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Empirical Evidence that Declining Species Diversity May Alter the Performance of Terrestrial Ecosystems

Shahid Naeem, Lindsey J. Thompson, Sharon P. Lawler, John H. Lawton and Richard M. Woodfin

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Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems

SHAHID NAEEM*, LINDSEY J. THOMPSON, SHARON P. LAWLER§, JOHN H. LAWTON AND RICHARD M. WOODFIN

NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.

SUMMARY

We examined experimentally the association between species diversity and ecosystem processes in a series of terrestrial mesocosms. We developed and maintained 14 mesocosms whose biota were assembled from a single pool of plant and animal species and whose environmental conditions were identically controlled. Each community contained four trophic levels: primary producers (annual herbs), consumers (herbivorous molluscs and phloem sucking insects), secondary consumers (parasitoids) and decomposers (earthworms, Collembola and microbes). All mesocosms received the same diurnal pattern of light, temperature, relative humidity and water. The initial volume of soil, soil structure, composition, nutrient content and inocula of both soil microbes and nematodes were also identical among replicates. The only experimentally manipulated factor was the number of plant and animal species within each trophic level. High, medium and low diversity communities had nine, 15 or 31 plant and animal species, respectively. We measured five ecosystem processes as response variables in these mesocosms over the course of 206 days: (i) community respiration; (ii) productivity; (iii) decomposition; (iv) nutrient retention; and (v) water retention.

The manipulation of diversity produced communities that differed significantly in their ecosystem processes. Our results provide the first evidence (obtained by a direct manipulation of diversity under controlled environmental conditions) that ecosystem processes may be affected by loss of diversity.

1. INTRODUCTION

Biological communities and their associated chemical and physical processes are collectively referred to as ecosystems (Tansely 1935; Odum 1971, 1993). Within ecosystems, physical and chemical processes governed by biological activities are known variously as ecosystem processes (Odum 1993), biogeochemical processes (reviewed in Schlesinger 1991), ecosystem functions (reviewed in Schulze & Mooney 1993) or, anthropocentrically, as ecosystem services (e.g. Ehrlich & Wilson 1991). Species within an ecosystem can be divided either into functional groups defined by a commonality of biogeochemical activities among group members or into trophic groups defined by a commonality of resource use by group members. These species groups contribute both to the gross flow of energy through, and the cycling of nutrients within an ecosystem. The loss of a functional group (e.g. all nitrogen fixers) or trophic group (e.g. all primary producers) would clearly alter the biogeochemical processes of an ecosystem. What is less clear, however, is whether the loss of a few or a fraction of the species within a functional or trophic group also affects the biogeochemical performance of an ecosystem.

Soulé (1991) estimated that as much as 50% of biotic diversity will be lost in the next century as a direct result of activities associated with human expansion. Although exact numbers and timescales for extinctions are difficult to derive (Lawton & May 1995), it is well documented that biodiversity – species richness and community complexity – is declining in the face of human expansion (Wilson & Peter 1988; Groombridge 1992). Global declines in biotic diversity imply that the world's ecosystems are losing species, posing the question: 'will depauperate, but nevertheless intact, ecosystems (containing primary producers, consumers and decomposers) perform differently from the more species-rich systems from which they are derived?'

Considerable experimental research has been devoted to the understanding of the factors which control diversity in ecosystems (Ricklefs & Schluter 1993) beginning with the early work on distribution and abundance of Elton (1927) to the more recent syntheses of the 1970s and 1980s (Cody & Diamond 1975; Price *et al.* 1984; Strong *et al.* 1984; Diamond & Case 1986; Kikkawa & Anderson 1986; Gee & Giller 1987). Similarly, research has been centred on the under-

* Current Address: Department of Ecology, Evolution and Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, Minnesota 55108, U.S.A.
§ Current Address: Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506, U.S.A.

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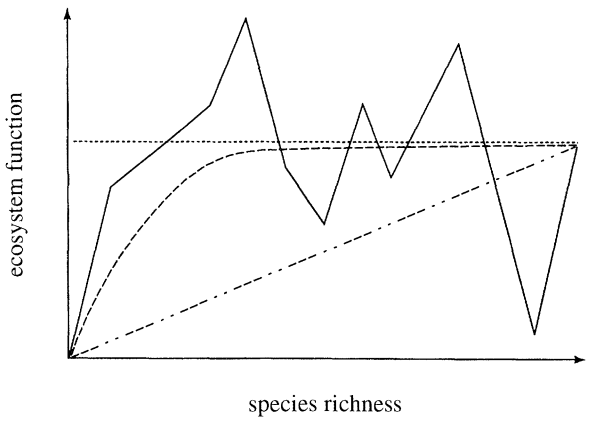

Figure 1. Hypothetical relations between species diversity (richness) and the level of expression of an ecosystem process, such as community respiration, community productivity or rate of decomposition. Dashed line, 'redundant species' hypothesis; dot-dashed line, 'rivet' hypothesis; solid line, 'idiosyncratic response' hypothesis; dotted line, 'null' hypothesis. The point of conversion to the right of the figure represents current level of species richness, not necessarily the maximum richness possible in a community.

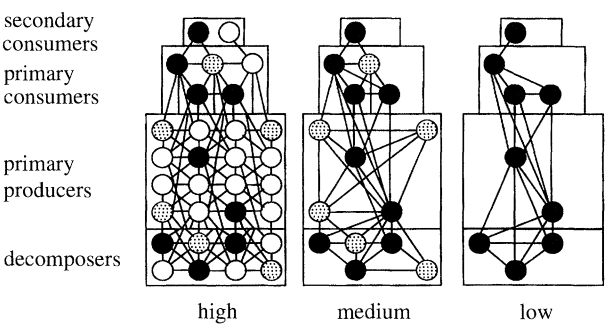

Figure 2. Schematic representation of the Ecotron experiment. The experiment consisted of terrestrial communities that were either 'high', 'medium', or 'low' in species diversity (numbers of species and biotic complexity). Circles represent individual species present in the different types of communities (see table 1). Shading of circles illustrates nested heirarchy of species representation in each community. Filled circles indicate species in all communities, grey circles indicate species only in high and medium diversity and open circles indicate species only in high diversity communities. Thus, communities to the right represent increasingly depauperate versions of communities on their left. Lines indicate biotic interactions among the species (for clarity, not all interactions are shown). Boxes indicate trophic levels. Note that each community contained species in all four trophically defined functional groups, irrespective of the total number of species in each community (from Naeem *et al.* 1994).

standing of nutrient and energy flows (Odum 1993), beginning with the early work of Lindeman (1942) to more modern syntheses (e.g. Margalef 1968; Odum 1971; De Angelis 1992). Recent reviews of the literature (Mooney & Schulze 1993) show, however, that less attention has been paid to how these changes in diversity are associated with changes in nutrient and energy flow.

