

Does removal of an alien predator from small islands in the Baltic Sea induce a trophic cascade?

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Changes in carnivore abundance can alter the distribution and abundance of plants on a community wide basis, an effect known as a trophic cascade. Because alien predators can have a disproportionate impact, compared to native predators, on herbivore populations, they may induce stronger trophic cascades in plant communities than native predators. We studied the indirect effects of the removal of an alien predator, the American mink *Mustela vison* on plant communities on small islands in the Baltic Sea, SW Finland. Mink had been removed from a group of islands for 12 yr, while another group of islands with mink presence served as a control area. Field voles *Microtus agrestis* and bank voles *Myodes glareolus* exert strong grazing pressure on the island vegetation and are an important part of mink diet. On nine islands of the mink removal area and five islands of the control area we studied the vegetation in ten randomly chosen plots; five in herbaceous and five in woody (i.e. dwarf shrub) vegetation. We studied the cascading impacts of mink predation on grassy and woody vegetation using the Shannon diversity and equitability indices and comparing abundances of different species between mink removal and control islands. Diversity and equitability of plant communities were higher on mink removal islands. In grassy patches, abundances of several species differed between mink removal and control islands. Our results demonstrate, for the first time, that alien predator removal may induce a trophic cascade on small islands.

A central question in ecology and conservation is the degree to which the environment or interactions between species affect community processes and thus the biodiversity of an ecosystem (Oksanen and Oksanen 2000). In terrestrial systems, recent studies have shown that top-down processes can have fundamental effects on population demography and community composition (Pace et al. 1999, Maron and Simms 2001). Changes in carnivore abundance can alter the distribution and abundance of plants on a community wide basis, an effect known as a trophic cascade (Carpenter et al. 1985). Trophic cascades have been shown to occur following the removal of predators preying upon herbivores (Schmitz et al. 2000, Norrdahl et al. 2002), but controversy still exists whether community-level trophic cascades might be widespread and strong in terrestrial ecosystems (Polis and Strong 1996, Polis et al. 2000, Schmitz et al. 2000). A cross-ecosystem comparison of the strength of 102 trophic cascade experiments showed that plants in aquatic ecosystems responded more strongly to predator reductions than those in terrestrial ecosystems (Shurin et al. 2002). However, the issue is debated and some authors maintain that trophic cascades are common even in vertebrate terrestrial food webs (Oksanen and Oksanen 2000, Terborgh et al. 2006, Aunapuu et al. 2008) which are

underrepresented in the data sets underlying the recent meta-analyses (Halaj and Wise 2001, Shurin et al. 2002, 2006, Borer et al. 2005).

Alien predators may induce even stronger trophic cascades than native predators do, because they have an impact double that of native predators (Salo et al. 2007) on prey populations, which often lack the behavioural traits to avoid alien predators (Banks and Dickman 2007) and have little resilience to additional heavy predation (Dickman 1996). For prey on small islands, where the potential of extirpation by predators is higher and re-colonisation processes are slow (Adler and Levins 1994), the impacts of alien predators can be exacerbated. Indeed, island ecosystems have suffered the highest extinction rates for vertebrate animals, and introduced predators are thought to have been a major cause (Courchamp and Sugihara 1999, Owens and Bennett 2000, Ceballos and Ehrlich 2002).

Herbivores influence the structure and diversity of plant communities by reducing the abundance of preferred forage species and changing competitive interactions between plant species (Whitham et al. 1991). In his Intermediate Disturbance Hypothesis (IDH) Connell (1978, see also Grime 1973) argues that areas where strong disturbances occur at intermediate frequency should be characterized by

high diversity of plants and sessile animals, because under such circumstances, mosaics of different successional stages are created, allowing for the coexistence of quickly dispersing ruderal species and slower but more competitive species. The islands of the outermost archipelagos of the Baltic Sea have probably never been much used by humans and only have small patches of meadow and heath vegetation. Disturbance to plants used to be created by voles (especially *Microtus agrestis*), which have colonized even the outermost islands with, and have periodically increased rapidly to hundreds or even thousands of individuals per ha of vegetated area (Pokki 1981, Banks et al. 2004). The runways and depleted patches thus provided opportunities for seeds to germinate and seedlings to grow (Ericson 1977). This source of disturbance has been recently weakened or eliminated by an alien predator, the American mink Mustela vison, hereafter mink.

