

that allows the expected contribution of each source population to the founding group to be a function of its productivity and its distance from the new colony,

$$E(x_i) = \frac{[(1-S) + S\pi_i]e^{-R\delta_i}}{\sum_j [(1-S) + S\pi_j]e^{-R\delta_j}}$$

where  $R$  is the rate of decay with distance  $\delta_i$ , and  $S$  is the contribution of productivity  $\pi_i$ . Distance between sources and new colonies is measured along the path that a seal would use to move between colonies. Productivity is obtained from the time series for pup production (see Supplementary Information) and describes both how strong the density-dependent effects within a source are and how large the source population is. It is obtained as

$$\pi_i = \Phi_i(\Delta_m - \Delta_i), i = 1, 2, \dots, s$$

where

$$\Delta_i = \frac{1}{(t_{c-2} - t_{c+2} + 1)} \sum_{j=t_{c-2}}^{t_{c+2}} N_{ij}$$

is the growth rate of source  $i$  per individual during the period  $[t_{c-2}, t_{c+2}]$  ( $t_c$  is the year in which the colonization event occurred and  $N_{ij}$  is the number of pups born in colony  $i$  on year  $j$ ),  $\Delta_m$  is the maximum growth rate per individual, and

$$\Phi_i = \frac{\sum_{j=t_{c-2}}^{t_{c+2}} N_{ij} / (t_{c-2} - t_{c+2} + 1)}{\sum_{i=1}^s \sum_{j=t_{c-2}}^{t_{c+2}} N_{ij} / (t_{c-2} - t_{c+2} + 1)}$$

is the average relative size (measured in number of pups) of source  $i$  for the period  $[t_{c-2}, t_{c+2}]$ .

We specify a Dirichlet  $(\alpha_1, \alpha_2, \dots, \alpha_s)$  distribution for  $\text{Pr}(\mathbf{x})$  with parameters  $\alpha_i$  given by  $\alpha_i = \alpha_0 E(x_i)$ , where  $\alpha_0 = \sum_j \alpha_j$  is a parameter that determines the variance of the  $x_i$  values and has to be estimated. The prior for  $\text{Pr}(\alpha_0)$  is uniform (non-informative) from  $s$  to 100, whereas those for  $\text{Pr}(w)$  and  $\text{Pr}(S)$  are uniform from 0 to 1. The prior for  $\text{Pr}(R)$  is uniform from 0 to 5. Having observed the data  $y$  (that is, the genotypes in the new populations and the allele frequency distributions of the potential sources), our knowledge about  $w$  and  $\mathbf{x}$  is given by the posterior distribution

$$\text{Pr}(w, S, R, \alpha_0, \mathbf{x} | y) \propto \text{Pr}(w) \text{Pr}(\alpha_0) \text{Pr}(R) \text{Pr}(S) \text{Pr}(\mathbf{x} | S, R, \alpha_0) \text{Pr}(y | w, \mathbf{x})$$

We used the maximum-likelihood estimates of the allele frequencies rather than including them as nuisance parameters, after verifying with synthetic data with the same  $F_{ST}$  and sample size that this had negligible effect on the estimation. The posterior distribution was estimated by using the Metropolis–Hastings algorithm<sup>14,15</sup>.

The DIC scores were produced from MCMC chains of length 520,000 for four models: with  $R$  and  $S$  unconstrained, with  $R$  set to 0, with  $S$  set to 0, and with both  $R$  and  $S$  set to 0. The measure of model complexity was estimated as the difference between the sample mean of the simulated values of the deviance minus an estimate of the deviance by using the simulated values of the parameters  $\theta$

$$p_D = \overline{D(\theta)} - (\bar{\theta}).$$

The function  $D(\theta)$  is the Bayesian deviance given by

$$D(\theta) = -2 \log p(y | \theta) + 2 \log f(y)$$

where  $f(y)$  is a standardizing function of the data,  $y$ , alone. In our case we used the null standardization obtained by assuming that  $f(y)$  is the perfect predictor that gave probability 1 to each observation. DIC was calculated as  $p_D + \bar{D}$ . The standard error on the DIC scores, estimated from the MCMC chains, was less than 0.040 for each of the estimates.

