core are within the range of variability observed during the LIA (Fig. 2) (*10*, *29*). Regardless of the date chosen for its termination, the LIA was one of the shortest cold intervals of the last 110,000 years (*30*) and was substantially shorter than some other major Holocene rapid climate change events (*2*). We suggest it is possible that, in terms of polar atmospheric circulation, conditions common during the LIA may have persisted into the 20th century and may still persist.

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11. High-resolution [2-cm intervals for the upper 24 m of core (~8 to 10 samples per year) and 25-cm intervals for 25- to 150-m core depth (~0.5 sample per year)] core samples were processed with contamination-free techniques and analyzed for major ion content (Na^+, Mg^{2+}, K^+, Ca^{2+}, NH_4^+, Cl^-, NO_3^-, SO_4^{2-}, and methanesulfonic acid) by ion chromatography similar to procedures described by C. F. Buck *et al.* [*J. Chromatogr.* **594**, 225 (1992)]. Annual layer counting of the Siple Dome core was accomplished with a combination of discrete and continuous (Cl^-, NO_3^-, and liquid conductivity) chemical measurements, stratigraphic layer analysis, and marker horizons (radioactive bomb layers and volcanic events).
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32. We thank R. Alley and Q. Yang for the stratigraphy measurements used in dating the Siple Dome core and D. Giles and D. Kahler (Polar Ice Coring Office), Navy Squadron VXE-6, and Antarctic Support Associates for field assistance. Supported by the Office of Polar Programs, NSF.

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The Influence of Island Area on Ecosystem Properties

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Island area is frequently a major determinant of the species composition of biological communities; community structure, in turn, often has important effects on ecosystem-level properties. Fifty islands of varying area were selected in an archipelago in the northern Swedish boreal forest zone, in which larger islands burn more frequently than smaller ones through wildfire arising from lightning strike, thus inducing a significant relationship between island area and plant species composition. This relationship was found to be a major factor in determining several ecosystem-level properties of these islands, including standing biomass, plant litter decomposition, nitrogen mineralization, terrestrial carbon partitioning, humus accumulation, and plant nitrogen acquisition.

Gradients of island area have frequently been used to help understand the factors responsible for structuring ecological communities (*1*), and it is apparent that the area of islands is important in regulating the occurrence and abundance of component species (*2*) as well as their interactions (*3*). There is an increasing awareness that individual species effects in communities are important determinants of ecosystem-level properties and, consequently, of functioning of the ecosystem (*4*). Therefore, it is expected that islands with different areas and thus different species compositions would contain different ecosystem-level attributes (*5*). However, there have been few attempts at using

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island-area gradients for evaluating processes and factors that operate at the ecosystem-level of resolution (5).

We selected an island archipelago in the northern boreal forest zone of Sweden, located within two adjacent lakes—Lake Hornavan and Lake Uddjaure (65°55′–66°09′N; 17°43′–17°55′E). We chose 50 islands, ranging in area from 0.02 to 15.0 ha (and with these areas being distributed lognormally) which were formed on morainic deposits created by the retreat of land ice 9000 years ago. Our island system is ideal for testing hypotheses relating to island area effects because all the islands are of the same age and origin, and because they have all been subjected to comparatively minor human interference (6). The main disturbance regime on the islands is wildfire by lightning strike; lightning (and therefore wildfire) appears to strike larger islands more frequently than smaller ones, presumably because they have a larger area to intercept. This is reflected in both the vegetation composition (7) and fire history data (8) collected from each of these islands (Table 1). The vegetation data demonstrated that larger islands are dominated by earlier-successional plant species which dominate in the presence of regular wildfire, for example, *Pinus sylvestris* and *Vaccinium myrtillus*, whereas smaller islands show a greater abundance of late successional species which occur in the prolonged absence of fire, for example *Picea abies* and *Empetrum hermaphroditum* (9). Further, evaluation of fire history with both fire-scar data and ^{14}C dating of charcoal particles in humus profiles reveals that the larger islands, in general, have burned much more recently than the smaller ones and have a greater fire frequency (Table 1).

