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Ecosystem Properties and Forest Decline in Contrasting Long-Term Chronosequences

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During succession, ecosystem development occurs; but in the long-term absence of catastrophic disturbance, a decline phase eventually follows. We studied six long-term chronosequences, in Australia, Sweden, Alaska, Hawaii, and New Zealand; for each, the decline phase was associated with a reduction in tree basal area and an increase in the substrate nitrogen–to-phosphorus ratio, indicating increasing phosphorus limitation over time. These changes were often associated with reductions in litter decomposition rates, phosphorus release from litter, and biomass and activity of decomposer microbes. Our findings suggest that the maximal biomass phase reached during succession cannot be maintained in the long-term absence of major disturbance, and that similar patterns of decline occur in forested ecosystems spanning the tropical, temperate, and boreal zones.

After catastrophic ecosystem disturbance, primary succession occurs; this involves an initial period of ecosystem development leading to a maximal biomass stage. The build-up phase has been extensively studied and is characterized by broadly predictable changes in ecosystem productivity, biomass, nutrient availability, and soil processes (*1–4*). However, in the prolonged absence of catastrophic disturbance in either late primary or secondary succession, a decline or regressive phase often follows, during which there is a significant reduction in ecosystem productivity and standing plant biomass (*5–7*). Unlike the build-up phase, the decline phase and associated ecosystem-level changes are poorly understood. Yet an improved understanding of this decline phase is essential for evaluating the mechanistic basis of forest decline as well as the long-term importance of disturbance in maintaining ecosystem properties and processes.

Here we assess changes that occur in several properties that can be related to the functioning of ecosystems in the long term (that is, on the order of at least several thousand years) along each of six well-established chronosequences (Table 1, table S1, and fig. S1). Each chronosequence represents a series of sites varying in age since surface formation or catastrophic disturbance, but with all other extrinsic driving factors being relatively constant. In any chronosequence, the older stages would previously have been subjected to climatic regimes that were different from the present regime; however, our study seeks only to relate ecosystem properties under the present climatic regime to substrates of varying ages since their formation. Each of the six sequences has previously been shown to endure long enough for a decline in standing plant biomass to occur. They range from 6000 to over four million years old and represent a range of locations, macroclimatic conditions, parent materials, and agents of disturbance forming the chronosequence.