Mink have continuously escaped from Fennoscandian fur farms for >60 yr and are now resident along the coastlines of the Baltic Sea and in the archipelago (Kauhala 1996). Mink have a diverse diet comprising mainly fish and migratory birds, but they also feed on small rodents as a supplemental component of their diet (Niemimaa and Pokki 1990). Because none of the native terrestrial predators of the region have had a corresponding ability to exploit both marine and terrestrial resources, the invasion of this alien predator has created a qualitatively new situation: an area which was previously practically free from all mammalian predators has now a fairly dense predator population, suppressing the densities of voles (Banks et al. 2004, 2008, Fey et al. 2008).

The scope of the present paper is to test the hypothesis, that an alien predator, which has an especially strong capacity to influence its prey, can initiate trophic cascades on the small islands in the outer archipelagos of the Baltic Sea. We have manipulated the predation pressure from alien mink (through mink erradication) and recorded plant abundance on mink and mink-free islands. We expected that the plant communities would differ between mink-free and mink islands, plant diversity being higher on mink-free islands, where grazing pressure of voles and hence disturbance is higher than on mink islands.

Material and methods

Study area

We studied indirect impacts of mink on vegetation on small islands in the outer archipelago of the Baltic Sea (59°N, 21°E), SW Finland. The experimental islands were exposed rocky skerries, ranging from 1 to 5.8 ha in size. Vegetation on these islands is sparse and typically dominated by grasses (mainly *Deschampsia flexuosa*), low juniper *Juniperus communis* bushes, crowberry *Empetrum nigrum* and bog bilberry *Vaccinium uliginosum* (see Nordström et al. 2002, 2003, Nordström and Korpimäki 2004 for additional details).

In the archipelago, two native herbivorous rodent species are found: the field vole *M. agrestis*, which is the most common herbivorous small mammal in the archipelago, and the bank vole *Myodes glareolus*, which is more patchily distributed and generally more abundant closer to the mainland (Kostian 1970, Ebenhard 1988), but also occurs in remote areas (Banks et al. 2004). Grasses are the main food source for voles, but in the winter voles also feed on buds and bark of the berries (Pokki 1981).

The mink is the most important and, essentially, the only mammalian predator of voles in the study area. Other mammalian predators, such as the red fox *Vulpes vulpes* and the raccoon dog *Nyctereutes procyonoides*, are extremely rare on the islands of the outer archipelago (Nordström et al. 2002, 2003), and we did not observe any signs of other mammalian predators than mink during the study. Black adders *Vipera berus* and, during spring- and autumn migration, short- and long-eared owls *Asio flammeus* and *A. otus* and kestrels *Falco tinnunculus* may exert some predation pressure on voles.

We manipulated mink impacts using a large-scale predator removal experiment. Since autumn 1992, mink have been consistently removed by gamekeepers during spring and autumn from 60 islands in a 72 km^2 area (R) around Trunsö near Nauvo (59°49'N, 21°48'E). A control area with mink present (C) consisting of 77 islands across 90 km² was established >10 km east in Vänö near Dragsfjärd (59°48'N, 22°11'E) (see Nordström et al. 2002, see 2003 for methods of removing mink and annual numbers removed and Banks et al. 2004, Fig. 1, for a map of the study area). We surveyed the vegetation on five islands of the control area and ten islands of the mink removal area in June 2004. Numbers of control and mink removal islands differed because the survey of the mink removal islands was also planned as the starting point of another long-term experiment, but due to logistic constraints we were not able to survey the same number of islands in the control area.



Figure 1. Mean and SE of numbers of voles trapped per island on mink removal islands and control islands in August 2004, August 2005 and August 2007. N represents numbers of mink removal islands/mink islands included in the data set. **Denotes significance levels of differences between mink removal and control islands at the level p < 0.005.

Data collection

On each island we randomly chose ten plots at least 5 m apart; five in grassy and five in woody (i.e. berry shrubs) vegetation. The vegetation in these plots was sampled using a point intercept method (Levy and Madden 1933, Bråthen and Hagberg 2004). We placed a 100×50 cm plexiglass table with 100 randomly distributed holes over the plot and passed a pin vertically through the holes. All species hit by the pin were recorded, each species not more than once per hole. If the pin hit bare ground or dead vegetation, that was recorded as "open space". The abundance of each species was estimated by the number of holes through which it was hit.

