gest much earlier divergence events. One possible explanation for this discrepancy is that part of the early Tertiary burst in avian and mammalian diversity would reflect dispersal from previously isolated India to Laurasia, rather than actual phylogenetic radiation. Indeed, similarly to ranid frogs, several modern land vertebrate lineages may have originated and been isolated on the drifting Indian subcontinent until they could colonize the world after India collided with Eurasia. Analyses of molecular data in acrodont lizards (27) and ratite birds (28) are consistent with this biogeographical hypothesis.

Krause and Maas (29) suggested that "among early Tertiary large landmasses, the Indian subcontinent is unique in its combination of having been in the right places at the right times to provide for the development and the subsequent disembarking of several new higher taxa of mammals" (p. 96). Our analyses provide molecular evidence extending this zoogeographical perception to amphibians and suggest that the origin of other vertebrate lineages might need to be sought in India, despite extensive isolation and massive volcanism.

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Rising CO₂ Levels and the Fecundity of Forest Trees

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We determined the reproductive response of 19-year-old loblolly pine (Pinus taeda) to 4 years of carbon dioxide (CO_2) enrichment (ambient concentration plus 200 microliters per liter) in an intact forest. After 3 years of CO_2 fumigation, trees were twice as likely to be reproductively mature and produced three times as many cones and seeds as trees at ambient CO_2 concentration. A disproportionate carbon allocation to reproduction under CO_2 enrichment results in trees reaching maturity sooner and at a smaller size. This reproductive response to future increases in atmospheric CO_2 concentration is expected to change loblolly dispersal and recruitment patterns.

Under elevated atmospheric CO_2 concentrations, the biodiversity of forests will depend on both changes in growth rates that confer competitive advantage to some species over others and on reproductive success, a key

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element of fitness. Greenhouse and growth-chamber studies demonstrate that although there is an average 31% growth enhancement of herbaceous plants and tree seedlings at doubled ambient CO_2 concentration, this response varies widely among species (1, 2). Tropical (3) and temperate (4–6) tree assemblages are "recruitment-limited." Tree population growth rates are constrained by low seed availability and low seedling establish-

ment in forest understories. If there is inter-specific variation in reproductive enhance-ments under CO_2 enrichment, then advantag-es gained by some species could have dra-matic consequences for their competitors.

Developing seeds are strong carbon sinks (1, 7), so potentially large responses are likely. Experiments on herb and crop plants demon-strate species differences that include increased reproductive biomass or seed number (8–10), decreased reproductive biomass (8, 11, 12), and no reproductive response (8, 13, 14). Some studies have indicated accelerated ontogeny (15) with plants maturing more quickly under elevated CO_2 concentration ([CO_2]). The ef-fects of CO_2 enrichment on forest tree repro-duction are unknown, because there are few studies of reproductive response in woody spe-cies (16–18). These studies have not been con-ducted in intact forests, and the few controlled studies of intact, fumigated forest communities have not examined reproduction (19, 20). Here we demonstrate that 19- to 20-year-old loblolly pine (Pinus taeda) trees in an intact forest ex-posed to 560 μl liters^{-1} [CO_2] since 1996 are twice as likely to be reproductively mature and produce three times as many cones and seeds as trees under ambient conditions. Because repro-ductive output is generally believed to be pro-portional to tree diameter, this response might be expected simply as a result of vegetative growth enhancement under CO_2 enrichment. However, the increased fecundity that we found results both from earlier reproductive matura-tion and higher proportionate allocation to reproduction.

The experiment was conducted in Duke Forest, in the Piedmont region of North Caro-lina (35°97'N, 79°09'W). In August 1996, a free-air CO_2 enrichment (FACE) system was installed in a 13-year-old loblolly pine plan-tation (pines were planted as 3-year-old seed-lings). Trees (P. taeda) in this plantation are half-sibs, have a density of 1733 stems per hectare, and account for 98% of the basal area (19, 21). Each of six 30-m-diameter FACE rings in the forest is surrounded by 32 vertical pipes that extend above the 14-m-high forest canopy. In the three fumigated rings, these pipes deliver CO_2 to maintain an atmosphere at ambient plus 200 μl liter^{-1} [CO_2]. The three ambient plots are identical to treatment rings without the addition of CO_2 (22). The FACE system allows CO_2 manipulation of the entire ecosystem including vegetation and soil processes.