From the limited literature available on the subject, four hypotheses summarize the possible general responses of ecosystems to declining species diversity. The first hypothesis, the 'redundant species' hypothesis, suggests that there is a minimum diversity necessary for ecosystem function but beyond that, most species are redundant in their roles (Lawton & Brown 1993). A second, contrasting view is the 'rivet' hypothesis which suggests that species are largely unique in their contribution to ecosystem performance (Ehrlich & Ehrlich 1981). This hypothesis likens species to the rivets holding together a complex machine and postulates that the function of an ecosystem will be altered or impaired as its rivets (species) fall out. A third view, the 'idiosyncratic response' hypothesis suggests that ecosystem processes change when diversity changes but that the response is unpredictable. Finally, the 'null' hypothesis is that ecosystem functions (i.e. processes) are insensitive to species deletions or additions (Vitousek & Hooper 1993). Although these hypotheses are general, serving as primarily heuristic devices to facilitate scientific discourse, they are nevertheless testable because each predicts a specific relation between diversity and ecosystem function (see figure 1).

There are currently no direct, empirical tests of figure 1 in which species richness only has been manipulated. Studies of the levels of expression of ecosystem processes across diversity gradients created by succession (e.g. Ewel *et al.* 1991), nutrient additions (e.g. Tilman & Downing 1994) or geographic clines in geological or climatic conditions (reviewed in Rosenzweig & Abramsky 1993) are difficult to interpret. Ecosystem responses in these studies are correlated not only with varying levels of diversity but also with the factor responsible for creation of the diversity gradient in the first place (for example, successional age, nutrient level, or the temperature, rainfall and edaphic changes that occur along geographical gradients).

Ideally, a direct manipulation of diversity would hold all other ecological factors constant while manipulating species richness as a single experimental factor alongside replication. It would also ensure that entire functional or trophic groups are not removed from the experimental community. Including representatives from all major groups provides a reasonable test of the hypotheses because there is no *a priori* reason for the level of expression an ecosystem process to be seriously impaired if all functional or trophic groups are present but species richness is altered. Response variables would be one or more ecosystem processes and population responses within functional or trophic groups could be monitored to gain insight into possible mechanistic explanations for the observed responses.

We have provided a brief report (Naeem *et al.* 1994) of such an experiment: to our knowledge the experiment reported here is unique. Previous experiments have either manipulated only one species group or manipulated diversity indirectly. Intercropping experiments directly manipulate crop diversity in agroecological experiments but they seldom manipulate more than two or three species, generally manipulating only one trophic group, for example plant species (Swift & Anderson 1993). Ewel *et al.* (1991), Tilman & Downing (1994) and McNaughton's New York grass

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experiments (1993) similarly manipulate only plant species, manipulating diversity only indirectly. Note that manipulations of plant and animal diversity have a long history in community ecology (Begon *et al.* 1986; Ricklefs & Schluter 1993) and our experiment builds on results from these earlier works.

We conducted the present experiment (Naem *et al.* 1994) using a controlled environmental facility called the Ecotron (Lawton *et al.* 1993). We manipulated species richness experimentally within trophic groups in replicate model terrestrial communities while holding all other experimental variables constant. Biotically complex communities were constructed with species diversity varied between them so that some replicates represented depauperate versions of others. All mesocosms, however, contained the same number of trophic levels and the same initial densities of individuals in trophic groups. We monitored both ecosystem and population responses to the treatment. Figure 2 presents a schematic summary of the experimental design.

2. MATERIALS AND METHODS

(*a*) *Mesocosm development and maintenance: controlled environmental facility*

The Ecotron (Lawton *et al.* 1993) consists of two banks of eight chambers, each chamber measures 2 m × 2 m × 2 m. Temperature, humidity, light and water are controlled by a computer and a 24 h diurnal pattern without seasonality was maintained (see figure 3). Each mesocosm was grown in a separate chamber. Increasingly, this type of approach (using micro- and mesocosms) is being used to examine complex issues of community and ecosystem ecology (e.g. Bazzaz & Carson 1984; Drake *et al.* 1989; Lechowicz & Romer 1990; Leonard & Anderson 1991; Strain 1991; Oechel *et al.* 1992; Körner & Arnone 1992; Diaz *et al.* 1993). To our knowledge, this is the first replicated, four-trophic level experiment conducted with terrestrial mesocosms.

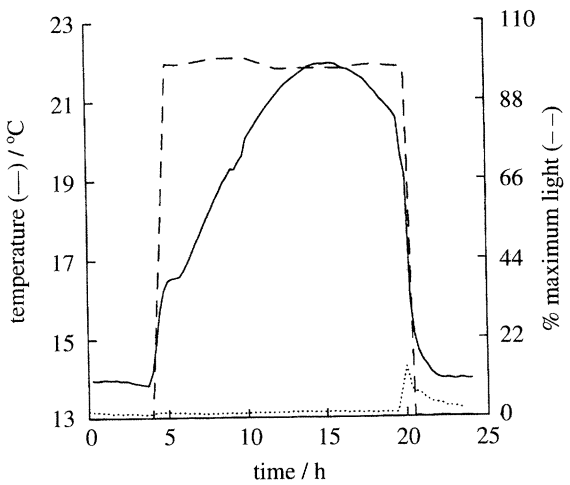

Figure 3. Temperature, light and humidity profiles for the Ecotron experiment. Shown are average temperature, light and humidity readings taken from sensors within each chamber on a typical single day (5 September 1993). Computer-delivered humidified air varied continuously between 57.97% during day and 70.0% during night (Lawton *et al.* 1993). Dashed line at bottom shows deviation in chamber humidity in millibars partial pressure (m.b.p.p.) from computer set points. Peak deviation (3.70 m.b.p.p.) from computer set point occurred transiently after rain. For clarity, humidity scale is not shown. Note that temperature rise is associated with the radiant energy from the lights in the chamber once they come on and the sharp decrease in temperature is associated with the coincident onsets of the rain and dark cycles within the chambers. See text and Lawton *et al.* (1993) for further detail.

Rainfall (deionized water) was delivered from an irrigation lance 150 cm above the soil surface. The lance provided a conical spray and lances were rotated biweekly among chambers to reduce the effects of individual variation in lance delivery patterns. Irrigation occurred at 20h30 ('dusk' in the Ecotron) delivering water at a rate of 1.75 l min^{-1} in two, 2 min intervals. (Intervals varied somewhat but averaged 120 s with a range of 90–135 s.) Thus, each chamber received approximately 7 l day^{-1}.

The soil was sterilized by methyl bromylation and consisted of 0.1 m^3 gravel topped with 0.3 m^3 of 40:60 sand:Surrey loam mix (40.83 p.p.m. nitrogen, 12.45 p.p.m. phosphorus, 10.69 p.p.m. potassium) placed in 0.4 m^3 containers. Each container received 120 ml of a microbial inoculum prepared from a Whatman number 4, 20–25 μm pore filtrate of Silwood Park soil. This treatment also, inevitably, introduced nematodes to all soil chambers.

The photoperiod was set at 16 h, with lights on between 04h30 and 20h30. A gradual dusk and dawn was simulated by varying lamp voltage over 1 h intervals during the first (04h00) and last (20h00) hour of each simulated day. The average light intensity at canopy surface (1 m from lights) when the lights were on was 300 μm s^{-1} m^{-1}.

(*b*) *Biotic components*

Selection criteria for our species are described in Lawton *et al.* (1993). The communities consisted of four trophic species groups. Within trophic groups we chose species that were ecologically similar in their biology and capable of growing and reproducing under the conditions of the Ecotron. These species are listed in table 1.