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**Spatial scale dictates the productivity–biodiversity relationship**

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The diversity of life is heterogeneously distributed across the Earth. A primary cause for this pattern is the heterogeneity in the amount of energy, or primary productivity (the rate of carbon fixed through photosynthesis), available to the biota in a given location<sup>1–12</sup>. But the shape of the relationship between productivity and species diversity is highly variable<sup>10–14</sup>. In many cases, the relationship is ‘hump-shaped’, where diversity peaks at intermediate productivity<sup>7,9,10,12,10,15–18</sup>. In other cases, diversity increases linearly with productivity<sup>4–6,10–12</sup>. A possible reason for this discrepancy is that data are often collected at different spatial scales<sup>10,12,14</sup>. If the mechanisms that determine species diversity vary with spatial scale, then so would the shape of the productivity–diversity relationship. Here, we present evidence for scale-dependent productivity–diversity patterns in ponds. When the data were viewed at a local scale (among ponds), the relationship was hump-shaped, whereas when the same data were viewed at a regional scale (among watersheds), the relationship was positively linear. This dependence on scale results because dissimilarity in local species composition within regions increased with productivity.

A wide variety of ecological models predict that local-scale species diversity should first increase with slight increases in productivity, but then decline to low levels when productivity is high<sup>7,9,15,16</sup>. That is, they predict that the productivity–diversity relationship should be ‘hump-shaped’, and this pattern is often seen in empirical studies at relatively small spatial scales<sup>7,9,10,12,10,15–18</sup>. At regional spatial scales, considerably less theory is available<sup>8</sup>. However, empirical studies performed at this larger scale often show a very different pattern from those performed at local scales. Instead of being hump-shaped, species diversity often monotonically increases with increasing productivity<sup>4–6,8–12</sup>. Because studies performed at different spatial scales often consider disparate systems and employ different methodology, it remains unclear as to whether relationships are scale-dependent or whether a single relationship holds across scales.

## letters to nature

In this study, we explicitly compared the relationship between primary productivity and species diversity within ponds at two different spatial scales: (1) at the local scale of an individual pond, where local interspecific interactions are likely to have a prominent effect on patterns of species diversity; and (2) at the regional scale of a watershed. We standardized each watershed to include three ponds that were similar in productivity and total area (see Methods). Here, regional processes, such as dispersal among ponds, can interact with local processes to influence patterns of species diversity.

At the local scale (among ponds), both producer and animal species diversity had a statistically significant hump-shaped relationship with primary productivity (Fig. 1a). This result is consistent with other local-scale studies in ponds and lakes<sup>15,18</sup>. In contrast, at the regional scale (among watersheds), species diversity linearly increased with productivity (Fig. 1b). Thus, we show here that the shape of the productivity–diversity relationship depends on spatial scale.

If the productivity–diversity relationship is scale-dependent, as we observe and as suggested elsewhere<sup>8–12,14</sup>, then the difference in species composition among localities within regions must increase with productivity. Formally, this can be depicted using the basic diversity equation where regional diversity ( $\gamma$ ) is a function of local diversity ( $\alpha$ ) and species compositional differences among localities ( $\beta$ -diversity) ( $\gamma = \alpha\beta$  or  $\gamma = \alpha + \beta$ )<sup>19–21</sup>. Given this simple relationship, if the pattern between primary productivity and local ( $\alpha$ ) diversity is hump-shaped while the relationship between primary productivity and regional ( $\gamma$ ) diversity monotonically increases, then species compositional differences among localities ( $\beta$ -diversity) must increase with productivity.