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Fig. 1. Tree basal area in relation to stage of chronosequence. For the Arjeplog succession, island size is used as a surrogate for successional age (time since the last fire), with island size decreasing with increasing age; there is a strong negative relation between island size and the time since the island last burned (5, 9). Each R^2 value was determined using polynomial regressions, with each data point representing an independent data value; for all sequences except Arjeplog, the independent variable (chronosequence stage) was treated as a rank variable, whereas for Arjeplog the independent variable was log-transformed island area (19). The use of rank-transformed values for chronosequence stage is justified because of the high level of uncertainty in assigning precise ages for many of the chronosequence stages. Polynomial terms (linear, quadratic, or cubic) were only included in each regression when they significantly improved R^2 values at $P = 0.05$. Information on ages and vegetation for each stage for each chronosequence is given in table S1 and fig. S1, and the total length of each sequence is given in Table 1.
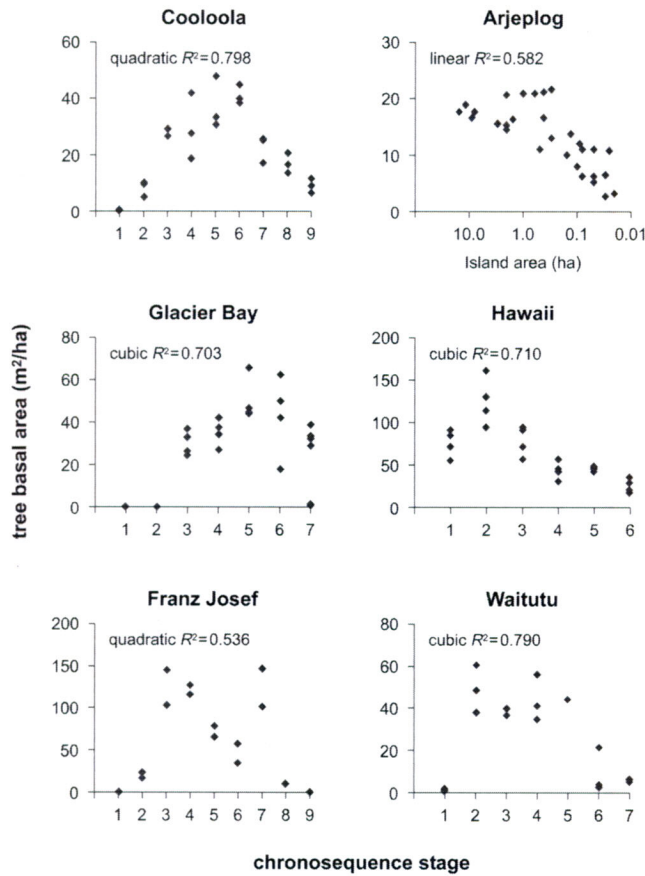
The six sequences that we studied are the Cooloola sand dune sequence in eastern Australia (6, 8), the Arjeplog lake island sequence in northern Sweden (5, 9), the Glacier Bay sequence in Alaska (10, 11), the Hawaiian islands chronosequence (7, 12), and the Franz Josef (13–15) and Waitutu (16–18) sequences in New Zealand. These chronosequences have been formed by very different processes: aeolian sand movement, wildfire, glacial retreat, volcanic lava flow, glacial retreat, and uplift of marine terraces, respectively. In all six cases, long-term ecosystem development has taken place after a catastrophic disturbance event or an event of sufficient severity to significantly reset the successional clock; in five of these cases, this has involved the creation of an entirely new surface for primary succession to occur on. The sixth case (the Arjeplog sequence) represents a secondary succession reset by wildfire, but we argue that ecosystem processes in the decline phase of either primary or secondary succession are comparable (3). In combination, these six sequences represent a natural experiment for studying whether predictable changes in ecosystem properties occur during the decline phase of ecosystems. We focus on whether similar trends occur across these chronosequences, with particular emphasis on the decline phase, for a suite of variables that are relevant to ecosystem functioning, biogeochemical cycling, and the performance of the decomposer subsystem.

Table 1. Characteristics of chronosequences investigated. Details on the vegetation and estimated age of each stage of each chronosequence are given in table S1.

| Chronosequence	Latitude and longitude	Mean temp. (°C)		Mean annual precipitation (mm)	Cause of chronosequence	Parent material	Duration of chronosequence (years)	Refs.
		January	July					
Cooloola, Australia	27°30'S, 153°30'E	25	16	1400–1700	Sand dunes of varying age caused by aeolian sand deposition	Sand derived from quartz grains	>600,000	(6, 8)
Arjeplog, Sweden	65°02'N, 17°49'E	−14	13	750	Islands with varying time since last major fire	Granite boulders; moraine	6,000	(5, 9)
Glacier Bay, Alaska	59°N, 136°W	−3	13	1400	Surfaces of varying ages caused by glacial retreat	Sandstone, limestone, igneous intrusions	14,000	(10, 11)
Hawaii	19–22°N, 155–160°W	14	17.5	2500	Surfaces of varying ages caused by volcanic lava flow	Basalt tephra	4,100,000	(7, 12)
Franz Josef, New Zealand	43°25'S, 170°10'E	15	7	3800–6000	Surfaces of varying ages caused by glacial retreat	Chlorite schist, biotite schist, gneiss	>22,000	(13–15)
Waitutu, New Zealand	46°06'S, 167°30'E	12	5	1600–2400	Terraces of varying ages caused by uplift of marine sediments	Mudstones and sandstones	600,000	(16–18)

Measurements of tree basal area (a surrogate of tree biomass) (19) show broadly consistent patterns across the six chronosequences (Fig. 1). For five of the six sequences, a build-up phase of tree biomass was apparent (the Arjeplog sequence did not include stands that were sufficiently young for the build-up phase to be assessed). In all cases, the maximal biomass phase was transient, although the duration of this phase varied across chronosequences. Further, all six sequences showed a distinct decline phase of tree basal area during the later stages of the sequence (Fig. 1). In all cases, the tree basal area of the final stage of the sequence was less than half that of the phase with the greatest basal area, and for one sequence (Franz Josef) the final phase no longer supported tree vegetation. For all the sequences, the decline in basal area became noticeable within thousands to tens of thousands of years after the start of the chronosequence. Therefore, despite the obvious differences in terms of extrinsic factors among the six systems that we investigated, there were reasonably similar patterns of ecosystem decline during the latter phases of each of the chronosequences. This means that the high standing biomass of forests during the maximal biomass phase represents a transitional state and cannot be maintained in the long-term absence of catastrophic disturbance.