Mesocosm communities were developed in stages; the sequence of additions to soil that had been *in situ* for three days was as follows. Seeds and microbes (day 1, 23 April 1993), earthworms and Collembola (day 26), snails and slugs (day 69), aphids (day 132), white flies (day 145), whitefly predators (day 165) and aphid predators (day 169). The experiment was terminated on day 206.

Because of the large number of species (31), common terms are used in our text (e.g. 'aphids' or 'plants') rather than the latin, generic or specific epithets listed in table 1.

(i) *Primary producers (plants)*

All plants (see table 1) were annuals that grew readily under the light, water and nutrient conditions

Table 1. *Ecotron communities of three differing diversities*

This table lists the nested sets of species in three types of communities used in this experiment. Each set of species is included in the set beneath it, for example, all comunities contain the basal species *Senecio vulgaris* but only community III contains *Lamium purpureum*.)

Community	Plant spp.	Herbivores, predators	Soil fauna
I	*Senecio vulgaris* *Stellaria media*	aphid, *Myzus ornatus* aphid parasitoid, *Aphidius colmanii* snail, *Helix aspersa* Slug, *Agriolimax reticulata*	earthworms, *Lumbricus terrestris*[a] Colembola, *Megalothorax incertus*[a] *Folsomia candida*
II (+I)	*Chenopodium album* *Spergula arvensis* *Cardamine hirsuta*	aphid, *Brevicoryne brassicae*	Collembola, *Sphaeridia* c.f. *pumilus* *Protaphorura* c.f. *armata*
III (+I+II)	*Aphanes arvensis* *Arabidopsis thaliana* *Capsella bursa-pastoris* *Conyza canadensis* *Lamium purpureum* *Poa annua* *Sinapis arvensis* *Sonchus oleraceus* *Tripleurospermum inodorum* *Veronica arvensis* *Veronica persica*	white fly, *Trialeuroides vaporariorum* white fly parasitoid, *Encarsia formosa*	Collembola, *Proisotoma minuta* *Pseudosineela alba*[a] *Mesaphorura machrochaeta*[a]

[a] Failed to reproduce over course of experiment.

of the Ecotron (Lawton *et al.* 1993). These plants require no pollinators, no special germination conditions and reproduce continuously in the absence of seasonality. They varied considerably in life form, size, growth rates and leaf morphology. Eighty individuals were established in each container by placing 80 patches of seeds on the soil surface according to a Poisson distribution. This step was accomplished by using the Poisson distribution to draw X and Y coordinates for points on a sheet of acetate. Holes were punched at these coordinates and the acetate laid over the container in the chamber where seeds were to be planted. Seeds were planted in positions marked by the holes in the acetate sheet. Only a single species was planted at each patch. Accordingly, the initial total number of individual plants of each species in the experiment fell as number of species increased. Each patch of seedlings produced from these seeds was weeded until one plant remained per position.

Plants were censused by analysis of the tri-weekly video recordings made from above the canopy from day 31 to 199. However, limited video camera resolution and overtopping by plants made reliable identification of species from video recordings difficult. Canopy structure was, therefore, determined by pin sampling (Goodall 1952). We recorded the height and species identity of each plant encountered by fine chains dropped from 24 positions in an evenly spaced grid with the outer chains 10 cm from the container edge. Heights were recorded in 10 cm increments from day 60 to 189.

(ii) *Primary consumers (herbivores)*

Insects and molluscs were used as herbivores. Because of their long generation time, molluscs provided a constant level of leaf-chewing herbivory within the Ecotron (approximately 0.5 generations for snails and 1.0 for slugs). Molluscs were introduced periodically, once plants were mature, reaching a final density of 20 snails and seven slugs per container. One final census was taken at the end of the experiment.

Insect herbivores were all homopteran phloem suckers (aphids and white flies) from cultures reared at Silwood Park. Initial densities were 50 *Myzus ornatus* and 30 *Brevicoryne brassicae*, although *M. ornatus* entered as a contaminant of some of the chambers at an earlier, unknown date. Whitefly initial densities were 50 with an additional 30 added on day 169. Because these insects have short generation times and fluctuate dramatically in density they were introduced late in the experiment.

The relative abundance of insects was sampled bi-weekly by counting all insects observed on leaves touching chains that were suspended from the top of the canopy to the soil surface along an evenly spaced 3×3 grid of points with outer chains 10 cm (or more) from the edge. More intensive sampling methods to

obtain absolute densities would have affected both plants and animals in our mesocosms, so we restricted ourselves to determining relative abundances.

(iii) *Secondary consumers (parasitoids)*

Predators were parasitoids of insect herbivores. Introduced densities were 15 *Aphidius colmanii* (in three sets of five) and five *Encarsia formosa* per container. These were censused at the same time as the insect herbivores (see preceding paragraph for methods) by counting mummified, successfully parasitized hosts.

(iv) *Decomposers (earthworms and Collembola)*

Earthworms and Collembola were used as metazoan decomposer species and were introduced after seedlings were established to prevent earthworm casting from damaging seedlings (Thompson *et al.* 1993) and to ensure that fungi and some litter were available for Collembola. On day 26, 49 earthworms were introduced into each chamber, they were then censused (by sifting through the entire soil contents of the containers of each chamber) as a final count when the experiment was terminated.

Over 30 individuals per collembolan species were introduced into each chamber on days 26 and 111. Collembola were sampled every 3–4 weeks using 5 cm × 6.5 cm diameter soil cores (232 cm^3, mean dry mass = 179 g, s.e. 6.7 g) samples and modified Kempson bowl extractors (where ethyl alcohol was substituted for picric acid preservative and heat was supplied by dimmable, quartz-halogen lamps).

(*c*) *Ecosystem processes*

(i) *Community respiration*

This was measured as the CO_2 flux in each chamber: a PP Systems infra-red gas analyser measured CO_2 chamber input and output every 15 min. Over weekeneds, when all chamber doors were closed and the system was isolated, readings were taken cumulatively, every 15 min period for the entire 48 h period.

(ii) *Productivity*

Productivity of each mesocosm was estimated by comparing the percent transmittance of photosynthetically active radiation (PAR), 400–700 nm, through the canopy. Assuming no significant differences in individual leaf transmittance among plant species (Monteith & Elston 1983; Nobel & Long 1985), which was confirmed as true for this study, percent transmittance serves as a good estimator of the leaf area index (the photosynthetic surface expanded over a given area). Percent transmittance was measured by recording mean differences between above and below canopy light measurements made with a PAR Quantum Sensor light meter. A uniform grid was used to record 24 measures per mesocosm at bi-weekly intervals.

(iii) *Decomposition*

Short-term surface

We used litter bags containing a 0.2 g mixture of grasses in the genera *Agrostis* and *Holcus* with an initial carbon to nitrogen (C:N) ratio of 35.5:1 The plant material in these bags was sterilized using methylbromylation to prevent introduction of contaminant soil organisms. Six bags were placed on the soil surface of each container for four weeks from day 126–194 and again from day 171–199.

Long-term below ground

Sets of three flat birch sticks (11.5 × 0.9 × 0.2 cm) were bundled using polyester thread and buried 1.5 cm below the surface. Changes in the dry mass of the central stick in the bundle was used to estimate decomposition. The wood had an initial C:N ratio of 311:1.

