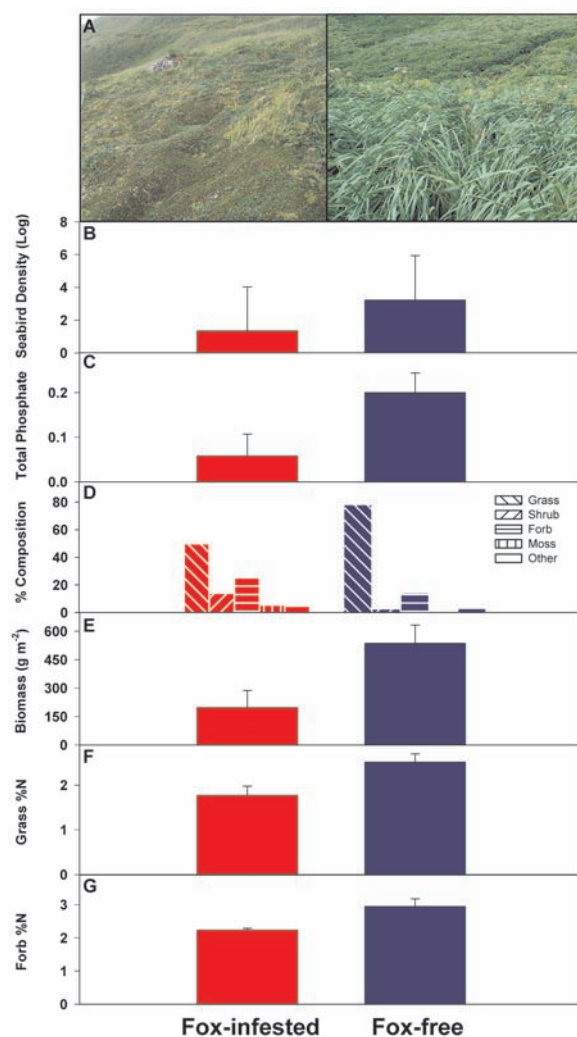


Fig. 1. The Aleutian archipelago with sample islands indicated in red (fox-infested) and blue (fox-free). Adak Island, the location of fertilization experiments, is indicated with a yellow dot.

Fig. 2. Mean (\pm SE) values for parameters sampled on fox-infested (red) and fox-free (blue) islands in the Aleutian archipelago. (A) Photographs of typical plant communities on fox-infested (Ogangan Island) versus fox-free (Buldir Island) islands. (B) Logarithm of the density (birds m^{-2}) of breeding seabirds estimated from population counts made by the U.S. Fish and Wildlife Service (26). (C) Soil Bray phosphorous (%). (D) Composition of island plant community from point contact counts of 1- m^2 photo quadrats. (E) Grass biomass ($g\ dry\ weight\ m^{-2}$). (F) Percent nitrogen composition of the dominant grasses (*Leymus mollis* or *Calamagrostis nutkanensis*). (G) Percent nitrogen composition of a common forb (*Achillea borealis*).



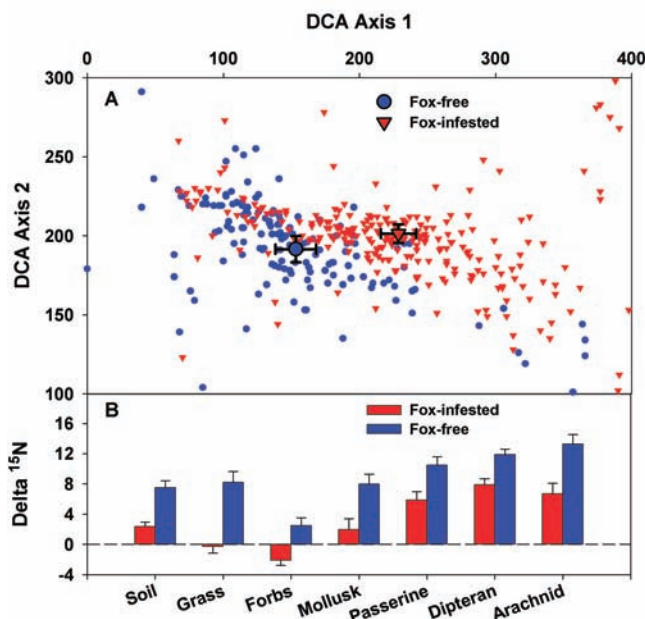
were based on contrasts among 18 islands (9 with foxes and 9 fox free) (Fig. 1) that were matched as carefully as possible for size and location in the archipelago (12).