In each of the chronosequences, the primary cause of the decline phase should be reduced favorability of the soil for plant growth. It has previously been proposed that in Hawaii and Franz Josef, the decline phase is due to phosphorus (P) limitation over time (7, 13) and that at Arjeplog and Glacier Bay, the decline is due to increasing nitrogen (N) limitation (9, 10). Stoichiometry of major elements [notably carbon (C):N:P], is increasingly being suggested as a major ecological driver (20, 21). For each stage in each succession, we assessed the ratios of C:N, C:P, and N:P for both the humus substrate and fresh litter for each of the dominant plant species present. For the humus, there were statistically significant increases toward the latter phase of each of the six chronosequences for both N:P (Fig. 2) and C:P ratios (22). For all six chronosequences, the humus N:P ratio exceeded the Redfield ratio (the ratio above which P becomes limiting for biological processes relative to N) (23) during the decline phase of the succession (Fig. 2). When the means of the litters of all the dominant plant species of each plot were considered, there was also a significant increase in the N:P ratio at the final stages of the Cooloola, Glacier Bay, and Franz Josef chronosequences. The Hawaiian chronosequence also showed a significant increase in mean litter N:P ratio over time when data

from the third chronosequence stage were excluded from the analysis; this third stage supported *Acacia koa* trees that fix N and had an anomalously high litter N:P ratio.

These results provide evidence that during the decline phase (which usually becomes apparent a few thousand years after chronosequence initiation), P becomes increasingly limiting relative to N in the humus layer, and that for some chronosequences this is subsequently followed by reduced concentrations of P in the litter that the vegetation produces. This is consistent with N being biologically renewable whereas P is not, and with P often being subjected to leaching and occlusion in strongly weathered soils (12). Therefore, over time, P should become depleted from the ecosystem, as well as less available, relative to N. In this light, it is relevant that significant biological N fixation has been measured in the decline phase of the Hawaiian sequence (24) as well as in late successional forests in northern Sweden that are comparable to the late decline stages of the Arjeplog succession (25). Furthermore, shrubs capable of symbiotic N fixation are common in the latest stages of the Cooloola sequence. The fact that the humus N:P ratio showed a relatively small increase during the decline phase in the Hawaiian sequence relative to the other five sequences may be because P is replenished in the later stages of that chronose-