For each plot we calculated the Shannon-Wiener indices of diversity

$$H' = -\sum_{i=1}^{s} pi \ ln \ pi$$

and equitability

$$J = \frac{-\sum_{i=1}^{s} pi \ln pi}{\ln S}$$

where S is the number of species, and p_i the relative abundance of each species, calculated as the proportion of individuals of a given species to the total number of individuals in the community.

Statistical analyses

Vole dynamics in the archipelago are influenced by metapopulation processes (Banks et al. 2004). Because data on vole abundances on study islands were only available for the year in which we conducted the vegetation survey, we decided not to use vole numbers as a covariate in the analyses as they may not reliably reflect past grazing pressure. To account for the possible influence of metapopulation processes on vole density, characteristics of island isolation [island size (ha), number of islands within 2 km radius, land area within 2 km radius (ha), and the distance to the closest island (m)] were included in all analyses. A 2 km area around islands was used to approximate the maximum distance from which voles might disperse in a patchy island landscape, fragmented by the open sea (although very occasionally field voles may also disperse over longer distances; Banks et al. 2004). Characteristics of island isolation were calculated on the basis of digitized maps of the area in MapInfo Professional 8.0. Island characteristics were reduced to two independent principal components using principal component analysis. PC1 explained 66% of the variation in the island isolation and was mainly related to the distance to the nearest island. PC2 explained a further 28% of variation and was mainly related to the island size (Table 1). Both principal components were then included as covariates in the analyses.

The impact of mink predation on vole populations can vary depending on weather conditions (Banks et al. 2004). We therefore used live-trapping data from three additional

Table 1. Factor loadings of each island characteristic used to derive two independent principal components using PCA on their correlation matrix.

PC1	PC2
-0.373	0.918
-0.962	-0.068
-0.843	-0.510
0.931	-0.165
2.643	1.134
66.07	94.41
	PC1 -0.373 -0.962 -0.843 0.931 2.643 66.07

years to confirm that mink removal increases vole densities. Data on vole densities were obtained from live-trapping in late summer (August) on islands of both mink removal and control areas in 2004, 2005 and 2007. In 2005, on some islands we recorded the number of visited traps after one day of pre-baiting with standard laboratory mouse pellets (estimated from the number of pellets disappearing from the traps) without actually trapping voles, because poor weather conditions and logistic constraints forced us to survey vole populations as quickly as possible. In a previous experiment on the small islands of the outer archipelago of the Baltic Sea (Fey et al. 2008), we have found that the number of visited traps the next day was positively correlated with the number of individuals trapped (Spearman rank correlation, $r_s = 0.672$, p = 0.047). We thus estimated vole numbers per grid using this correlation coefficient. To test for the effect of mink removal on vole densities we used general linear modelling (GLM), initially including vole numbers (both field and bank voles) trapped per grid as dependent variable, mink removal as the factor and PC1 and PC2 as covariates. Because the covariates did not have a significant influence on the dependent variable, we then excluded them from the analyses.

To test for the influence of mink removal on species composition, we used linear mixed models with diversity/ equitability averaged per island as dependent variable, mink removal as a factor, and PC1 and PC2 as covariates. SIMPER in Primer 5 was used to examine which species contributed most to differences between mink removal and control areas. In order to tease out the influence of mink removal on the abundances of single plant species, we used GLM with the relative abundance of each species averaged per island as the response variable.

Results

Mink removal significantly increased vole densities on the islands of the outer archipelago during two out of three summers (Fig. 1; August 2004: $F_{1,13} = 3.71$, p = 0.076; August 2005: $F_{1,13} = 19.69$, p = 0.002; August 2007: $F_{1,13} = 19.86$, p = 0.001).

We identified a total of 49 plant species on grassy patches and 20 species on woody patches. On both mink removal and mink islands, grassy patches were dominated by *Deschampsia flexuosa*, woody patches by *Empetrum nigrum* and *Vaccinium uliginosum* (Table 3).

Mink removal significantly increased both diversity (mink free islands: $H' = 0.64 \pm 0.36$ mean \pm SD, mink islands: $H' = 0.58 \pm 0.44$) and equitability (mink free

Table 2. ANCOVA on the effects of mink removal and isolation indices (PC1 relates mainly to the distance to the nearest island and PC2 relates mainly to island size) on plant species diversity and equitability in the outer archipelago of the Baltic Sea.