A geographical information system (GIS) was used to superimpose spatially explicit grids over maps of each island. All islands were sampled at the completion of the growing season (August) between 2001 and 2003. We established a 30 m by 30 m plot at each of the grid crosspoints (12 to 32 per island, depending on island size) (12), within which we sampled plant species presence and cover; aboveground plant biomass; total soil N, P, and $\delta^{15}N$; and %N and $\delta^{15}N$ from a common grass (in most cases *Leymus mollis* but in some instances *Calamagrostis nutkanensis*) and forb (*Achillea borealis*) (12). At each island, we also haphazardly sampled $\delta^{15}N$ in at least five individuals from a diverse group of terrestrial consumers, including a mollusk (*Deroceras laeve*), arachnid (*Cybaeus reticulatus*), dipteran (*Scathophaga impudicum*), and passerine bird (Lapland longspurs, *Calcarius lapponicus*, and song sparrows, *Melospiza melodia*). $\delta^{15}N$ was measured to determine the degree to which nitrogen-based nutrients were marine derived. Soils and organisms that obtain their N from locally fixed sources have lower $\delta^{15}N$ values than those that obtain their N from higher trophic levels, such as marine fish and zooplankton (15, 16).

Breeding seabird densities were almost two orders of magnitude higher on fox-free than on fox-infested islands (Fig. 2B) (Mann-Whitney rank sum, $T = 36$, $P < 0.001$) (12). We estimate that this reduction in seabird abundance translates to a decline in annual guano input from 361.9 to 5.7 $g\ m^{-2}$ (median values; $T = 42$, $P = 0.005$) (12). The resulting difference in marine nutrient input is reflected in soil fertility. Total soil phosphorus on fox-free islands was more than three times that on fox-infested islands (Fig. 2C) ($F_{1,16} = 8.01$, $P = 0.012$) (12). Although seabird colonies are often concentrated on the perimeter of islands, guano-derived nutrients can be broadly redistributed across islands and not solely concentrated within the colonies (17).

The different soil fertilities between fox-free and fox-infested islands corresponded with strong shifts among island types in the biomass and nutrient status of terrestrial plants, as well as overall composition of the plant community (Figs. 2, A to D, and 3A). Grass biomass was almost a factor of 3 higher (Fig. 2E) ($F_{1,15} = 10.58$, $P = 0.005$), shrub biomass was a factor of 10 lower (0.48 ± 0.31 versus $4.95 \pm 0.84\ g\ m^{-2}$; $F_{1,15} = 19.97$, $P < 0.001$), and the nitrogen content in grasses and forbs was significantly greater on fox-free versus fox-infested islands (Fig. 2, F and G) ($F_{1,16} = 8.28$, $P = 0.01$ and $F_{1,13} = 12.51$, $P = 0.004$ for grasses and forbs, respectively). Plant communities on fox-free islands were graminoid dominated, whereas those on fox-infested islands had a

Fig. 3. (A) Detrended correspondence analysis (DCA) comparing plant assemblages (based on the presence or absence of species) on fox-infested (red triangles) and fox-free (blue circles) islands. Analysis was conducted on species presence data from one of the three 1-m² quadrats within 30 m by 30 m plots on the two island types. Each small point represents a census of plant species occurrence within a 1-m² quadrat. Large points represent the mean \pm 99% confidence interval axis scores from all samples taken across each island type. (B) Stable nitrogen isotope ($\delta^{15}\text{N}$ mean \pm SE) analyses of soils and a suite of common species across trophic levels on fox-infested (red) and fox-free (blue) islands.



more equitable distribution of graminoids, shrubs, and forbs (Fig. 2D).