Fig. 2. N:P ratios for humus and fresh litter (the mean of all dominant species for each plot) in relation to stage of chronosequence. The Redfield ratio (N:P = 16) is shown in each panel as a horizontal dashed line. For the Arjeplog succession, island size is used as a surrogate for successional age, with island size decreasing as age increases. All R^2 values were determined using polynomial regressions as described in Fig. 1. For the R^2 determination for Hawaii (litter), data from stage 3 are omitted because anomalously high ratio values are attributable to dominating effects of an N-fixing tree (*Acacia koa*) that is absent from all other stages. Waitutu humus ratio values were log-transformed before R^2 determination.
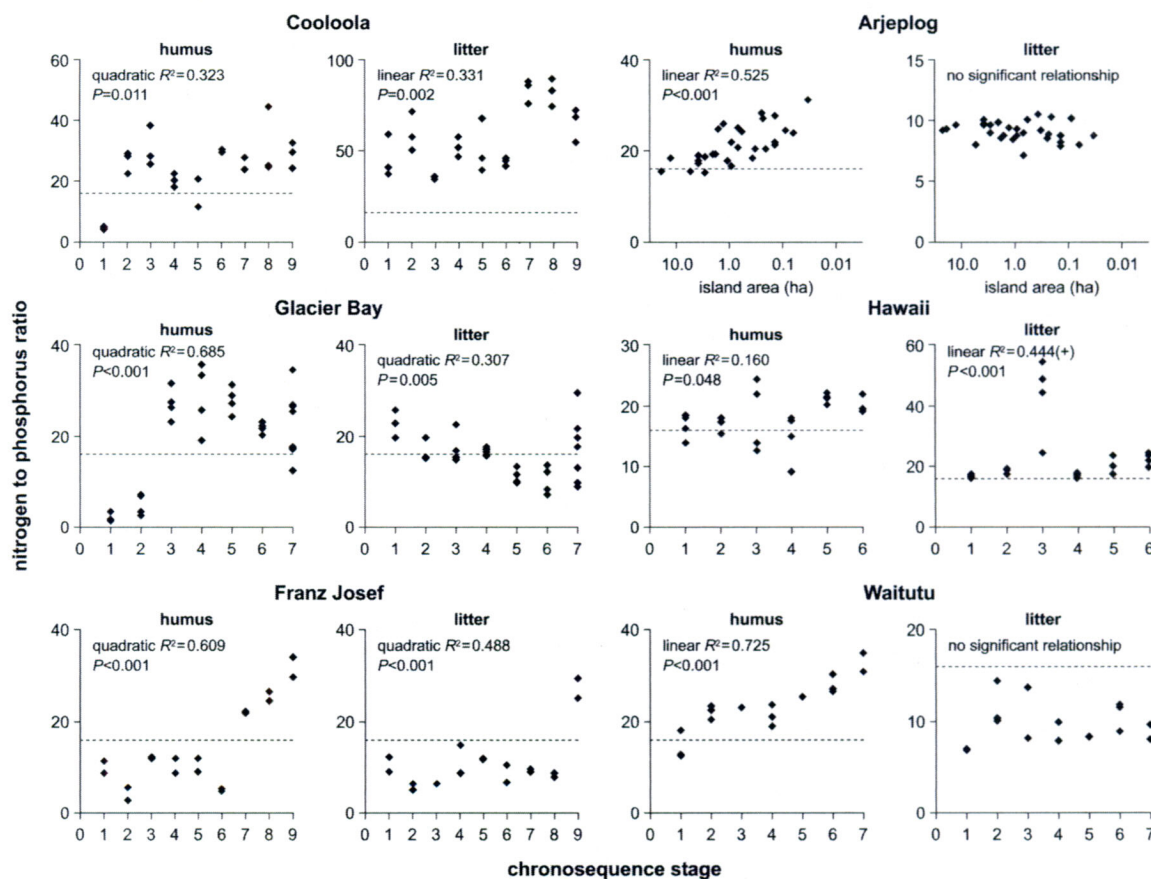
Table 2. Relations between properties indicative of decomposer activity or biomass and ecosystem developmental stage for each of six chronosequences, shown as R^2 values and the nature of relation. All R^2 values were determined using polynomial regressions as described in Fig. 1. PLFA, phospholipid fatty acids; NS, no significant relation at $P = 0.05$.

Response variable	Cooloola	Arjeplog	Glacier Bay	Hawaii	Franz Josef	Waitutu
Litter decomposition rate	Negative linear 0.211*	NS	Positive linear 0.530***	Positive linear 0.530***	Negative linear 0.544***	Negative quadratic 0.505***
Litter N loss rate	Negative linear 0.293**	NS	Positive cubic 0.519***	NS	NS	NS
Litter P loss rate	Negative quadratic 0.313*	NS	Negative quadratic 0.183*	Negative cubic 0.482**	Negative linear 0.303*	Positive linear 0.386**
Humus basal respiration	Negative cubic 0.495***	Negative linear 0.269*	Negative quadratic 0.447***†	NS	Negative linear 0.667***	Negative quadratic 0.431*
Humus microbial biomass	Negative cubic 0.495***	Negative linear 0.191*	Negative quadratic 0.697***†	Positive linear 0.195*†	Negative linear 0.476**	Negative quadratic 0.340*
Humus total microbial PLFAs	Negative quadratic 0.434***	NS	Negative quadratic 0.621***	Negative cubic 0.479***†	NS	Positive quadratic 0.610***
Humus bacterial-to-fungal ratio	Negative quadratic 0.595***	Positive linear 0.191*	Negative quadratic 0.555***	NS	NS	Negative quadratic 0.637***

*, **, ***Relation statistically significant at $P = 0.05$, 0.01, and 0.001 respectively.   †Response variable log-transformed before analysis.

quence from significant deposits of wind-blown dust from Asia (*26*).