(iv) *Nutrient retention*

Using tri-weekly chemical analyses of soil samples taken from each pot, nutrient retention was monitored. Small samples (less than 100 g) were analysed for total nitrogen, available nitrites, nitrates, amonium, phosphorus and potassium by NRM Laboratories, Berkshire.

(v) *Water retention*

Each container was fitted with one horizontal exit port at its base. Water outflow was measured weekly after soil had settled and vegetation had matured. Inflow was occasionally irregular due to problems with irrigation but the randomization of treatment assignment to chambers prevented any treatment bias from occurring. Containers received an excess of water to ensure some runoff.

(*d*) *Experimental design*

In this experiment, the single treatment factor was diversity with three treatment levels: high, medium, and low diversity (six, four and four replicates for each level, respectively). High diversity mesocosms contained all the species listed in table 1 and an initially uniform, but unknown, number of microbial and nematode species introduced with the soil inocula. Medium and low diversity systems represented increasingly depauperate versions of the high diversity mesocosms (see figure 2), each lacking species listed in table 1, parts II and III, accordingly.

Because the 16 chambers were divided into two separate banks, each with a separate air handling unit, treatment levels were assigned equally to each bank. Thus, the first bank contained three high-, two medium- and two low-diversity mesocosms. The second bank also had high-, medium- and low-diversity mesocosms. In both cases these were assigned randomly to chambers within the banks.

(*e*) *Test of robustness*

The large number of possible combinations of species that can be drawn from our species pool provides a very large number of possible more depauperate communities, of which our experimental communities

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are only a small sample. For example, for 16 species of plants there are 120 two-species combinations, one of which was used in the Ecotron experiment, and 4368 possible combinations of five species, again, only one of which was used in the experiment. The particular combinations used were chosen at random and could, by chance, give unusual results that lie well outside the range of average performances for all possible assemblages of these species.

To determine where our particular systems lay in the range of possibilities, we examined experimentally the general response of a single ecosystem process – plant productivity – to changes in diversity over a larger diversity gradient in an auxiliary experiment. We constructed a representative subset of the 4493 possible plant species combinations, using 182 combinations sampled across a $\log_2$ scaled gradient of diversity from monocultures to full richness polycultures. The subset included four replicates each of the 16 possible monocultures: 20, 30 and 40 replicates each of intermediate richness polycultures of two, four and eight species respectively; eight replicates of the particular five species combination used in the Ecotron medium diversity treatment; and ten replicates of full richness (16 species) polycultures. Intermediate richness polycultures with two, four and eight species were constructed by using a random number generator which selected species from the pool, discarding duplicate combinations. Thus all 90 of the intermediate polycultures were unique. Each replicate in every treatment consisted of 16 individual plants in an evenly spaced grid, produced by *in situ* selective weeding of seedlings, grown on the same soil as used in the Ecotron experiment, in 7.5 l pots (20 cm in diameter), placed randomly on benches in an outdoor environmentally controlled glasshouse.

We then measured total productivity (dry mass of above ground plant biomass for each pot) for each combination and compared these to the specific combinations of two, five and 16 species (see table 1) used in the Ecotron.

(*f*) *Stastical methods*

Temporal series of measurements from the Ecotron for census data and ecosystem processes were analysed using repeated measures of analysis of variance (RMANOVA). We used the MGLH module of SYSTAT (1992) for calculating RMANOVA's. Each diversity level was a treatment, with six, four and four replicates per level for low, medium and high diversity systems, respectively. The variance was partitioned into among-group variance, within-group variance and the interaction between among- and within-group effects, where 'group' refers to diversity level.

If among-group variation accounts for a significant part of the overall variance, this indicates that different diversity mesocosms show different mean levels of expression of the variable over the course of the experiment. If the within-group variation accounts for a significant part of the overall variance, this indicates that the mean expression of the variable changed significantly from one point in time to the next during the experiment. Significance in this term, however, does not indicate that high-, low- and medium-diversity mesocosms are necessarily different. Finally, if the interaction between among-group and within-group variation accounts for a significant part of the overall variance, it indicates that different diversity mesocosms show different temporal patterns of expression of the variable. (Note, that this significant result can be obtained even if among-group differences are not significant.) Other statistical methods are described, as appropriate, as the results are presented.

3. RESULTS

(*a*) *Community development*

(i) *Primary producers*

Percent cover of surface by vegetation showed a divergence among treatments that remained constant throughout the duration of the experiment (see table 2). Higher diversity replicates showed a significantly greater percentage cover than lower diversity systems (see figure 4).

Chains encountered greater numbers of plants at a greater range of heights in the higher diversity systems (see figure 5, table 2). These results imply that higher diversity systems filled the available space more densely than lower diversity systems.

(ii) *Primary consumer*

There was no difference in final adult snail abundances among treatments (ANOVA; d.f. 2,11; $p = 0.80$) with final mean densities of 6.25, 7.0 and 5.67 in high, medium and low diversity mesocosms, respectively. All containers contained numerous second-generation, immature snails but these were not included in the census. Slugs wandered from the

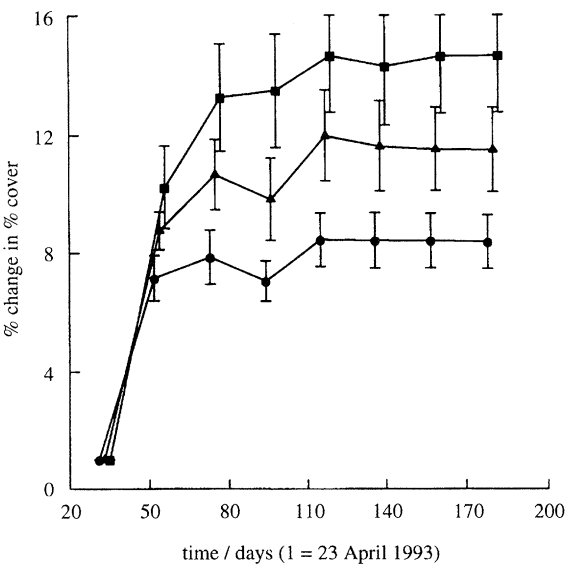

Figure 4. Percent change in percent cover of vegetation. Each line shows the means and standard errors for measures of percent change in percent vegetation cover as determined from the analyses of above canopy video images. Measurements were made on the same date at each interval, but means are shown scattered along the time axis for clarity (from Naeem *et al.* 1994). Circles, low diversity; triangles, medium diversity; squares, high diversity.