Source	DF	MS	F	р
Diversity (H')				
Mink removal	1	0.66	4.369	0.038
PC1	1	0.656	4.342	0.039
PC2	1	0.001	0.004	0.947
Error	136	0.151		
Equitability (J)				
Mink removal	1	0.683	8.768	0.004
PC1	1	0.377	4.844	0.029
PC2	1	0.217	2.791	0.097
Error	136	0.078		

islands: $J = 0.58 \pm 0.27$ mean \pm SD, mink islands: $J = 0.48 \pm 0.31$) of plant communities; both were also influenced by distance to the nearest island (Table 2).

The abundance of a number of species was significantly influenced by mink removal. Several species on both grassy patches (*Phalaris arundinacea*, *Phragmites australis*, *Rhinanthus minor*, *Sanionia uncinata*, *Senecio sylvaticus*, *Stellaria graminea*, *Tanacetum vulgare* and *Veronica longifolia*; Table 4) and woody patches (*Calliergonella cuspidata* and *Tanacetum vulgare*; Table 5) were either not present or present in significantly lower abundances on mink free islands compared to mink islands.

Discussion

Long-term mink removal has clearly altered the vegetation on the study islands during the twelve years since removal started. Both diversity and equitability, i.e. the evenness with which individuals are distributed amongst the species, were higher on islands from which mink had been removed. This suggests that plant communities on the small islands are more diverse under periodically higher grazing pressure by voles induced by the absence of mink predation (Banks et al. 2004; Fig. 1), as predicted by the IDH (Grime 1973, Connell 1978).

On the species level, we found the largest number of differences between mink islands and mink free island in grassy patches. The statistically significant species level differences concerned tall herbs and grasses and some palatable species, for which the presence of the mink was a positive factor. The species' level results in the opposite

Table 3. Average abundance of plant species in grassy and woody patches which contribute to the similarity among islands in mink removal and mink areas.

Species	Mink removal	Mink present
Grassy patches:		
Deschampsia flexuosa	65.76	61.28
(Open space)	10.24	8.16
Rumex acetosella	9.50	6.84
Carex canescens	3.07	2.88
Woody patches:		
Empetrum nigrum	66.18	79.64
Vaccinium uliginosum	47.16	31.60
(Open space)	2.91	3.08

direction were not statistically significant. A likely reason for this apparent contradiction is the large number of plant species with good colonizing ability and the randomness of the dispersal process. When voles create gaps in the vegetation, some of these plants predictably invade, and this is reflected in diversity and evenness indices. However, the identity of invading plants varies between islands and plots, depending on the surrounding vegetation. Therefore, it would require very large materials to obtain statistically significant results on the level of individual species.

In particular, we expected that mink removal should have produced a species-level trophic cascade resulting in increases of grazing resistant plant biomass and decreases in edible plant biomass (Leibold 1989, Schmitz 1994). Abundances of a number of plant species, which appear related to palatability, differed between mink free and mink islands. Although in general the grazing impact may be higher on winter food plants than on plants available during summer, it is likely that at least the most preferred summer food plants of voles might also be affected by reduced grazing pressure. In agreement with this, the abundances of Rhinanthus minor and Stellaria graminea, two preferred food plants, were greater in the presence of mink, i.e. under reduced grazing pressure by voles. Norrdahl et al. (2002) showed in a predator-exclusion experiment on agricultural areas that field voles were able to reduce the coverage of three preferred food plants in summer (the grasses *Elymus* repens and Phleum pratense, and the herb Vicia cracca). The impact on preferred herbaceous plants observed in our study and by Norrdahl et al. (2002) contrasts with the results of Hambäck et al. (2004), who reported that, in the tundra, only woody plants were influenced by vole grazing, even in the absence of predators. Difference in the length of the growing season between study systems probably accounts for or at least contributes to this contrast. On the tundra, microtine rodents seem to become satiated during the short arctic summer, their impact being overwhelmed by the rapid growth of the plants. At lower latitudes, the winter bottleneck is less severe, allowing for the survival of voles in numbers sufficient to influence preferred herbaceous plants.