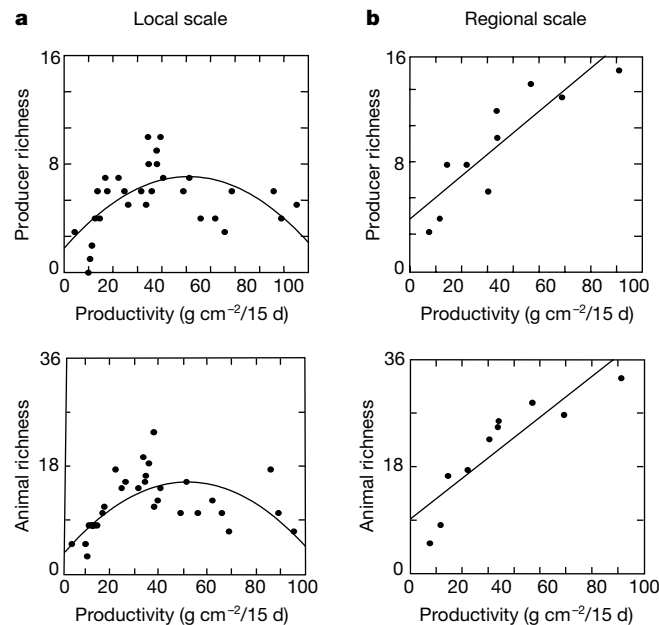
To test this, we calculated species dissimilarity of each watershed by quantifying the species compositional differences among the three ponds that comprise each watershed (see Methods). Although species dissimilarity is not directly analogous to  $\beta$ -diversity, it is conceptually very similar, and the two measures are highly correlated<sup>20</sup>. It also provides a way of evaluating the difference in species composition among localities without statistically confounding it with estimates of local ( $\alpha$ ) and regional ( $\gamma$ ) diversity<sup>20,21</sup>.

We found that species dissimilarity increased with productivity (Fig. 2). Ponds within watersheds of low productivity shared the majority of their species, whereas ponds within watersheds of high productivity shared few species. Any individual pond within a high-productivity watershed had relatively few species, but the species composition between ponds was quite different, so that the entire watershed had many species. Thus, the positive correlation between productivity and species dissimilarity (Fig. 2) explains the scale-dependent productivity–diversity relationship (Fig. 1). Further, we suggest that whenever a scale-dependent productivity–diversity relationship is observed in natural ecosystems, the explanation for this pattern will include covariation between productivity and species dissimilarity.

There are three primary mechanisms that would cause species dissimilarity to increase with productivity. First, regions with higher average productivity may also have a larger degree of heterogeneity in environmental factors (including productivity itself), which could increase species dissimilarity. In this study, we did not find a relationship between the variance in productivity among ponds within a watershed and the average productivity of watersheds (linear regression,  $P < 0.3$ ). We also measured a variety of standard physical and chemical variables in these ponds (see Methods). For every variable, we found no relationship between its variance within a watershed and the average productivity of watersheds (for all linear regressions,  $P > 0.2$ ). We conclude that this mechanism is unlikely for this system.

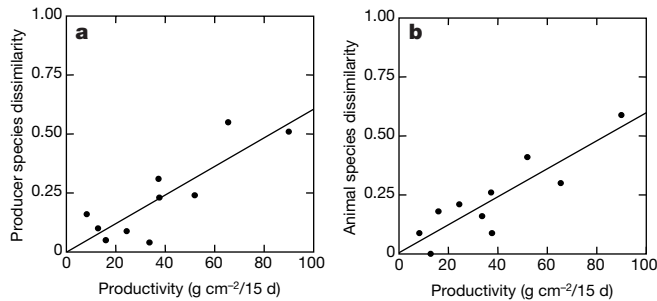
Second, regions with higher average productivity may also have a higher propensity for temporal variation in local species composition, which could increase species dissimilarity. Because of the limited temporal scale of our study (two years), we are unable to evaluate whether this mechanism may have influenced our results.

Third, in some cases, community composition can strongly depend on the order in which species initially entered a community; a phenomenon known as multiple stable states<sup>17</sup>. If communities with higher average productivity are more likely to obtain multiple stable states than regions with low average productivity, then species compositional dissimilarity would increase with productivity.