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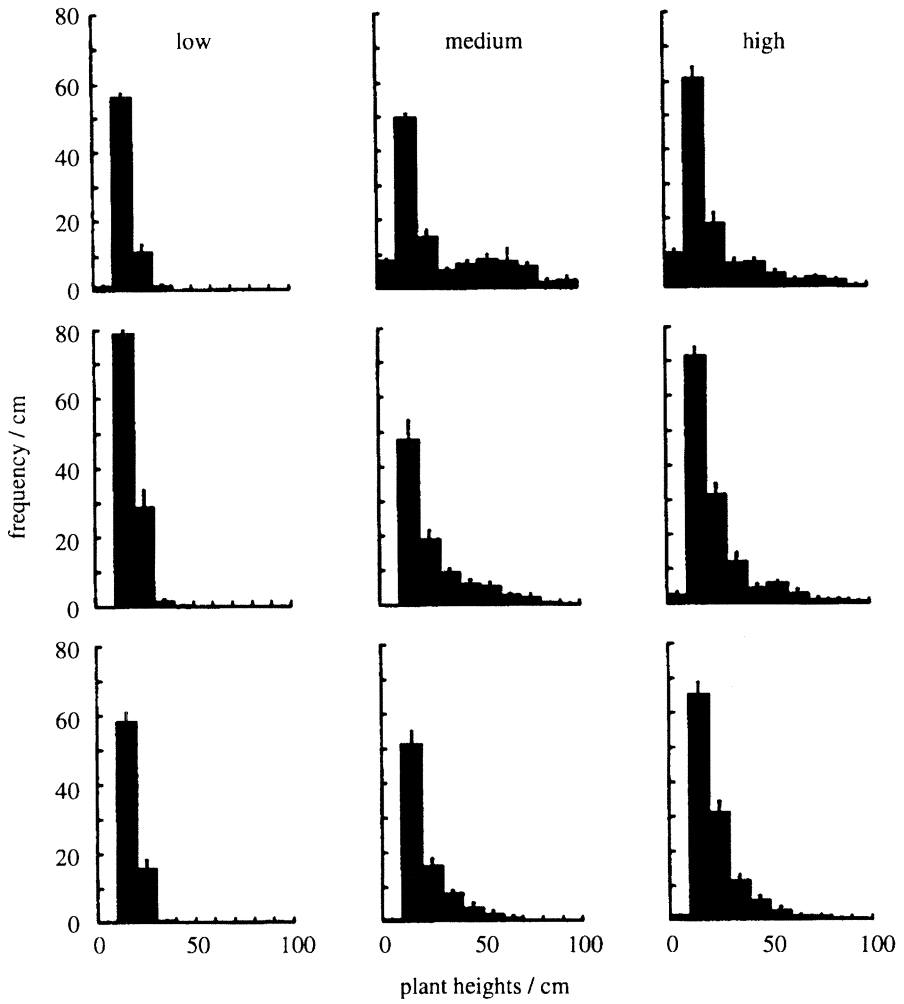

Figure 5. Pin (fine chain) encounters with vegetation as a measure of canopy architecture. Shown are histograms for fine chain encounters with vegetation when lowered from grid positions above the canopy (see text for methods). Vegetation is classed in heights of 10 cm increments. For clarity, only three, evenly spaced dates are shown out of seven possible; top = day 81, middle = day 123, and bottom = day 165.

containers into numerous regions of the chamber and could not be retrieved. Only two chambers contained mature, second generation slugs (one in each) by the end of the experiment.

Myzus ornatus was the only insect herbivore sufficiently abundant to merit statistical analysis for treatment effects. Densities of *M. ornatus* were quite variable both within and among treatments (see figure 6) but did show higher densities in higher diversity mesocosms (see figure 6 and table 2). *Brevicoryne brassicae* were abundant on several crucifers but our sampling rarely encountered these plants in the high and medium diversity systems. Similarly, whitefly populations became numerous but because of their patchy distribution were only detected in our final census.

(iii) *Secondary consumers*

Although adult parasitoids were abundant by the end of the experiment, our sampling methods rarely encountered these or the patchily distributed parasitized hosts. Numerous parasitized hosts were found by direct search and parasitoids successfully emerged from 100% of the sample collected. Data were too few to subject to statistical analyses.

(iv) *Decomposers*

Earthworms were more abundant in higher diversity systems (ANOVA; d.f. 2,11; $p < 0.05$) with final mean earthworm abundances at 16.0, 12.75 and 8.25 in the high, medium and low diversity systems, respectively. This decline in earthworm abundance from the initial densities is not uncommon for such mesocosm experiments (Thompson *et al.* 1993).

Collembolan abundances were variable and showed no significant differences among treatments (ANOVA; d.f. 2,11; $p = 0.26$) with final mean densities of 275.8, 578.6 and 508.7 Collembola per 100 g surface soil in mesocosms, respectively.

(*b*) *Ecosystem processes*

(i) *Community respiration*

Carbon dioxide flux differed significantly among treatments (see figure 7, table 3). Higher diversity assemblages showed higher rates of CO_2 consumption averaged over the duration of the experiment.

(ii) *Productivity*

Productivity differed significantly among treatments (see table 3). Higher diversity systems showed a higher

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Table 2. *Community dynamics and repeated measures analysis of variance of results*

Bold type highlights values that indicate significant diversity effects. In analysis 1, video data is grouped by diversity treatment in the ROMANOVA. In analysis 2, pin sampling uses two grouping factors: diversity treatment and height class (in 0 cm increments) of pin encounters. Highlighted significance terms indicated significant results important to hypotheses stated in the text. Statistical interactions between factors indicated by terms on either side of asterisks. Among = among treatment groups; d.f. = degrees of freedom associated with F; diversity = among diversity treatment groups effects; error = error term in breakdown of sums of squares for RMANOVA; height = among height (10 cm increment) groups; interact = interaction between within group temporal response and treatment; within = within temporal series for groups of replicates; p = significance probability with critical levels set at 0.05; NS = not significant ($p > 0.05$).

population measure	term	d.f.	f	p
1. percent vegetative cover (arcsine-square root transformed)	diversity	2, 11	159.6	< **0.001**
	within	7, 77	5929.2	< 0.001
	within* diversity	14, 77	65.5	< **0.001**
2. pin encounters with vegetation	diversity	2	57.6	< **0.001**
	height	10	1273.0	< **0.001**
	diversity* height	20	11.6	< **0.001**
	error	121		
	within	6	12.2	< 0.001
	within* diversity	12	7.4	< **0.001**
	within* height	60	9.4	< **0.001**
	within* diversity[a] height	120	3.4	< **0.001**
	error	726		
3. relative abundance of *Myzus ornatus*	among	2, 11	12.3	< **0.01**
	within	4, 44	1.3	NS
	interact	8, 44	1.2	NS

[a] Arcsine-square root transformed.

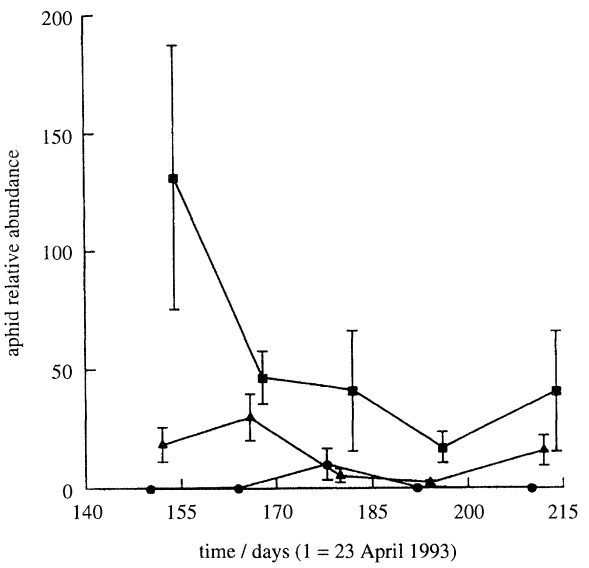

Figure 6. *Myzus ornatus* abundance. Each line shows means and standard errors for relative abundance by pin (fine chain) sampling methods (see text for methods). Measurements were made on the same date at each interval, but means are shown scattered along the time axis for clarity. Circles, low diversity; triangles, medium diversity; squares, high diversity.