Those late successional plant species that dominate on the smaller islands typically produce foliage and litter of poor quality with high levels of secondary metabolites, principally phenolics (10), and these compounds have the potential to reduce the ability of the soil microflora to decompose substrates and mineralize nutrients (11). Measurements of soil chemical and biological properties (12) were consistent with this—we found higher concentrations of water-soluble phenolics, reduced microbial biomass, and reduced microbial activity in the humus of the smaller islands (Fig. 1). This retardation of microbial activity was also reflected in a reduction of the rates of decomposition and N mineralization of *V. myrtillus* litter placed on the smaller islands (13). Further, the N concentration of both the humus and the added litter was highest on the smaller islands, suggesting that on these islands organic N becomes bound in protein-phenolic complexes, which are notoriously resistant to microbial attack (14). The inhibition of soil biotic processes on the smaller islands probably contributes to the substantial accumulation of

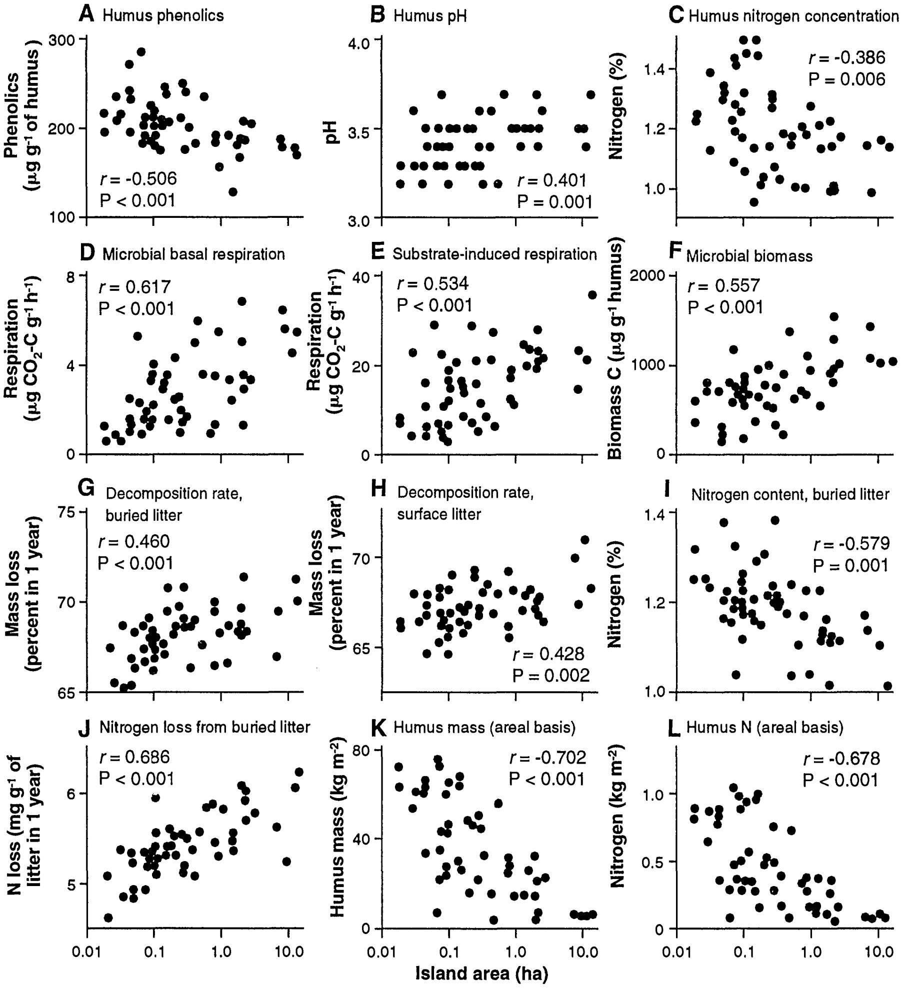

Fig. 1. Humus chemical and biological characteristics in relation to island area. (**A** through **F**) Chemical and biological properties are shown for humus samples collected from each island. Concentrations of phenolics are expressed as microgram of gallic acid equivalent per gram of humus. (**G** through **J**) Properties are shown for leaf litter of *V. myrtillus* placed in litter bags and left to decompose for 1 year. (**K** and **L**) Total mass of humus and humus N was determined on an areal basis.