Trees were not reproductively mature at the start of the experiment, so our 4-year study spans the onset of seed production [seeds collected in 0.16-m^2 seed traps were gathered monthly and sorted by species (5)]. Loblolly cone development requires 2 years (23); thus, seed censuses in May 1997 repre-sent pretreatment. In September 1999, the first year of significant cone production, and in September 2000, cones on all P. taeda trees within the six rings were counted from above-canopy towers with binoculars (24). Counts were also made of cones produced the previous year (those having open scales and borne by the previous year's growth) and of cones on the ground in each ring.

The effects of elevated [CO_2] were deter-mined on both seed and cone production. We used an intervention analysis to test for a change in the difference between ambient and CO_2 treatment seed and cone production since the onset of CO_2 fumigation in 1996. Our probability model for cone production per tree simultaneously estimates effects of elevated [CO_2] on the mean μ and variance σ^2 of tree diameter d when cone production begins, and on the proportionate increase a in cone production with tree diameter. The probability of being reproductively mature (producing cones) $\theta(d)$ increases with diam-eter, as described by the probit (cumulative normal distribution)

$$\theta(d) = \Phi(d;\mu,\sigma^2)$$

(first onset of cone production is normally distributed). The normal distribution best fit the data when compared with other distribu-tions. After reproductive maturation, cone production $\lambda(d)$ increases with the square of diameter (4, 5)

$$\lambda(d) = ad^2$$

This model accommodates the two ways to observe zero cones. A tree may be immature with probability $1 - \theta(d)$ or it may be mature with probability $\theta(d)$ and produce no cones, the zero category of the Poisson distribution. Cone production is the joint probability of being mature [with probability $\theta(d)$] and of producing at least one cone. The likelihood of observing c cones is thus

$$L(c|a,\mu,\sigma^2) =$$
$$\begin{cases} 1 - \theta(d) + \theta(d)e^{-\gamma(d)} & c = 0 \\ \theta(d) \times \dfrac{\gamma(d)^c e^{-\gamma(d)}}{c!} & c > 0 \end{cases}$$

We hypothesized that CO_2 treatment might affect the average diameter at which repro-duction begins (μ), the variance among indi-viduals in diameter at maturation (σ^2), and/or the proportionate allocation to seed produc-tion once mature (a). We obtained maximum likelihood estimates for parameters fitted to data from both ambient and fumigated plots separately and combined. We tested for treat-ment effects using likelihood ratio tests of the deviance $D = -2LR$, where LR is the loga-rithm of the ratio for nested models.

There was no treatment effect before the 1999 cone crop (Fig. 1). In 1998, cones per tree were rare in all elevated and ambient rings (0.073 ± 0.004 versus 0.051 ± 0.003 cones per tree; $D = 1.72$, $P = 0.19$, df = 2). But differences were large by fall 1999, when trees fumigated with CO_2 were twice as like-ly to be reproductively mature ($D = 23.46$, $P < 0.0001$, df = 2) and produced three times more cones per tree (2.85 ± 0.15 ver-sus 0.90 ± 0.05, $D = 355$, $P < 0.0001$, df = 2). The difference between elevated and am-bient cone production was maintained in fall 2000 counts (Fig. 1). Trees in the enriched rings were twice as likely to be reproductive ($D = 13.13$, $P = 0.00029$) and produced 2.4 times more cones per tree than in the ambient rings (3.48 ± 0.19 versus 1.46 ± 0.08; $D = 277.21$, $P < 0.0001$).