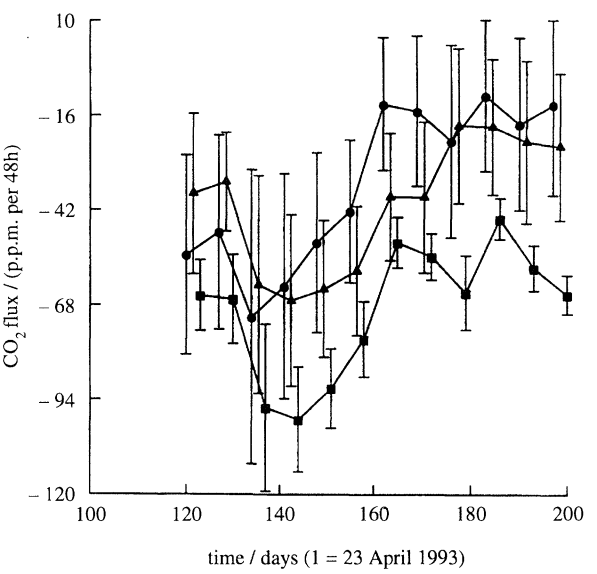

Figure 7. Community respiration. Each line shows means and standard errors for CO_2 flux in chambers measured over 48 hour periods with chamber doors sealed. Note that more negative fluxes indicate higher rates of photosynthesis or greater fixation of carbon by communities. Measurements were made on the same date at each interval, but means are shown scattered along the time axis for clarity (from Naeem *et al.* 1994). Circles, low diversity; triangles, medium diversity; squares, high diversity.

absorption of PAR light over the duration of the experiment (see figure 8).

(iii) *Decomposition*

Short term; surface litter decomposition showed different rates among the treatments but no clear association with diversity was apparent (see table 3). Long term; below ground decomposition showed no

Table 3. *Ecosystem processes monitored in communities, and repeated measures analysis of variance of results*

Bold type highlights values that indicate significant diversity effects. Among = among treatment groups; d.f. = degrees of freedom associated with *f*; interact = interaction between within group temporal response and treatment; within = within temporal series for groups of replicates; *p* = significance probability with critical level set at 0.05; NS = not significant ($p > 0.05$).

Ecosystem function	statistical analyses term	d.f.	f	*p*
1. community respiration	among[a]	2, 8	4.5	**< 0.05**
	within	11, 88	0.2	NS
	interact	22, 88	2.7	**< 0.001**
2. decomposition	among	2, 11	5.4	**< 0.05**
short term, surface	within	1, 11	17.5	< 0.01
litter	interact	2, 11	2.9	NS
long term, below	among	2, 11	0.6	NS
ground, wood	within	3, 33	145.2	< 0.001
	interact	6, 33	0.8	NS
3. nutrient retention	among	2, 25	1.9	NS
available amonium	within	7, 175	74.7	< 0.001
	interact	14, 175	6.7	**< 0.001**
available nitrate	among	2, 25	2.0	NS
	within	7, 175	1.5	NS
	interact	14, 175	1.8	**< 0.05**
available total	among	2, 25	2.6	NS
nitrogen	within	7, 175	65.4	< 0.001
	interact	14, 175	6.2	**< 0.001**
available phosphorus	among	2, 25	5.2	**< 0.05**
	within	7, 175	129.6	< 0.001
	interact	14, 175	4.3	**< 0.001**
available potassium	among	2, 25	9.9	**< 0.01**
	within	7, 175	40.1	< 0.001
	interact	14, 175	3.9	**< 0.001**
4. productivity[a]	among	2, 11	38.1	**< 0.001**
	within	6, 66	402.5	< 0.001
	interact	12, 66	15.1	**< 0.001**
5. water retention	among	2, 7	2.0	NS
	within	10, 70	8.1	< 0.001
	interact	20, 70	1.8	**< 0.05**

[a] Arcsine square root transformed.

response to differences in diversity (see figure 9, table 3).

(iv) *Nutrient retention*

Figure 10 shows the results for changes for nitrogen, phosphorus and potassium with an additional presentation of ammonium as part of the nitrogen response. All nutrients showed significant treatment responses (see table 3), although only available potassium and phosphorus showed higher retention (higher average levels) in higher diversity systems. Total nitrogen, ammonium and nitrate showed no clear pattern of association with the different diversity levels, although they showed significant treatment effects (see table 3).

(v) *Water retention*

Problems in the computer controlled irrigation system became apparent after day 160. We, therefore, analysed only the first 160 days' data and found significant treatment effects (see table 3). Neither before or after our irrigation problems, however, did a clear pattern of association with diversity appear (see figure 11).

(*c*) *Test of robustness*

Productivities of plant assemblages in the auxiliary experiment covered a wide range of possible outcomes (see figure 12). Two replicate monocultures and one two-species replicate were damaged and discarded, leaving 179 replicates. The low and medium diversity combinations used in the Ecotron experiment were unusually productive compared to alternative combinations and unusually similar compared with many other combinations (see figure 13). However, consistent with the data from the Ecotron experiment, the mean productivity of the plant assemblages is significantly

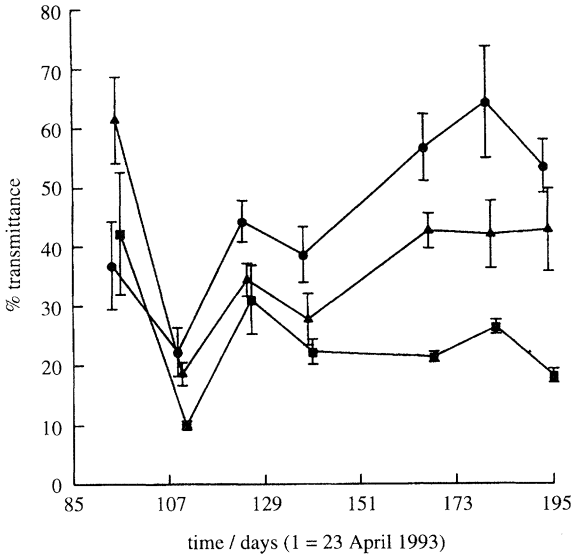

Figure 8. Community productivity as measured by percent trasmittance of photosynthetically active radiation. Lines show means and standard errors for percent transmittance. Note that productivity is inversely related to percent transmittance, thus lower values indicate denser vegetation. Measurements were made on the same date at each interval; means are shown scattered along the time axis for clarity. Circles, low diversity; triangles, medium diversity; squares, high diversity.

