are other potentially deleterious greenhouse gases such as nitrous oxide and dimethyl sulphide. Furthermore, buoyant rising particles[25,26] may also effect a flux of dissolved materials to the ocean's surface and thus serve to accelerate the ocean-to-atmosphere transfer of certain gaseous constituents. □

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Declining biodiversity can alter the performance of ecosystems

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COMMUNITIES of species and their associated biological, chemical and physical processes, collectively known as ecosystems, drive the Earth's biogeochemical processes[1,2]. Currently most ecosystems are experiencing loss of biodiversity associated with the activities of human expansion[3–5], raising the issue of whether the biogeochemical functioning of ecosystems will be impaired by this loss of species[6–8]. Current ecological knowledge supports a wide range of views on the subject[9–13], but empirical tests are few[9,14–16]. Here we provide evidence from direct experimental manipulation of diversity by over an order of magnitude, using multi-trophic level communities and simultaneous measures of several ecosystem processes, that reduced biodiversity may indeed alter the performance of ecosystems.

The experiment used 14 model, terrestrial microcosms, each 1 m^2, individually developed, maintained and randomly placed in separate chambers of the Ecotron, a system of controlled environmental chambers designed for such experiments[17,18]. Air temperature, air flow, relative humidity, water, initial soil conditions, initial densities of organisms, and numbers of trophic levels were the same for all chambers (Table 1).

Plant and animal diversity was manipulated to create low, intermediate, and high diversity microcosms, with 9, 15 and 31 species, structured such that lower-diversity systems contained a subset of higher-diversity species. This manipulation produced a set of microcosms in which lower-diversity communities functionally resembled depauperate descendants of higher-diversity communities that had lost species uniformly across all trophic categories (Table 1 and Fig. 1). This is analogous to what is currently occurring globally in natural ecosystems.

We measured five ecosystem processes: (1) community respiration; (2) decomposition; (3) nutrient retention; (4) plant productivity; and (5) water retention (Table 2). We focused on energetic and chemical ecosystem functions related to the biogeochemical processes of natural ecosystems. We did not measure community stability, an ecosystem function discussed in other studies[9,12,13,15,16].

Statistically, the three levels of diversity represented three treatments: 6, 4 and 4 replicates of high, medium and low diversity treatments were assigned randomly to chambers. Ecosystem functions were measured repeatedly at fixed intervals and analysed using repeated measures analysis of variance (RMANOVA[19]). Significance in the highlighted RMANOVA terms (Table 2) supports the hypothesis that different levels of biodiversity are associated with different levels of ecosystem functioning.

The three levels of biodiversity showed significantly different ecosystem performances in the majority of functions (Table 2).

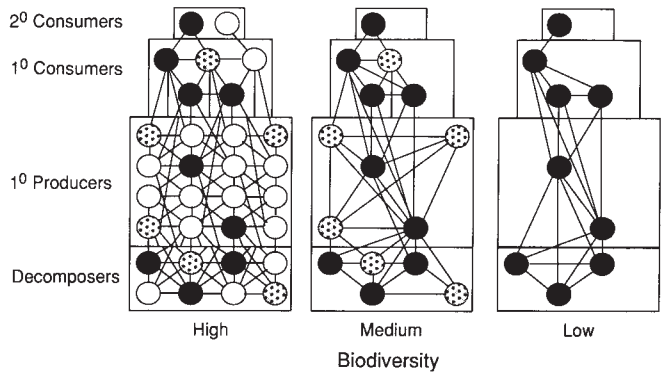

FIG. 1 Community diagrams of the three types of model terrestrial ecosystems developed in the Ecotron. Circles represent species and lines connecting them represent biotic interactions among the species (solid circle, species present in all 3 systems; speckled circle, two systems; open circle, just in the most diverse system). Note that each lower-diversity community is a subset of its higher-diversity counterpart and that all community types have four trophic levels. Primary (1°) producers are plants (self pollinating herbaceous annuals). Primary (1°) consumers are herbivores (molluscs and insects). Secondary (2°) consumers are predators (parasitoids). Decomposers are Collembola and earthworms. See Table 1 for list of species. Larger organisms, such as plants, snails and earthworms, were introduced to achieve equal final densities across all replicates (Table 1) to assure some balance in initial biomass among trophic levels in all replicate ecosystems. Biotic interaction (within level) and trophic (between level) links between species are illustrated; although we have documented trophic links by feeding trials, for clarity we have illustrated only some of the interactions to demonstrate that a loss of species richness is accompanied by a loss in community complexity as well, which is why we use the term biodiversity.