Producer and decomposer subsystems function in tandem to maintain ecosystem functioning (*27*). Therefore, we also assessed whether plant biomass reduction during the decline phase was matched by impairment of decomposer processes and organisms. We assessed the loss of mass, N, and P from litter of each of the dominant plant species from each plot along each chronosequence, by using a standardized laboratory bioassay (*19*) (Table 2). Consistent with predictions that litter quality should decline during the ecosystem decline phase of succession (*27, 28*), we found that litter mass loss rates declined throughout each of the Cooloola, Franz Josef, and Waitutu chronosequences (Table 2). Unexpectedly, two chronosequences showed the reverse trend. Only two sequences showed significant trends for litter N release, but for four of the sequences there were statistically significant reductions in litter P release rates during the decline phase (Table 2). These reductions point to increased retention of P within plant litter during the chronosequence stages in which the growth of plants was being impaired.

Soil microbial biomass is an important driver of decomposition processes and regulates the supply of plant-available nutrients from the soil (*29*). For all sequences except Hawaii, microbial biomass and respiration showed a marked decline during the latter (decline) phase (Table 2). Furthermore, for the Glacier Bay and Waitutu sequences, these two variables were optimized at the intermediate stage of the sequence, coincident with the time when tree basal area is also maximal. For three of the sequences, the soil bacterial-to-fungal biomass ratio was optimized

in the intermediate stages of the sequence (Table 2), indicating that fungi become increasingly important relative to bacteria as ecosystem decline proceeds. Because fungal-based soil food webs promote less leaky nutrient cycles that are more retentive of nutrients than do bacterial-based food webs (*30*), nutrient cycles become increasingly closed during retrogression and nutrients therefore become less available.

Our results show that characteristic changes occur in forested ecosystems when they are not subjected to catastrophic disturbances over time spans on the order of thousands of years. There is a consistent pattern of plant biomass decline, accompanied by an increased limitation of P relative to N and a reduced rate of release of P from decomposing litter. At least half of the chronosequences also showed similar trends in other properties related to the decomposer subsystem during the decline phase, such as reduced decomposability of litter from dominant plant species, reduced soil respiration and microbial biomass, and reduced ratios of bacterial to fungal biomass.

Our results have several implications. First, they suggest that the decline of natural forests, which is often observed in the long-term absence of catastrophic disturbance, may arise through increasing limitation by P and reduced performance of the decomposer subsystem. Although N is frequently proposed as the primary limiting nutrient in forests [especially in the temperate zone (*31*)], P is arguably more limiting for systems that have been free of such disturbances for lengthy periods. Second, the results show that the maximal biomass phase (and associated rates of ecosystem processes) attained after primary or

secondary succession cannot be maintained in the long-term absence of major disturbances. Finally, they point to consistencies in patterns of ecosystem decline after the long-term absence of disturbance in very different systems representing the tropical, temperate, and boreal zones.

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Shifts in Deep-Sea Community Structure Linked to Climate and Food Supply

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A major change in the community structure of the dominant epibenthic megafauna was observed at 4100 meters depth in the northeast Pacific and was synchronous to a major El Niño/La Niña event that occurred between 1997 and 1999. Photographic abundance estimates of epibenthic megafauna from 1989 to 2002 show that two taxa decreased in abundance after 1998 by 2 to 3 orders of magnitude, whereas several other species increased in abundance by 1 to 2 orders of magnitude. These faunal changes are correlated to climate fluctuations dominated by El Niño/La Niña. Megafauna even in remote marine areas appear to be affected by contemporary climatic fluctuations. Such faunal changes highlight the importance of an adequate temporal perspective in describing biodiversity, ecology, and anthropogenic impacts in deep-sea communities.