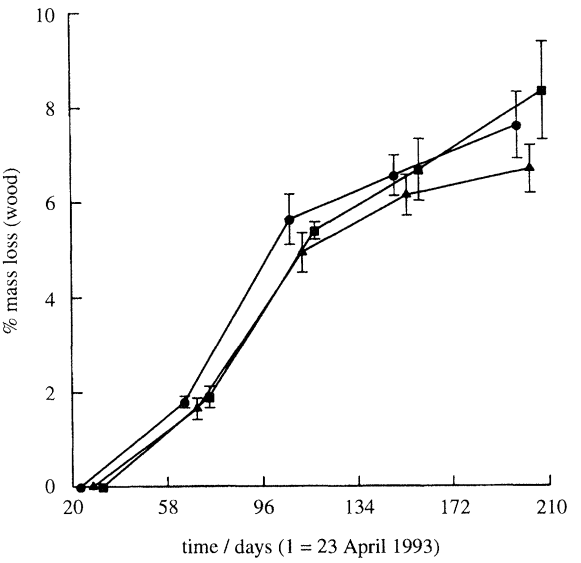

Figure 9. Rates of below surface decomposition. Lines show means and standard errors for change in weight of wood (birch) sticks buried on day 20 just below the soil surface. Measurements were made on the same date at each interval; means are shown scattered along the time axis for clarity. Circles, low diversity; triangles, medium diversity; squares, high diversity.

positively correlated with diversity (least-squares regression weighted by the standard deviation of the diversity group to correct for the heterogeneity of variances: d.f. 1, 169; $F = 2\ 108.3$; $p < 0.001$). But it is also clear from figure 13 that some individual monocultures and simple polycultures are more productive than the average for species rich systems.

4. DISCUSSION

(*a*) *Summary of findings*

The model terrestrial ecosystems established in the Ecotron varied in the dynamics of some of their trophic groups and in most ecosystem processes, in association with different levels of species richness. Higher diversity systems had more dense, more complex canopies, higher numbers of earthworms and insect herbivores, greater rates of CO_2 flux, greater productivity and greater accumulation of phosphorus and potassium. Other variables (surface decomposition, water retention, available nitrogen, ammonium and nitrates) showed temporal responses to different diversity levels but without any consistent or clear correlation with diversity.

Correlations between population and community structure offer some explanation for the differences we observed. Greater CO_2 absorption and productivity may have occurred in higher diversity systems because there was greater light interception in higher diversity systems. Figures 4 and 5 show that the canopies of higher diversity systems filled more of the available space. This is due to the greater variety of leaf forms, growth forms and heights of the different plants in the more complex plant assemblages of the higher diversity systems, similar to both theory and observations on 'overyielding' in intercropping systems (e.g. Vandermeer 1989).

The auxiliary experiment showed that the higher productivity of more diverse systems is a consistent result for other combinations of these plants drawn from the 16 species pool (see figure 13) and is not likely to be an artifact of the particular combinations we used. Indeed, our specific low and medium diversity communities were, by chance, highly productive systems leading us to believe that we would have found even stronger results with other possible communities.

(*b*) *Extrapolation of results to natural ecosystems*

The Ecotron mesocosms, although modeled on a British ruderal community, are not meant to be exact analogues of any natural ecosystem. Because of this, some precautions should be considered before extrapolating these results to natural systems.

1. Our experiment lasted less than a year and the communities were small. Without further experimentation, extrapolations to natural systems are necessarily qualitative rather than quantitative.

2. Our systems are open; continuous loss of nutrients means that successional effects account for some of the change we observe. However, because most ecosystems go through succession we do not regard this as a serious problem.

3. The developmental sequence of constructing complex communities required the late introduction of top trophic levels, dependent on the establishment of lower levels. Although time constraints prevented us from running the Ecotron mesocosms for longer, we believe that longer running times would only allow the different treatments to diverge further in their different levels of expression of ecosystem processes.

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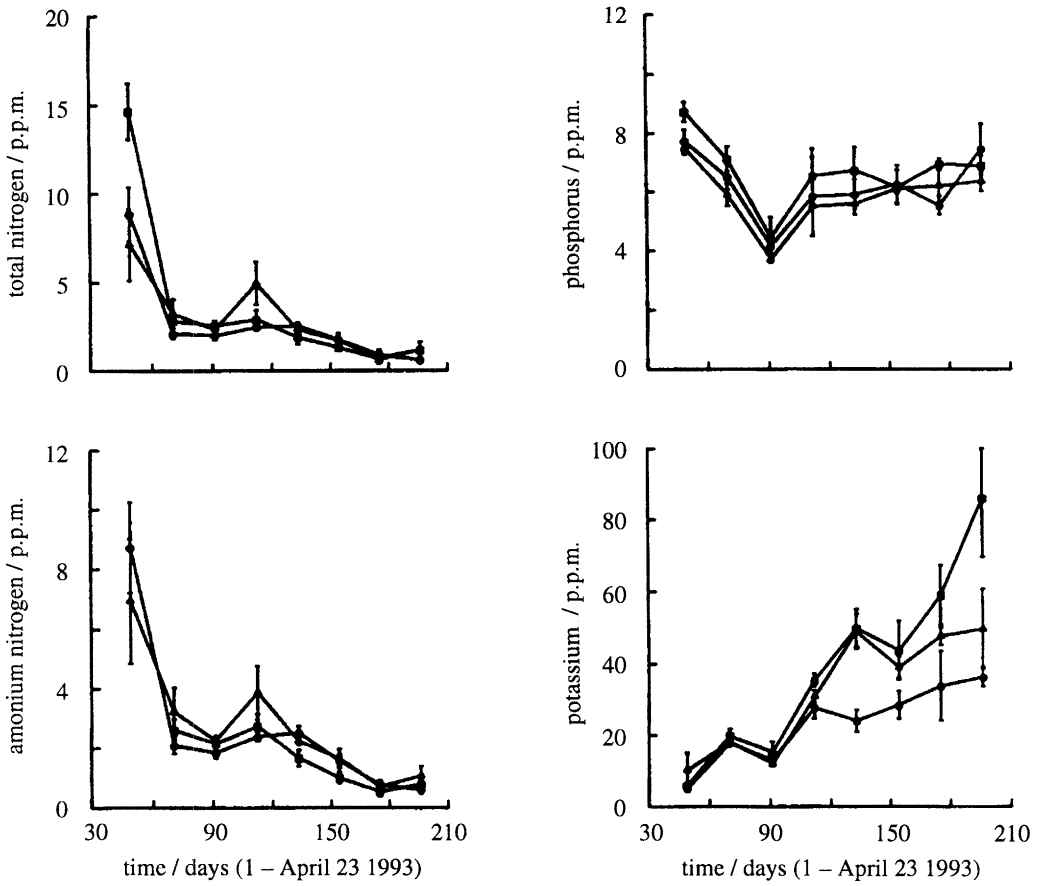

Figure 10. Nutrient retention: lines show means and standard errors for changes in abundance of nitrogen (total nitrogen and ammonium), phosphorus and potassium in soil. Circles, low diversity; triangles, medium diversity; squares, high diversity.