Higher-diversity communities consumed more CO_2 than lower-diversity communities (Fig. 2*a*). Short-term decomposition rates differed among treatments, but not in any consistent way. Long-term decomposition showed no significant treatment effects. Nutrient retention was different among treatments as measured by total available soil nitrogen, potassium and phosphorus, but with no consistent pattern of variation among treatments. Plant productivity, related in part to community respiration, was higher in the high-diversity ecosystems (Fig. 2*b*). Water retention was also different among treatments (Table 2), but without any consistent pattern of variation. The positive association between plant diversity and productivity finds some confirmation in the intercropping literature[20]. It is difficult, however, to compare our results with intercropping experiments because the latter have seldom manipulated more than three species of plants, rarely manipulated other trophic levels, and results have been equivocal[21].

TABLE 1 Ecotron communities of three differing biodiversities

Community	Plant spp.	Herbivores, predators	Soil fauna
I	*Senecio vulgaris* *Stellaria media*	aphid, *Myzus ornatus*	earthworms, *Lumbricus terrestris**
		aphid parasitoid, *Aphidius colmanii*	Collembola, *Megalothorax incertus** *Folsomia candida*
		snail, *Helix aspersa* slug, *Agriolimax reticulata*	
II (+I)	*Chenopodium album* *Spergula arvenis* *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** *Mesaphorura machrochaeta**

This 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 communities contain the basal species *Senecio vulgaris* but only community III contains *Lamium purpureum*. Seeds were planted on day 1 (23 April 1993). Initial densities of seedlings were held at 40 individuals per plant species in type I, 16 individuals per plant species in type II and 5 individuals per plant species in type III. Initial densities of earthworms were 49 on day 26. Initial Collembola densities were >30, introduced on day 26 with a second introduction on day 111. Initial snail and slug densities were 4 and 5, respectively, introduced on day 69. Additional snails were added each month to bring the final density to 20. Initial densities of aphids, *Myzus ornatus* and *Brevicoryne brassicae*, were 50 and 30, respectively, introduced on day 132, though *M. ornatus* began as a contaminant at an unknown earlier date. Initial white fly densities were 50, added on day 145. Total initial parasitoid (*Aphidius*) densities were 15, established in three introductions of 5, started on day 169. Initial white fly parasitoid densities were 5, introduced with 30 additional white flies on day 165. The experiment ended on day 206. All plant species flowered by day 206. All animals reproduced successfully except those marked with an asterisk. Average environmental conditions for the experiment were: photoperiod, 16 h, between 04:30–20:30, with gradual dusk and dawn durations of 1 h; average light intensity at canopy surface (1 m from lights) when lights were on was 300 $\mu m\ s^{-1}\ m^{-2}$; pot volume, 0.4 m^3; initial soil was 0.1 m^3 gravel topped with 0.3 m^3 of 40:60 sand/Surrey loam mix, 40.83 p.p.m. N, 12.45 p.p.m. P, 10.69 p.p.m. K; temperature varied smoothly between maximum of 20 °C day and minimum of 12 °C night; relative humidity varied smoothly between maximum of 70% after watering and minimum of 58% before onset of next watering cycle.

The effects of plant community architecture on light interception[22] suggests a mechanistic explanation for the differences observed in productivity and community respiration. We measured plant community architecture by two methods (Table 2, rows 6, 7), with higher-diversity systems showing greater per cent cover (Fig. 2*c*), and a greater number of contacts with sampling pins distributed among greater numbers of height classes (Fig. 2*d*). Hence, higher-diversity ecosystems intercepted more light because they had better three-dimensional, space-filling canopies, probably accounting for differences in productivity and community respiration. As all ecosystem functions are affected by energy input, it is also possible that this mechanism indirectly accounts for the differences observed in nutrient, water, and decomposition processes, but direct confirmation is not possible for our data.