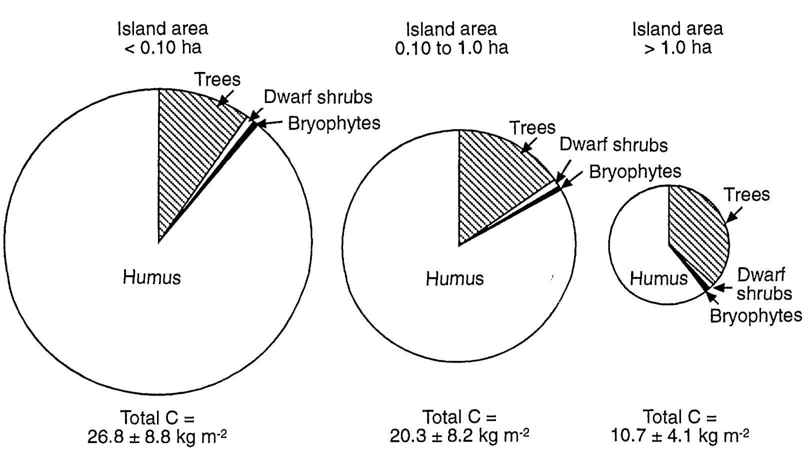

Fig. 2. Proportion of terrestrial C present in humus and plant pools in relation to island area. Total C values are mean ± SD.

humus that occurs on them (Fig. 1); the smallest islands contain up to 10 times more humus per unit area than do the largest ones. Therefore, our results demonstrate that island area is critical in regulating key ecological processes (and therefore ecosystem function) and that this is most likely attributable to plant species effects.

Carbon partitioning is clearly regulated by island area. With increasing island size, there is a distinct trend of an increasing proportion of organic C that is bound in living organisms, especially trees (Fig. 2). Because smaller islands contain much higher terrestrial C levels on an areal basis than do larger ones, our data indicates that wildfire is of critical importance (either directly or indirectly) in reversing C lock-up in boreal forest ecosystems. This finding suggests that deliberate anthropogenic supression of fires in boreal forests over the past century has the potential to lead to retardation of soil biological processes and substantial terrestrial C sequestration (*15*), which is likely to be of global significance given the role of boreal forests in the global C cycle (*16*).

Table 1. Vegetation and fire history characteristics in relation to island area. Values presented are means ± SE.