**Figure 1** Results from the survey of pond species diversity relative to *in situ* primary productivity at local and regional scales. Top panels, producers (vascular plants and macroalgae); bottom panels, benthic animals (insects, crustaceans, amphibians, and so on). **a**, Local, within-pond, species diversity ( $N = 30$ ). Both relationships are significantly unimodal ( $P < 0.05$ ) (see text for explanation of statistical methodology). The line

represents the estimated quadratic function. **b**, Regional, within-watershed, species diversity. For both producers (regression:  $N = 10$ ,  $R^2 = 0.74$ ,  $P < 0.001$ ) and benthic animals (regression:  $N = 10$ ,  $R^2 = 0.75$ ,  $P < 0.001$ ) regional species diversity was linearly related to primary productivity.



**Figure 2** The relative dissimilarity in species composition among local ponds within the watersheds (calculated as one minus Jaccard's index of similarity). Each point represents the average of the dissimilarity estimates from each two-way comparison of species composition among the three ponds within a watershed (see Methods). Regional dissimilarity of both producers **(a)** (regression:  $N = 10$ ,  $R^2 = 0.69$ ,  $P < 0.002$ ), and animals **(b)** (regression:  $N = 10$ ,  $R^2 = 0.74$ ,  $P < 0.001$ ) was linearly positively related to regional productivity.

Again, however, this mechanism cannot be assessed in this study, because the history of these communities is unknown.

We have thus shown how species diversity, when viewed at different spatial scales, can respond in fundamentally different ways to the same environmental factor (productivity in this case). This supports the notion that considerable insight can be gained by increasing the scale, both spatially and temporally, in which species diversity is viewed.

Our results also have implications for understanding how patterns of species diversity might respond to anthropogenic influences. The input levels of nitrogen and phosphorus, important limiting nutrients for productivity, have increased greatly in many ecosystems<sup>23,24</sup>. This cultural eutrophication often decreases local species diversity<sup>23,24</sup>. In order to fully understand and manage damaged ecosystems, we must consider the effects of cultural eutrophication on both local and regional species diversity. If, as we found in our study, higher productivity regions contain fewer species locally, but more species regionally, then cultural eutrophication may decrease local species diversity but increase regional species diversity. Alternatively, if cultural eutrophication homogenizes all of the habitats in an area and reduces species dissimilarity, then it can decrease both local and regional species diversity. Finally, species adapted to live in habitats with low productivity could be permanently lost from the ecosystem. Understanding the scale-dependence of these issues will be essential in order to predict and ameliorate the effects of humans on the earth's biota. □

**Methods**

**Estimating primary productivity and other variables**

Measuring total nutrient (nitrogen and phosphorus) availability in these ponds does not provide a realistic estimate of primary productivity because ponds also vary considerably in other limiting factors, such as temperature and light availability. Thus, we indirectly estimated primary productivity within each pond by measuring the rate of algal biomass accrual on artificial substrates in the absence of herbivory<sup>25</sup>. We also estimated several physical and chemical variables of each pond using standard methods<sup>25</sup>. These variables included pond area, average depth, tree canopy coverage, total nitrogen, total phosphorus, pH, average temperature, and average dissolved oxygen.

**Choice of ponds within watersheds**

We chose 30 ponds (local) nested within 10 watersheds (regional). To standardize the regional scale, we chose three ponds within each watershed, that occurred within 0.5 km of each other, and that owing to similar environmental conditions and chemical properties of the water and soil, had primary productivity values  $\pm 1 \text{ g cm}^{-2}/15 \text{ d}$  of each other (see below). The three chosen ponds within each watershed had a similar total surface area ( $\pm 500 \text{ m}^2$ ), so as not to confound the effect of area on species diversity.