The difference observed in cone production is consistent with seed trap data. From August 1999 through July 2000, we collected three times as many seeds from seed traps in the enriched rings than in ambient rings (282.0 ±

Fig. 1. (A) The differ-ence in number of loblolly seeds per square meter from May 1997 to Decem-ber 2000 and (B) mean cone produc-tion per loblolly tree for all elevated minus ambient rings. Cone production data are marked annually. The typical season for seed fall is shaded. Error bars mark 95% confidence intervals. Both data sets sug-gest that 1999 was the first significant cone crop at this site.
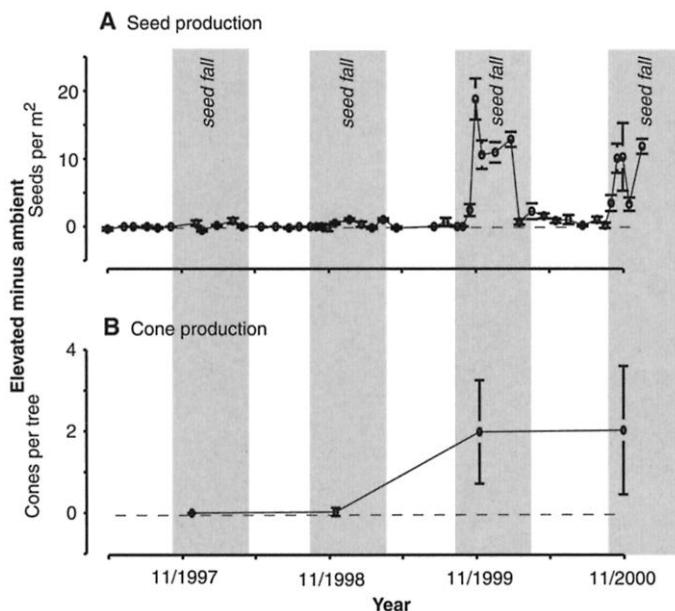
8.4 versus 94.8 ± 5.4 seeds per m², $P = 0.01$).

Trees subjected to elevated [CO_2] began cone production at smaller diameters and, once cone production began, produced disproportionately more cones per diameter than ambient trees. Trees in the enriched rings had a greater increase (a) in cone production per unit diameter than trees under ambient [CO_2] in 1999 (Table 1 and Fig. 2A). The distribution of maturation diameters (Fig. 2B) was shifted to smaller size classes in the elevated rings (Table 1). Although reproductive output is generally taken to be proportional to diameter, it is possible that shifts in leaf area–to–sapwood ratios may affect this relationship under CO_2 enrichment. In addition to elevated [CO_2], there were significant ring effects on reproductive effort ($P < 0.0001$, df = 12), indicating spatial variability in CO_2 responses. Despite spatial differences, CO_2 caused an overall significant increase in reproductive effort as measured by cone production and seed rain ($P < 0.0001$).

Recruitment limitation is pervasive in forest communities. Both temperate and tropical forests are limited by low seed availability (3, 5, 6). Recruitment limitation promotes diversity, because dominant species cannot co-opt the available recruitment opportunities (25–27). Our results suggest that, through increased seed production under elevated [CO_2], recruitment limitation will diminish for P. taeda, potentially affecting forest diversity. This is especially important in the southeastern United States, where P. taeda dominates many Piedmont forests and is a valued timber species. P. taeda may gain importance as accelerated maturation and increased reproductive effort increase its ability to exploit disturbed landscapes and track regional change due to greenhouse warming. Seventy-five percent of loblolly forests in the United States are naturally regenerated, closed stands that are profoundly seed-limited for at least 25 years (23). Under CO_2 enrichment, this period of seed limitation may be reduced.

The increased rate of ontogeny we observe under CO_2 enrichment may have implications for carbon accumulation. Development rate and life-span are inversely correlated across tree species (28). If this correlation applies within individuals, as a consequence of allocation trade-offs, then earlier maturation may result in more rapid turnover and not necessarily in increased stand biomass. The long-term impacts will depend on differences among species.