Species/measurement	Area class		
	<0.1 ha (n = 14)	0.1–1.0 ha (n = 24)	>1.0 ha (n = 12)
Tree stem density (N°/ha)			
Pinus sylvestris	206 ± 82	222 ± 48	410 ± 78
Betula pubescens	1233 ± 229	1707 ± 186	982 ± 214
Picea abies	278 ± 87	211 ± 48	45 ± 22
Total	1720 ± 198	2140 ± 169	1438 ± 201
Tree biomass (kg/m^2)			
Pinus sylvestris	1.697 ± 0.627	2.627 ± 0.563	6.160 ± 0.864
Betula pubescens	0.844 ± 0.198	1.287 ± 0.211	0.887 ± 0.199
Picea abies	1.329 ± 0.323	1.462 ± 0.289	0.332 ± 0.169
Total	3.869 ± 0.624	5.376 ± 0.466	7.385 ± 0.826
Dwarf shrub biomass (kg/m^2)			
Vaccinium myrtillus	0.069 ± 0.014	0.083 ± 0.011	0.119 ± 0.017
Vaccinium vitis-idaea	0.164 ± 0.030	0.215 ± 0.021	0.153 ± 0.025
Empetrum hermaphroditum	0.129 ± 0.024	0.075 ± 0.010	0.060 ± 0.018
Total	0.365 ± 0.022	0.383 ± 0.021	0.332 ± 0.033
Bryophyte biomass (kg/m^2)			
Pleurozium schreberi	0.152 ± 0.038	0.143 ± 0.030	0.155 ± 0.030
Hylocomium splendens	0.121 ± 0.021	0.061 ± 0.016	0.077 ± 0.021
Total	0.283 ± 0.033	0.217 ± 0.027	0.261 ± 0.035
Additional parameters			
Total vegetation biomass (kg/m^2)	4.517 ± 0.616	5.977 ± 0.455	7.979 ± 0.817
Shannon-Weiner species diversity index (H')*	1.784 ± 0.131	1.465 ± 0.065	1.178 ± 0.134
Number of fires in past 250 years	0.143 ± 0.097	0.208 ± 0.085	0.667 ± 0.256
Age of charcoal in years (^{14}C)†	2984 ± 340	2081 ± 428	1106 ± 495

*Index calculated by use of biomass values for each plant species. †Obtained by ^{14}C radiocarbon dating of uppermost charcoal layer in humus profile; n = 5 islands used for each area class.

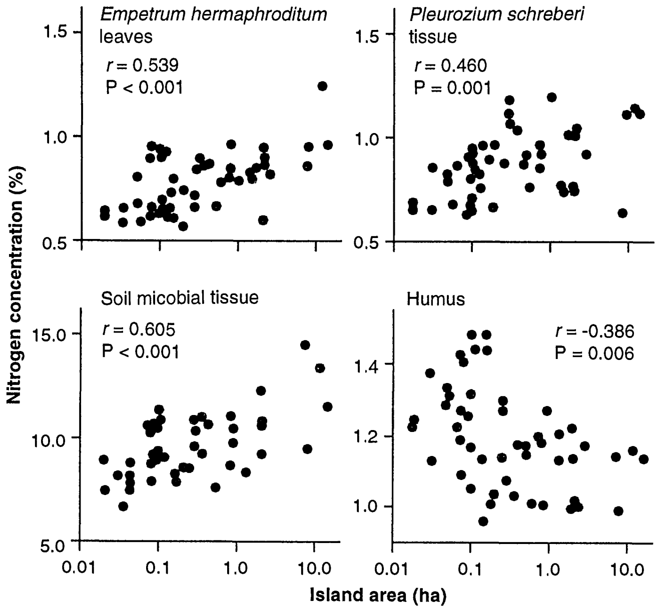

Fig. 3. Total N concentration of selected organisms in relation to island area. The relationship of humus N concentration to island area is included for comparative purposes. The N concentration of leaves from *V. myrtillus* and *V. vitis-idaea* did not show a statistically significant relationship with island area.

There is evidence that N partitioning is also likely to be affected by island area. Although the humus N content was negatively related to island area, the N concentrations of leaves of *E. hermaphroditum*, shoots of the moss *Pleurozium schreberi*, and the soil microbial biomass were all positively related to island area (Fig. 3). This is indicative of enhanced acquisition of N by these organisms, and means that the N present in the humus of the smaller islands is clearly less available to living organisms than that of the larger islands. This again supports the concept that higher levels of phenolics on the smaller islands contribute to reduced N availability. The lower plant tissue N content of plants on smaller islands would be expected to result in subsequently produced plant litter with a lower C:N ratio, and thus, a reduced rate of decomposition (*17*), ultimately resulting in further organic matter accumulation.