The deep sea occupies more than two-thirds of the Earth's surface. This vast area remains largely unexplored, especially in terms of its biota. Only a very small fraction of the deep sea has been sampled spatially, and few areas have been sampled temporally. The deep sea is isolated from ocean surface conditions in several ways, including the negligible penetration of light and millennial-scale vertical circulation of deep water masses (*1*). Time-series studies have shown, however, that the deep sea can experience rapid inputs of food supplies from overlying surface waters (*2*), as well as rapid responses by micro- and macrofaunal taxa such as foraminifera (*3*). It has since been hypothesized that climate fluctuations such as those related to El Niño/La Niña could be affecting deep-sea communities through long-term variations in the food supply (*4*). Here we examine variations in the abundance of mobile epibenthic megafauna at an abyssal location in the northeast Pacific over a 14-year study period. The influences of climate and food supply on megafaunal abundance and community structure are also assessed.

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A long time-series station, Station M (34°50′N, 123°00′W) was established in the northeast Pacific at 4100-m depth to study benthic boundary-layer processes and deep-sea ecology from 1989 through 2002. This study site is influenced by seasonal pulses of particulate organic matter that reach the sea floor after sinking from overlying surface waters (*5*, *6*). Echinoderms dominate the conspicuous mobile epibenthic megafauna on the sea floor at Station M (*7*), and they are known to rapidly ingest settling particles at the site (*8*). Short-term analysis over two 12-month periods before 1996 revealed no discernible temporal change in echinoderm abundance and no correlation with food supply (*7*, *9*).

We analyzed 48 photographic line transects across the sea floor from 1989 to 2002 at Station M to determine the abundance of mobile epibenthic megafauna (animals conspicuous in photographs and typically ≥1 cm in size). These transects were typically conducted seasonally, but this frequency was variable because of logistical constraints (*10*). Results indicate that the holothuroid *Elpidia minutissima* increased in abundance from 1989 through 1996, peaking at ~1 individual per m², but then decreased markedly during a hiatus in sampling from 1999 to 2000, as none were subsequently observed in 2001 to 2002 (Fig. 1A). Another

species of holothuroid, *Peniagone vitrea*, showed a similar overall trend in abundance, remaining relatively stable in numbers through 1998 but then declining sharply in 2001 and 2002 (Fig. 1A). In contrast, the holothuroids *P. diaphana*, *Abyssocucumis abyssorum*, *Scotoplanes globosa*, *Psychropotes longicauda* (Fig. 1B), the echnoid group *Echinocrepis* spp., and the ophiuroid group *Ophiura* spp. (Fig. 1C) occurred in lower abundances through most of the time series but increased substantially during 2001 and 2002. The abundance of *P. diaphana* also had a notable increase in 1995.

A Bray-Curtis similarity analysis was applied using the ten most dominant mobile epibenthic megafauna over the 14-year period and revealed a major dissimilarity in abundances between the 1989 to 1998 and 2001 to 2002 periods (*10*) (Fig. 2). When examined as separate species, the abundances of six taxa, *E. minutissima*, *P. vitrea*, *S. globosa*, *Ps. longicauda*, *Echinocrepis* spp., and *Ophiura* spp., were significantly different between the two periods (Mann Whitney U Test, $P < 0.05$).

Climate has been implicated in the fluctuations of many Pacific pelagic communities ranging from plankton (*11–14*) to fishes (*15*, *16*). There are also indications that a regime shift may have occurred in the north Pacific in 1998 to 1999 (*15–18*). Our studies have revealed that shifts in the abundance of epibenthic megafauna in the deep sea also correlate to three indices expressive of El Niño/La Niña (Table 1): the Northern Oscillation Index (NOI), the Southern Oscillation Index (SOI), and the Multivariate El Niño–Southern Oscillation Index (MEI) (*10*) (Fig. 1E). Cross-correlation coefficients between climate and abundance of the holothuroids *E. minutissima*, *P. vitrea*, *A. abyssorum*, *Synallactes* sp., and *S. globosa* peaked with abundance lagging climate by 11 to 22 months (Table 1). The relative temporal differences in correlations between climatic indices and megafauna abundance may be indicative of the connection between index parameters and pelagic-benthic processes at Station M, as well as the responsiveness of a particular taxon to any changes in climatic processes.

Further investigation explored whether climatic shifts were related to changes in food