Differences in plant life history did not seem to account for the differences in species' responses to mink removal as both annual and perennial plants were affected. We found an indirect impact of the mink on the only annual species found in our study, Rhinanthus minor, which is highly palatable to voles and probably had problems with getting mature seeds on islands with high vole densities. A similar phenomena occurs with the impact of voles on Melampyrum silvaticum, a relative of Rhinanthus minor which is also annual (Ericson and Oksanen 1987). The majority of the perennial plants reacting positively to mink presence, are tall forbs (e.g. Tanacetum vulgare) or tall grasses (Phalaris arundinacea, Phragmites australis), likely to be strong competitors. Their height makes them especially vulnerable to grazing for two reasons. First, big plants usually have strong apical dominance which means they are easily damaged when herbivores browse their juvenile shoots. Selective grazing on the most nutritious parts of the plants, the growing shoot tips, can have much more impact than would be expected on the basis of the amount of material consumed. Second, the bigger the plant, the

Table 4. Effects of mink removal on the average abundance of species in grassy patches which contribute to the dissimilarity between communities on mink removal and mink islands, i.e. the degree to which communities are unlike each other. Asterisks indicate species which are most likely to be found in the diet of voles. Abundance of species marked in bold differs significantly between mink removal and mink islands.

Species	Abund. ¹⁾	Abund. ¹⁾	Diss. ²⁾	SD ³⁾	Contrib.%4)
	Mink removal	Mink present	_		
Graminoids					
*Carex nigra	3.80	8.16	3.02	1.09	5.40
*Phalaris arundinacea	0.00	4.08	2.66	1.06	4.75
*Carex canescens	3.07	2.88	2.16	0.84	3.85
*Agrostis canina	1.87	0.64	1.52	0.68	2.72
*Agrostis stolonifera	3.11	5.36	1.46	0.68	2.61
*Festuca rubra	0.80	0.92	1.33	0.67	2.38
*Phragmites australis	0.00	0.68	0.78	0.49	1.40
*Eleocharis uniglumis	0.00	0.08	0.65	0.49	1.16
Herbs	0100	0.00	0100	0110	
Trientalis europaea	0.12	0.44	1 94	0.74	3 46
Internaris europaea	0.07	2 08	1.54	0.85	3.16
Calium verum	1.89	0.00	1.77	0.63	2 59
Tanacotum vulgaro	0.56	3.80	1.75	0.05	2.55
Voronica longitalia	0.38	1 12	1.20	0.09	2.29
Sodum tolophium	0.03	0.04	0.00	0.59	1.01
Securi (elepinum	0.07	0.04	0.90	0.39	1.01
Sellecio Sylvalicus	0.00	0.04	0.70	0.49	1.40
*Stellaria graminea *Dhimomthus minor	0.00	0.60	0.78	0.49	1.40
*Kninaninus minor	0.00	0.32	0.78	0.49	1.40
Valacious service de la contraction	0.00	0.08	0.65	0.49	1.10
Valeriana sambucifolia salina	0.00	0.08	0.65	0.49	1.16
Potentilla palustris	0.00	3.28	0.65	0.49	1.16
Deciduous woody plants					
Rubus idaeus	0.10	0.00	0.90	0.50	1.60
Evergreen woody plants					
Juniperus communis	0.87	0.00	1.85	0.83	3.30
Empetrum nigrum	0.20	0.04	1.73	0.67	3.10
Mosses					
Dicranium scoparium	0.67	0.72	2.34	0.89	4.19
Pohlia nutans '	0.02	0.12	2.14	0.80	3.83
Calliergonella cuspidata	0.29	3.60	1.73	0.81	3.09
Calliergonella stramineum	2.11	3.96	1.73	0.81	3.09
Hypnum cupressiforme	0.00	0.24	1.43	0.79	2.56
Bryum spp.	0.04	0.04	1.43	0.67	2.55
Ceratodon purpureus	0.36	0.20	1.43	0.67	2.55
Aulicomnium palustre	0.22	0.40	1 21	0.58	2.17
Sanionia uncinata	0.00	0.04	0.78	0.50	1 40
Warnstorfia exannulata	0.00	2.28	0.65	0.49	1.16
Lichens					
Cladina mitis	9.60	3 24	2 71	0.96	4 85
Cladonia spp	0.13	0.52	1 1 2	0.54	2 01
Cladina giliata	2 00	0.00	0.93	0.54	1.65
Chaina ginata	2.00	0.00	0.55	0.51	1.05

¹⁾ Average abundance.

²⁾ Average dissimilarity between groups.

³⁾ SD of the average dissimilarity.