Island area studies have potential for investigation of relationships between species diversity and ecosystem-level properties (*5*). In our study, plant species diversity was highest on the smallest islands (Table 1), meaning that ecosystem process rates were lowest on those islands with the greatest diversity. This finding is in direct contrast to other studies which have shown elevated process rates in more diverse communities (*18*). However, we found that the plant biomass of the larger islands was dominated by a single early successional competitive tree species, *P. sylvestris*, which has comparatively favorable litter quality but which contributes to a reduced species diversity. The greater ecological stresses on the smaller islands (due to higher phenolics, lower pH, and reduced N availability) presumably prevented dominance by a single competitive species, resulting in a greater diversity (*19*), but with a greater abundance of those plant species with traits likely to contribute to retarding ecosystem-level processes. Other possible explanations for the discrepancy between our results and earlier investigations (*18*) are that we considered the long-term effects of plant litter and belowground interactions on ecosystem properties, rather than the live-plant effects and productivity aspects that have characterized other studies (*20*); that possible artifact associated with those studies claiming positive effects of species diversity on ecosystem processes has led to incorrect conclusions (*21*); and that long-term feedbacks between plant species composition and ecosystem processes occurred in our study. Our results point to the utility of island archipelago studies in investigating relationships between biodiversity and ecosystem function, and reveal that the nature of such relationships are ultimately dependent on the ecological attributes of each of the plant species present (*22*).

Our study has demonstrated, through the assessment of a range of islands with differing plant communities, that species effects can be of critical importance in determining ecosystem properties, and we suggest that island archipelago studies provide unique, and largely unrealized, opportunities to test hypotheses relating to species effects in ecosystems. In using islands to address ecosystem-level questions, an obvious extension is to address relevant issues through experimentation rather than through the correlation-based approaches that have characterized island biogeography research to date. Ultimately, island-area effects are far more wide-reaching than simply influencing the structure of ecological communities; they are also important determinants of how the ecosystem itself functions.