Our study demonstrates for the first time under controlled environmental conditions, that loss of biodiversity, in addition to loss of genetic resources, loss of productivity[15], loss of ecosystem buffering against ecological perturbation[9,15,16], and loss of aesthetic and commercially valuable resources, may also alter or impair the services that ecosystems provide[3]. However, different ecosystem processes responded differently to loss of biodiversity, providing some support for several current hypotheses[3,9–11]. To

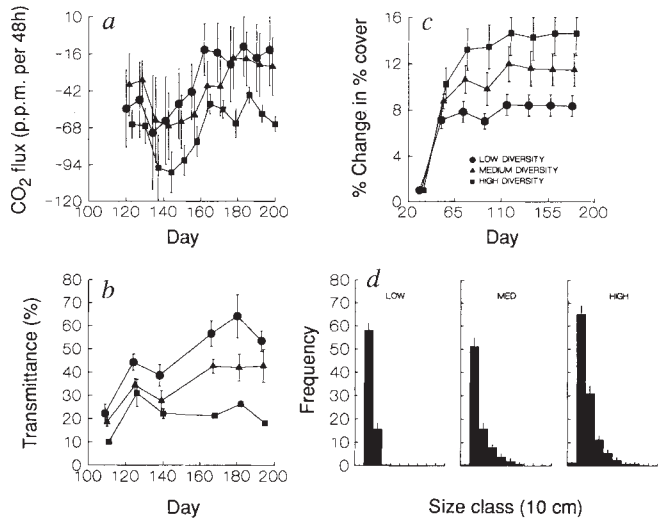

FIG. 2 *a*, Community respiration (mean ± 1 s.e.) as measured by CO_2 flux levels for each treatment. Note that the high-diversity ecosystems fixed more CO_2 (flux more negative) for the majority of the time. Measures are flux, in p.p.m. CO_2, over a 48 h period on weekends (no one entering the chamber), with an air flow of 0.25 $m^3\ 50\ s^{-1}$ per chamber. Cross flow fans within chambers caused turbulent airflow over chamber. Note that differences in fluxes between treatments were small, partly due to the small size of our microcosms; it is therefore difficult to predict the equivalent response of larger systems without further experimentation. *b*, Plant productivity as measured by per cent transmittance of photosynthetically active radiation. Productivity is correlated with the inverse of per cent transmittance[22]. Shown are means (±1 s.e.) of per cent transmittance for each treatment. Note that the high-diversity treatment was, from day 107, consistently more productive (lower per cent transmittance) than the low or medium diversity treatments. *c*, Per cent change in per cent vegetation cover (mean ± 1 s.e.) from initial conditions as determined by analysis of video images of canopies. ●, Low diversity; ▲, medium diversity; ■, high diversity. Day 1 was 23 April 1993. *d*, Canopy architectural complexity as measured by pin sampling. Shown are frequency diagrams for encounters of vegetation with vertical pins (24 per pot on a 6 by 4 grid). For clarity, we show only the sixth sample of the seven available, but a similar pattern is observed for other samples (see Table 2 for statistical analyses of all data).

TABLE 2 Ecosystem processes (1–5) and vegetation structure (6, 7) monitored in communities, and repeated measures analysis of variance of results