**Estimating species diversity**

Each pond was sampled twice per year (April–May and July–August) for two years (1997 and 1998), to incorporate both seasonal and year-to-year variation in species composition, for a total of four censuses per pond. Animals (excluding zooplankton) were sampled

using D-net sweeps (0.1-m width, 0.33-mm mesh). Individuals were identified in the field, and sorted to the lowest possible taxonomic category (usually species or in cases where species could not be reliably identified, we categorized them into operational taxonomic units). In each pond, D-net sweeps were made until a full series of ten sweeps revealed no new species. This methodology was used because we could not reliably standardize sampling across ponds that varied in area, and because ponds were highly variable in their bottom substrate and debris, making D-net sweeps difficult to compare directly among ponds.

Producers, including submerged and emergent macrophytes, filamentous macroalgae, and floating duckweeds (but not microscopic periphytic and planktonic algae), were sampled by identifying species along transects through each pond. In each pond, transects were censused until no new species were found per five transects.

For both producers and animals, local species diversity was calculated as the total number of species observed in each pond over all census periods. Regional species diversity was calculated as the total number of species observed in the three ponds within each watershed. We calculated the dissimilarity in species composition among ponds within each watershed (region) as one minus Jaccard's similarity index (if dissimilarity is zero, then all species are shared among local communities; if dissimilarity is one then no species are shared). Because this index is for pairwise comparisons of communities, and our 'regions' consisted of three ponds, we calculated each combination of pairwise dissimilarity values, and averaged them to attain a regional dissimilarity value. Our dissimilarity metric is similar conceptually to  $\beta$ -diversity, but retains slightly different statistical properties<sup>20</sup>. Nevertheless, dissimilarity is more appropriate for statistical comparisons among regions because  $\beta$ -diversity is confounded owing to its lack of independence from regional species diversity<sup>20,21</sup>.

**Statistical analyses**

For each data set, we first performed linear regression to determine whether there was a significant relationship between primary productivity and species diversity at the local or regional scales. We then performed quadratic regressions to see if there were significant deviations from linear relations. When we found significant quadratic effects, we then determined whether it was significantly unimodal (hump-shaped) using a statistical test developed by Mitchell-Olds and Shaw<sup>26</sup> (see refs 12, 15, 18 for its usage in the context of productivity–diversity relationships). This method uses quadratic regression to estimate the productivity associated with the peak of the relationship between productivity and diversity, as well as the 95% confidence interval around that peak. Next, the method uses  $t$ -tests to determine whether the estimated peak of a data set is significantly greater than species diversity at the minimum and less than species richness at the maximum productivity values.

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## Competing interests statement

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## Correlated binocular activity guides recovery from monocular deprivation

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Monocular deprivation (MD) has much more rapid and severe effects on the ocular dominance of neurons in the primary visual cortex (V1) than does binocular deprivation<sup>1</sup>. This finding underlies the widely held hypothesis that the developmental plasticity of ocular dominance reflects competitive interactions for synaptic space between inputs from the two eyes<sup>2</sup>. According to this view, the relative levels of evoked activity in afferents representing the two eyes determine functional changes in response to altered visual experience. However, if the deprived eye of a monocularly deprived kitten is simply reopened, there is substantial physiological and behavioural recovery, leading to the suggestion that absolute activity levels, or some other non-competitive mechanisms, determine the degree of recovery from MD<sup>3–7</sup>. Here we provide evidence that correlated binocular input is essential for such recovery. Recovery is far less complete if the two eyes are misaligned after a period of MD. This is a powerful demonstration of the importance of cooperative, associative mechanisms in the developing visual cortex.

In normal kittens, artificially induced strabismus, which misaligns the receptive fields of binocular neurons and hence effectively decorrelates the inputs from the two eyes, causes a substantial breakdown of cortical binocularity<sup>3,8</sup>. We have tested whether strabismus induced immediately after MD prevents physiological and behavioural recovery of the reopened deprived eye. The results demonstrate the role of correlated activity in the recovery process.