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7. For evaluation of tree species composition, two circular plots (each 10 m in radius) were established on each island, except for the smallest islands for which only one plot was usually used. In each plot, the diameter of each tree was measured at a height of 1.3 m. Established relationships for converting diameter into biomass for each species [L. G. Marklund, *Biomassafunktioner för Tall, Gran och Björk i Sverige* (Sveriges Lantbruksuniversiteit, Umeå, Sweden, 1988)] were used for determining total tree biomass on an areal basis. In the area used for these plots, four plots of 0.5 m by 0.5 m were also established, and all dwarf shrub and moss species were trimmed at ground level and sorted into component species. All trimmed material was dried at 80°C for 24 hours for biomass determinations, and leaf subsamples of the dwarf shrubs *E. hermaphroditum, V. myrtillus*, and *V. vitis-idaea* and shoot samples of the bryophyte *P. schreberi* were measured with micro-Kjeldahl analysis for N concentration. All plots were centered 5 to 15 m from the island edge and were always similar distances from the shore, regardless of island area, to prevent edge and climate effects from confounding the results.
8. The trees on each island were searched for fire scars to determine how many fires had occurred on that island in the past 250 years; the time elapsed since each fire was determined by counting tree rings [O. Zackrisson, *Oikos* **29**, 22 (1977)]. For five islands in each of the three area classes (<0.1 ha, 0.1 to 1.0 ha, and >1.0 ha), charcoal particles in the uppermost charcoal layer in the humus profile were sampled, and the time since the last fire was determined by ^{14}C analyses of these particles at the Tandemlaboratory, Uppsala, Sweden [I. U. Olsson, in *Handbook of Palaeoecology and Palaeo-Hydrology*, B. E. Berglund, Ed. (Wiley, London, 1986), pp. 272–310; S. Bouwman, *Radiocarbon Dating* (British Museum Publications, London, 1990)]. We emphasize that the age of the charcoal we measured is not necessarily the same as the time of the most recent fire, because charcoal from fires with low intensity is sometimes undetectable in humus profiles; fire-scar data on the largest islands indicated occurrence of fires that were obviously more recent than the uppermost charcoal we found.
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12. Humus samples were collected to the entire humus depth from each of the four plots used for ground-layer vegetation determination (*7*) and were combined for each island. Total water-soluble phenolics were measured for aqueous extracts by use of Folin-Ciocalteu reagent [G. Marigo, *Analytica* **2**, 106 (1973)]; nitrogen was determined by micro-Kjeldahl analysis. Microbial basal respiration and substrate-induced respiration (a relative measure of active microbial biomass) [J. P. E. Anderson and K. H. Domsch, *Soil Biol. Biochem.* **10**, 215 (1978)] were determined through the use of a modified form of infrared gas analysis [D. A. Wardle, *Funct. Ecol.* **7**, 346 (1993)]. The fumigation-extraction approach was used for determining total microbial biomass C [E. D. Vance, P. C. Brookes, D. S. Jenkinson, *Soil Biol. Biochem.* **19**, 703 (1987)] and N [P. C. Brookes, A. Landman, G. Pruden, D. S. Jenkinson, *ibid.* **17**, 837 (1985)].
13. Litter decomposition was determined by use of litter bags. We placed 10 litter bags on each island (approximately 10 m from the shore) on 22 to 27 June 1995; each contained 0.5 g air-dried litter of *V. myrtillus.* Five of these bags were placed on the humus surface, while the other five were buried at a depth of 8 cm. These were retrieved on 18 to 25 June 1996, and the litter weight remaining and litter N concentration were determined, the latter through micro-Kjeldahl analysis.
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20. Nearly all studies that have claimed to identify positive effects of species diversity on ecosystem function involve relatively short-term experiments in which species richness of live plants has been manipulated. However, most plant productivity eventually enters the decomposer subsystem as litter, where it has important long-term "afterlife effects" [S. Findlay, M. Carreiro, V. Krischic, C. J. Jones, *Ecol. Appl.* **6**, 269 (1996)]. Those studies that have explicitly investigated effects of species diversity of litter, or of organisms associated with litter breakdown, on ecosystem processes have failed to find simple cause-effect relationships [O. Andrén, M. Clarholm, J. Bengtsson, in *The Significance and Regulation of Soil Biodiversity*, H. P. Collins, G. P. Robertson, M. J. Klug, Eds. (Kluwer, Dordrecht, Netherlands, 1995), pp. 141–151; D. A. Wardle, K. I. Bonner, K. S Nicholson, *Oikos* **79**, 247 (1997)]. Our study represents a situation in which ecosystem properties are largely regulated by the decomposer subsystem in the long-term perspective.
21. A recent critique [M. A. Huston, *Oecologia*, **110**, 449 (1997)] of those experimental studies claiming evidence for cause-effect relationships between species diversity and ecosystem properties (*18*) proposes that the observed trends can be explained in terms of "hidden treatments" affecting plant productivity independent of species diversity, and which are manifested through problems with experimental design, inappropriate interpretation of data, and incorrect application of statistical techniques. If this is the case, then presumably cause-effect relationships between diversity and ecosystem properties could have been detected in those studies even if they did not exist.
22. Plant communities are not random assemblages of species [J. B. Wilson and S. H. Roxburgh, *Oikos* **69**, 267 (1994)], and plant species that dominate in low-diversity situations probably have very different ecophysiological traits from those that dominate in high-diversity situations. These traits regulate the ecological performance of plant species, including their participation in biotic interactions [P. D. Coley, J. P. Bryant, F. S. Chapin III, *Science* **230**, 895 (1985); J. P. Grime *et al.*, *Oikos* **79**, 259 (1997)] and responses to disturbances [C. W. MacGillivray *et al.*, *Funct. Ecol.* **9**, 640 (1995)]; this is, in turn, likely to have important effects at the ecosystem level of resolution [P. B. Raich, M. B. Walters, D. S. Ellsworth, *Ecol. Monogr.* **62**, 365 (1992)], including ecosystem function.

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