Ecosystem function		Method	Statistical analyses Term	DF	F	P
1.	Community respiration	Infrared gas analysis of atmospheric input and output for CO_2 flux, partially detrended for block effect	AMONG*	2, 8	4.5	**<0.05**
			WITHIN	11, 88	0.2	0.99 (NS)
			INTERACT	22, 88	2.7	**<0.001**
2.	Decomposition short-term surface litter	Change in weight of hay† sealed in inert bags and placed on surface for 6 weeks	AMONG	2, 11	5.4	**<0.05**
			WITHIN	1, 11	17.5	<0.01
			INTERACT	2, 11	2.9	0.09 (NS)
	long-term, below ground, wood	Change in weight of wood‡ sticks buried in soil at beginning of experiment	AMONG	2, 11	0.6	0.58 (NS)
			WITHIN	3, 33	145.2	<0.001
			INTERACT	6, 33	0.8	0.76 (NS)
3.	Nutrient retention available nitrogen	Change in soil concentrations	AMONG	2, 25	2.6	0.09 (NS)
			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 (plants)	Inverse of % light§ (wavelength, 44–700 nm) transmittance[28], arcsine-square-root transformed	AMONG	2, 11	38.1	**<0.001**
			WITHIN	6, 66	402.5	<0.001
			INTERACT	12, 66	15.1	**<0.001**
5.	Water retention	Rate of water outflow	AMONG*	2, 7	2.0	0.21 (NS)
			WITHIN	10, 70	8.1	<0.001
			INTERACT	20, 70	1.8	**<0.05**
Vegetation structure						
6.	Per cent vegetative cover (arcsine-square root transformed)	Analysis of video images made every three weeks from day 31 to day 199*	DIVERSITY	2, 11	159.6	**<0.001**
			WITHIN	7, 77	5,929.2	<0.001
			WITHIN × DIVERSITY	14, 77	65.5	**<0.001**
7.	Pin encounters with vegetation	Pin sampling of 24 positions from ceiling to soil surface in 10-cm increments. All contacts by pin with plants were recorded every three weeks from day 60 to 186‖	DIVERSITY	2	57.6	**<0.001**
			HEIGHT	10	1,273.0	**<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 × HEIGHT	120	3.4	**<0.001**
			ERROR	726		

In analyses 1–5: AMONG, among treatment groups; DF, degrees of freedom associated with *F*; INTERACT, interaction between within group temporal response and treatment; *P*, significance probability with critical level set at 0.05; NS, not significant ($P<0.05$); WITHIN, within temporal series for groups of replicates. Bold type highlights values that indicate significant biodiversity effects. In analysis 6, video data are grouped by diversity treatment in the RMANOVA. In analysis 7, pin sampling uses two grouping factors, one of diversity treatment and the other of height class, in 10-cm increments, of pin encounters. Bold type highlights significance terms important to hypotheses stated in text. Statistical interactions between factors are indicated (for example, WITHIN × DIVERSITY). DIVERSITY, among diversity treatment groups effects. ERROR, error term in breakdown of sums of squares for RMANOVA. HEIGHT, among height, 10-cm increment, groups. Other terms are as previously stated.

* Analysis adjusted for significant block effects.

† A mixture of grasses in the genera *Agrostis* and *Holcus* with a C:N ratio of 35.5:1.

‡ Wood sticks, 11.5 × 0.9 × 0.2 cm, with a C:N ratio of 311:1.

§ Assumes no significant differences in individual leaf transmittance among plant species, which is true for this study.

‖ Day 1, 23 April 1993.

the extent that loss of plant biodiversity in the real world means a reduction in the ability of ecosystems to fix CO_2, we also tentatively conclude that the loss of diversity may reduce the ability of terrestrial ecosystems to absorb anthropogenic CO_2 (refs 23–27). □

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Axonal sprouting accompanies functional reorganization in adult cat striate cortex

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REMOVAL of sensory input from a focal region of adult neocortex can lead to a large reorganization of cortical topography within the deprived area during subsequent months[1–9]. Although this form of functional recovery is now well documented across several sensory systems, the underlying cellular mechanisms remain elusive. Weeks after binocular retinal lesions silence a corresponding portion of striate cortex in the adult cat, this cortex again becomes responsive, this time to retinal loci immediately outside the scotoma. Earlier findings showed a lack of reorganization in the lateral geniculate nucleus and an inadequate spread of geniculocortical afferents to account for the cortical reorganization, suggesting the involvement of intrinsic cortical connections[4,10]. We investigated the possibility that intracortical axonal sprouting mediates long-term reorganization of cortical functional architecture. The anterograde label biocytin was used to compare the density of lateral projections into reorganized and non-deprived cortex. We report here that structural changes in the form of axonal sprouting of long-range laterally projecting neurons accompany topographic remodelling of the visual cortex.