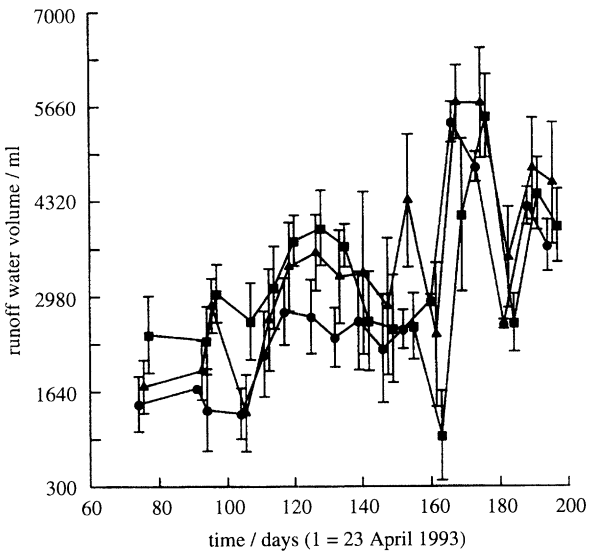

Figure 11. Water retention: lines show means and standard errors for volume of water collected from chambers through bottom drainage ports of containers. Measurements were made on the same date at each interval, but means are shown scattered along the time axis for clarity. Circles, low diversity; triangles, medium diversity; squares, high diversity.

4. Different communities with different species may show different patterns of ecosystem response to alterations in species diversity.

5. More ecosystem processes and population factors could be measured in such an experiment.

Just as the limited resources of this experiment constrained us to the five measures of ecosystem processes we chose, the small size of our mesocosms prevented us from sampling populations in ways that would either destroy or seriously disturb the communities. For example, our insect sampling methods had low resolution, earthworms could only be sampled at the end of the experiment and our resources did not permit measures of possibly important factors such as below grown productivity and nematode abundance. Although additional information on these and other factors might prove useful, our conclusions, that some ecosystem processes are affected by levels of species diversity whereas others are not, are likely to remain unchanged by additional data.

With these caveats in mind, we offer some tentative conclusions about natural systems which we draw from our results.

First, a decline in species diversity within an ecosystem can potentially alter ecosystem processes even if its trophic structure remains intact. To our knowledge, this is the first demonstration of this possibility via a direct manipulation of biotic diversity across four trophic levels. The large scale and long term implications of our results, however, are difficult to extrapolate to the global scale of declining species diversity on earth.

Second, if the decline in diversity is one in which the space filling property of the plant assemblage is altered, then the ecosystem may perform differently, showing

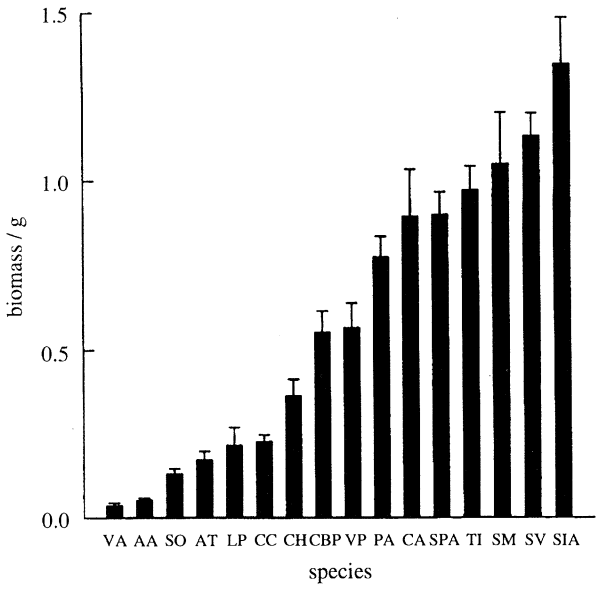

Figure 12. Species-specific plant productivities measured in a glasshouse. Bars show means and standard errors for total biomass (dry mass of above ground portion of plant) produced by monocultures of the species indicated on the bottom axis. Productivities are ranked in increasing order from right to left. AA = *Aphanes arvensis*, AT = *Arabidopsis thaliana*, CBP = *Capsella bursa-pastoris*, CH = *Cardamine hirsuta*, CA = *Chenopodium album*, CC = *Conyza canadensis*, LP = *Lamium purpureum*, PA = *Poa annua*, SV = *Senecio vulgaris*, SO = *Sonchus oleraceus*, SIA = *Sinapis arvensis*, SM = *Stellaria media*, SA = *Spergula arvensis*, TI = *Tripleurospermum inodorum*, VA = *Veronica arvensis*, and VP = *Veronica persica*.

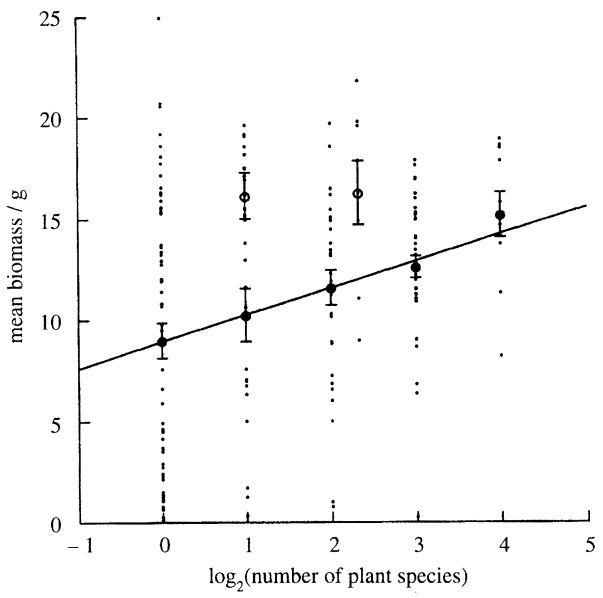

Figure 13. Productivities of Ecotron experimental plant assemblages and randomly constructed plant assemblages grown in a glasshouse. Filled circles show means and standard errors of productivities of communities with 1, 2, 4, 8, or 16 plant species, plotted on a $\log_2$ species richness gradient. Open circles show means and standard errors for combinations used in the Ecotron experiment, but grown in the same glasshouse conditions as those represented by closed circles. Points show actual values for each assemblage. Line is a least-squares regression line fitted to the data.

different rates of CO_2 flux and plant productivity. The relatively poor knowledge of the individual carbon budgets of plant species in natural ecosystems and a similarly poor knowledge of which species are likely to go extinct in the near future, makes predicting global change difficult. These results suggest, however, that if the decline in diversity reflects a decline in architectural complexity of a plant community, then that community may show similar declines in CO_2 fixation (Naeem *et al.* 1994).

Third, different ecosystem processes may show a variety of responses to changes in species richness. Some changes in the levels of expression of an ecosystem's processes are correlated with changes in species richness, some are insensitive and others show idiosyncratic responses. In other words, ecosystems undergoing declines in species richness can exhibit patterns of association between changing levels of expression of ecosystem processes (ecosystem function) and changing diversity that fit any of four current hypotheses (species-redundant, rivet, idiosyncratic, or null). No one pattern will suitably describe the breadth of possible outcomes for one or any number of ecosystems.

Finally, from an applied standpoint, our study augments a growing list of reasons for conserving species (Ehrlich & Wilson 1991; Beattie 1992, 1994; Ehrlich & Ehrlich 1992; Goombridge 1992). The list ranges from aesthetic and moral to practical, including the conservation of economic, genetic, and agricultural resources and the ability of communities to recover from disturbances (e.g. Tilman & Downing 1994). The present experiment supports the addition to this list of the possibility that loss of diversity alters the biogeochemical processes of ecosystems. Changes in current biogeochemical processes attributable to species extinction may or may not have detrimental consequences for environmental conditions but if they do, the irreversibility of extinction means that the environmental change may also be irreversible.

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