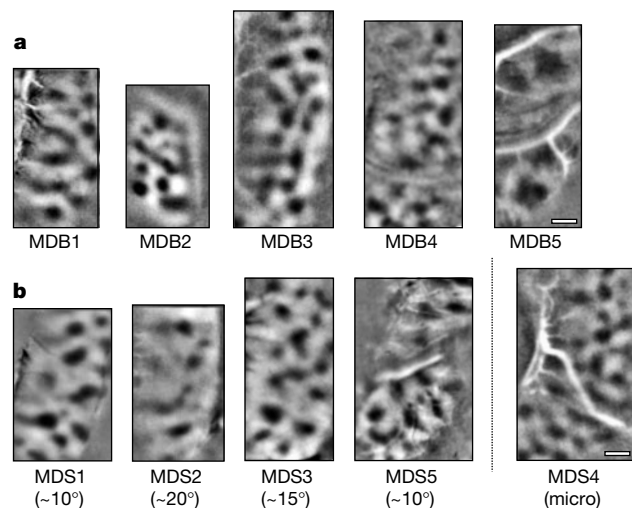
Ten kittens were monocularly deprived for 10 days, starting at 5 weeks of age. In five animals, MD was followed by normal binocular experience (MDB). In the other five cats, a convergent strabismus (esotropia) was induced in the nondeprived eye when

the deprived eye was reopened (MDS). In four of these cats, an esotropia of between 10° and 20° persisted throughout the recovery period, as judged from the positions of the corneal reflexes, whereas in one animal (MDS4), the visual axes seemed to become realigned within a few days of the strabismus surgery.

Intrinsic-signal optical imaging of V1 of both hemispheres was performed at least 14 days after the deprived eye had been reopened. In two additional control kittens we performed optical imaging, immediately after a 10-day period of MD, to obtain maps of activation through each eye. In these animals, in agreement with previous results<sup>9</sup>, deprived-eye responses were weak and restricted to small ‘islands’ that occupied, on average, only 14.3% of cortical territory in V1 ipsilateral to the deprived eye and 18.2% of V1 contralateral to the deprived eye (see Fig. 3a).

All five MDB cats exhibited remarkable recovery of responses through the previously deprived eye; the maps were generally indistinguishable from monocular responses in normal cats of similar age. In the ipsilateral hemisphere (Fig. 1a), on average the previously deprived eye dominated 48.2 ± 3.5% (mean ± s.d.) of the cortical surface, compared with 48.8 ± 3.8% in four normal kittens. In the contralateral hemisphere, the deprived eye’s domains occupied 52.6% (±4.2%), compared with 51.2% (±3.8%) in normal kittens.

In contrast, representation of the deprived eye was still much reduced in all four kittens in which inputs from the two eyes were decorrelated because of a persistent strabismus (MDS1–3 and MDS5). In the hemisphere ipsilateral to the deprived eye, responses to stimulation of that eye were often restricted to ‘islands’ (Fig. 1b; for example, animals MDS2 and MDS3). The deprived eye’s territory covered just 36.7% (±3.6%) of the imaged region, significantly less than in the kittens with normal binocular recovery ( $P < 0.002$ , one-tailed  $t$ -test; see Fig. 2). Even if the data were included from the additional animal (MDS4) in which the visual axes became realigned, the mean cortical territory dominated by the deprived eye was 39.4% (±6.8%), significantly smaller than in the five MDB kittens ( $P < 0.02$ ). The results also differed significantly from data for the ipsilateral eye in four kittens of similar age



**Figure 1** Ocular-dominance maps from left-hemisphere V1 of cats with 10-day MD of the left eye. **a**, Five cats in which MD was followed by concordant binocular vision (MDB); **b**, five cats which were strabismic during the binocular recovery period (MDS). Dark islands represent regions dominated by the left (originally deprived) eye. In all the MDB animals, dark and light areas occupy roughly equal areas (**a**). In the MDS cats (except the microstrabismic cat MDS4 (micro)), dark (left-eye) regions often form relatively isolated patches in a lighter ‘sea’ of cortex dominated by the right (nondeprived) eye (**b**). Blood vessel artefacts appear as light-grey linear and branching patterns (for example, MDS4 and MDB5). Scale bar, 1 mm. In all images the posterior pole is at the bottom.