⁴⁾ Contribution (in %) of the species to the dissimilarity between groups.

greater the leaf surface supported by a single shoot and thus also the damage that the plant suffers if the shoot is clipped. Changes in community structure are also predicted given that big plants are likely to monopolize places, and subordinate, smaller plants will gain benefit from their damage.

Our study suggests, for the first time, that the effects of an alien predator on herbivores can cascade to the lower trophic levels, in this case to plant communities. Although the influence of 12 yr of mink removal on the vegetation community level was generally not strong, it is likely that plant communities probably need even more time until changes will become more obvious. Trophic cascades can arise in two ways: through direct population effects in which predators kill herbivore prey, thereby decreasing herbivore densities resulting in reduced impacts on the plant trophic level, or through non-lethal effects in which herbivore prey respond to apparent predation risk by changing habitat use and decreasing foraging effort (Preisser et al. 2005). These behavioural changes can result in reduced herbivore feeding time and increased starvation risk which leads to reduced survival and reproductive output (Lima 1998), again reducing the impact of herbivores on vegetation. A recent review showed that predator intimidation of prey populations is even more important than direct consumption of prey by predators when considering the cascading effects of predators on resources of herbivore prey (Preisser et al. 2005). In our Table 5. Effects of mink removal on the average abundance of species in woody patches which contribute to the dissimilarity between communities on mink removal and mink islands, i.e. the degree to which communities are unlike each other. Asterisks indicate species which are most likely to be found in the diet of voles. Abundance of species marked in bold differs significantly between mink removal and mink islands.

Species	Abund. ¹⁾	Abund. ¹⁾	Diss. ²⁾	SD ³⁾	Contrib.%4)
	Mink removal	Mink present	_		
Graminoids					
*Deschampsia flexuosa	3.42	1.72	3.68	0.87	10.26
*Carex nigra	0.62	0.40	3.27	0.87	9.11
*Festuca rubra	0.20	0.04	1.76	0.59	4.92
Herbs					
Rubus chamaemorus	2.51	1.76	4.85	1.16	13.54
Angelica sylvestris	0.00	3.88	3.13	0.80	8.73
Trientalis europaea	0.38	0.16	2.83	0.79	7.90
Rumex acetosella	0.20	0.00	1.68	0.52	4.70
Tanacetum vulgare	0.00	0.20	1.50	0.49	4.19
Epilobium angustifolium	1.22	0.00	1.46	0.52	4.07
Evergreen woody plans					
Juniperus communis	3.22	3.00	3.21	0.78	8.95
Ferns					
Dryopteris carthusiana	0.00	1.00	1.30	0.49	3.64
Mosses					
Calliergonella cuspidata	0.00	0.32	1.50	0.49	4.19
Aulicomnium palustre	0.00	0.20	1.30	0.49	3.64
Hypnum cupressiforme	0.00	0.12	1.30	0.49	3.64

¹⁾ Average abundance.

²⁾ Average dissimilarity between groups.

³⁾ SD of the average dissimilarity.

⁴⁾ Contribution (in %) of the species to the dissimilarity between groups.

study system it is possible that both density-mediated and trait-mediated interactions between mink and voles reduce grazing pressure (Preisser et al. 2005). Direct consumption of voles leads to generally lower vole densities on mink islands than in mink free islands, but we have earlier found that field voles respond to mink presence with a microhabitat shift from grassy patches and dwarf shrubs to juniper (Fey et al. 2006) which would release these patches from grazing pressure.

Our study provides evidence that the alien mink not only have detrimental effects on many bird species (Nordström et al. 2002, 2003) and amphibians (Ahola et al. 2006) and limit vole populations (Banks et al. 2004, 2008, Fey et al. 2008) but is also, via reducing the grazing pressure by voles, reducing plant diversity in the archipelago. Because the alien mink has also been shown to decrease the diversity of breeding bird assemblages in the outer archipelago (Nordström and Korpimäki 2004), alien predation is not only devastating for native prey populations, but can have detrimental effects on the diversity of three trophic levels (piscivorous birds, herbivores and plants) of the ecosystem. American mink should therefore be carefully managed to avoid further damage to the archipelago ecosystem. Constant removal could probably lead to a restoration of the ecosystem, since densities of piscivorous birds (Nordström et al. 2002, 2003) and herbivores will increase again, as shown in the present study.

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