$\delta^{15}\text{N}$ measures from soils, plants, and consumers all indicate that fox introductions reduced nitrogen input from sea to land. $\delta^{15}\text{N}$ was significantly greater in soils from fox-free islands compared with fox-infested islands (Fig. 3B) ($F_{1,16} = 14.07$, $P = 0.002$). Similar patterns in $\delta^{15}\text{N}$ between fox-free and fox-infested islands were evident in grasses, forbs, mollusks, passerines, dipterans, and arachnids (Fig. 3B). These findings demonstrate that fox-free islands are strongly subsidized by marine-derived nutrients, which in turn assist in fueling the ecosystem at higher trophic levels.

To test whether differences in the magnitude of nutrient subsidies transported by seabirds onto fox-free versus fox-infested islands could have produced the observed differences in plant communities, we conducted a fertilization experiment on a large fox-infested island. Experimental nutrient additions to a community representative of fox-infested islands over 3 years caused a 24-fold increase in grass biomass ($24.33 \pm 6.05 \text{ g m}^{-2}$) compared with control plots ($0.51 \pm 0.38 \text{ g m}^{-2}$ increase; two-factor analysis of variance, $F_{1,20} = 23.96$, $P < 0.001$) and a rapid shift in the plant community to a grass-dominated state. In fertilized plots, grass increased from 22 ($\pm 2.7\%$) to 96 ($\pm 17.3\%$) of total plant biomass, whereas grass biomass in control plots was relatively unchanged ($11.4 \pm 3.0\%$ and $12.1 \pm 1.2\%$ of total biomass at the start and end of the experiment, respectively) (12). In a parallel experiment (18), we disturbed and fertilized plots to mimic the effects of both seabird burrowing and guano addition. Here we found that disturbance negatively rather than positively affected grass biomass; the effects of fertilization alone were

far greater than the joint effects of disturbance and fertilization. These results confirm the importance of nutrient limitation in these ecosystems and establish that nutrient delivery in the form of seabird guano is sufficient to explain observed differences in terrestrial plant communities between islands with and without foxes.

In total, our results show that the introduction of foxes to the Aleutian archipelago transformed the islands from grasslands to maritime tundra. Fox predation reduced seabird abundance and distribution, in turn reducing nutrient transport from sea to land. The more nutrient-impooverished ecosystem that resulted favored less productive forbs and shrubs over more productive grasses and sedges.

These findings have several broad implications. First, they show that strong direct effects of introduced predators on their naïve prey can ultimately have dramatic indirect effects on entire ecosystems and that these effects may occur over large areas—in this case across an entire archipelago. Second, they bolster growing evidence that the flow of nutrients, energy, and material from one ecosystem to another can subsidize populations and, importantly, influence the structure of food webs (19–21). Finally, they show that the mechanisms by which predators exert ecosystem-level effects extend beyond both the original conceptual model provided by Hairston *et al.* and its more recent elaborations (22). Trophic cascades (23, 24) have traditionally been thought to involve a series of strictly top-down interactions, where predators, by affecting herbivore populations and altering the intensity of herbivory, ultimately influence plant production at the base of food webs (25). Our work illustrates that predators, by thwarting the transport of nutrients between systems, can have powerful indirect effects on systems via

a route different from that of classic trophic cascades. The impact of highly mobile predators and their prey on the transport of materials between ecosystems remains poorly understood. Because few ecosystems support food webs that are undisturbed either through introductions or extirpations, it may be that the all-too-common addition or deletion of predators from systems have had substantial but largely unexplored effects.

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- There are several reasons why the Aleutian archipelago provides an ideal large-scale experimental system to study the effects of introduced predators: (i) Most islands are small; (ii) high-latitude floral diversity is relatively low; (iii) there are no native vertebrate herbivores; (iv) the islands are geologically and climatologically homogeneous with similar overall soil properties; (v) the large number of islands in the archipelago provides the opportunity for meaningful replication; (vi) the islands are isolated from anthropogenic nutrient inputs; and (vii) fox introductions were not targeted for particular island types, and the history of introductions is reasonably well known.
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References and Notes

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