To investigate the presence of sprouting of laterally projecting cortical neurons in functionally reorganized cortex, a comparison was made between axon fibres within normal and reorganized cortex. Receptive field (RF) maps were first documented before, immediately following and 3–9 months after making retinal lesions (Fig. 1 and Table 1). The cortical reorganization observed over this time period extended over an area 7–8 mm in diameter (Fig. 1). Because we were able to conclude from previous work (refs 4, 10 and C.D.-S. and C.D.G., manuscript in preparation) that changes occur largely at the cortical level, the present study focused on intracortical circuitry, particularly the horizontally projecting plexus of cortical neurons[11–13]. These connections extend laterally for 6–8 mm, and are thought to play a modulatory role in integrating visual information across neighbouring receptive fields. Although the horizontal connections can exhibit use-dependent changes in synaptic weights[14], these changes can occur within seconds and minutes. The reorganization described here, however, takes shape over several months. Our findings indicate these connections may provide the substrate through which visual information is transferred from normal to deprived cortical areas, and through which cortical circuitry is functionally and structurally redefined.

Intrinsic axonal projections were examined by placing extracellular injections of biocytin into cortex just outside the original boundary of the deprived region (cortical scotoma). This allowed labelled axons to be followed laterally from the same injection sites many millimetres into both normal and reorganized cortex. In this instance 'normal' refers to cortical areas representing unlesioned parts of retina, but because there could be distant effects in these areas as well, we also included controls in unlesioned animals. Three-dimensional reconstructions of axons (Fig. 2) projecting through layer III into reorganized cortex revealed a greater exuberance of terminal branching than seen in published examples of horizontally projecting neurons[11–13], and suggested that terminal sprouting might accompany functional reorganization. To examine this quantitatively, a comparison of fibre density was made between normal and reorganized cortex as documented physiologically. Fibre density was defined as the sum of the lengths of all fibre fragments found within the sampled volume of cortex. The selected sample regions were positioned at equal distances from the injection strip (see insert in Figs 2 and 3), and extended through the full cortical depth.

Axon fibres were always denser within reorganized than within normal cortex. In three of the four hemispheres analysed, the differences were highly significant (Fig. 3 and Table 1), with fibre densities 57-88% greater in reorganized than in normal cortex. Although in the fourth hemisphere the difference was not statistically significant, the trend was nonetheless similar, and there was a significant increase in density of axonal boutons

TABLE 1 Experimental details of the six hemispheres used

Cat number	Post-lesion survival	Δ Fibre density ($P<0.05$)	Scotoma size (°)	Distance from injections (mm)	Reorganization extent (mm)	Sample size (mm)
1	8 months	+66%, $P=0.008$	R = 8 × 16 L = 9 × 17	3.0	R ~ 2.9 L ~ 3.0	3.5 × 0.5
2	14 weeks	+16%, $P=0.133$	R = 10 × 17 L = 10 × 17	2.0	R ~ 2.5 L ~ 2.5	2.5 × 1.0
3R	8.5 months	+88%, $P=0.000$	R = 15 × 20 L = 15 × 22	1.0	R ~ 2.0 L ~ 2.2	2.5 × 1.0
3L	8.5 months	+57%, $P=0.003$	R = 15 × 20 L = 15 × 22	1.0	R ~ 2.0 L ~ 2.2	2.5 × 1.0
4R	Control no lesions	+13%, $P=0.443$	—	1.3	—	3.0 × 1.0
4L	Control no lesions	+6%, $P=0.692$	—	1.3	—	3.0 × 1.0

A paired sample *t*-test was used to compare the fibre densities in sample areas (dimensions in furthest right column), through the full sequence of sections cut tangentially from pia matter to white matter. Δ Fibre density is percentage difference between the summed fibre length (across 11–16 sections) in reorganized and normal sample cortex. Analogous sample regions were used for the control hemispheres. R and L, right and left hemispheres in column 1 and left and right eyes in column 4.