If the rate of photosynthesis decreases with long-term exposure to elevated [CO_2], and if increased reproductive effort depends on a high rate of carbon assimilation (29), then cone and seed production may

not remain at the high rates we observed. Responses of trees subjected to CO_2 enrichment from germination might also differ from those reported here. However, crop studies have demonstrated that down-regulation of RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase) activity may become apparent when plants reach reproductive maturity (30). Because our trees have already reached this developmental stage, the results of long-term enrichment may be sustained. The multiyear response we observed extends longer than the interval typically used to identify an acclimation response. It represents the most realistic insight currently available, because previous studies come from isolated plants in growth chambers.

Although we document only the first few years of reproduction, the reproductive output is substantial. For comparison with mature stands under optimal conditions, loblolly seed orchard trees [25 cm diameter at breast height (DBH)] can produce 100,000

seeds per hectare (23). Our juvenile trees (mean 16.5 cm DBH) already produce close to 50,000 seeds per hectare in the elevated rings. By contrast, ambient trees produced 17,100 seeds per hectare (mean 15.5 cm DBH).

Perhaps most important when considering dynamics of forest composition and diversity are the expected species-specific CO_2 responses, as suggested by vegetative responses in trees (31, 32) and reproductive responses in crops (8, 30). Our study demonstrates that P. taeda, a fast-growing, evergreen species, has a large fecundity response. Interspecific variation in response to changing climate will alter forest dynamics of the future. We do not demonstrate species differences, but differences are more likely than not. Not only will species with large reproductive response to CO_2 enrichment be the most likely to track regional climate change, but they will also be favored in competition with less responsive species.
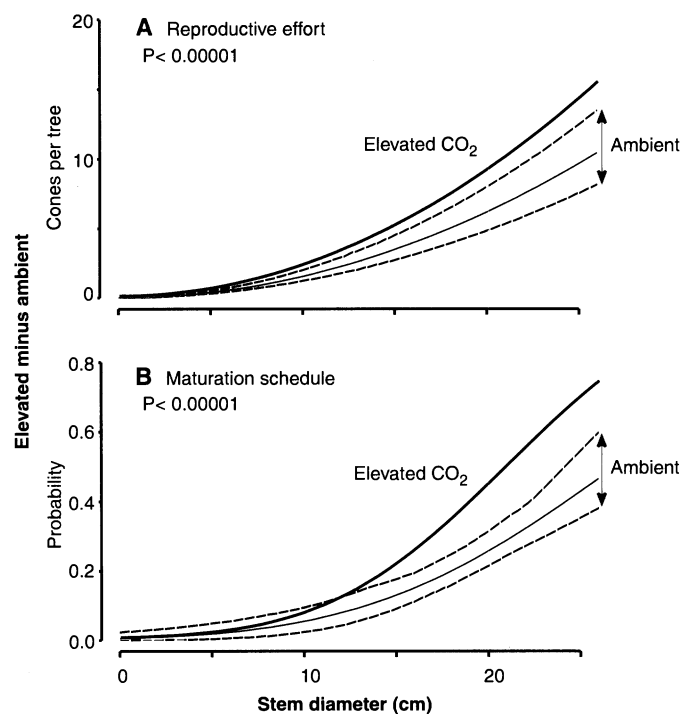
Fig. 2. (A) Cone production per tree increases with stem diameter. Fitted model (upper solid line) for elevated [CO_2] trees is significantly different from the fitted ambient model (lower solid line) and bootstrapped 95% confidence intervals (dashed line). (B) Probability of reproductive maturation as a function of stem diameter. Fitted model for probability of being reproductively mature in elevated [CO_2] rings is significantly different from the ambient probability and bootstrapped 95% confidence interval.

Table 1. Maximum likelihood parameter estimates and bootstrapped 95% confidence intervals for loblolly pinecone production in ambient and elevated [CO_2] plots are significantly different ($P < 0.0001$).

	Cone allocation a (cm⁻²)	Mean maturation diameter μ (cm)	Standard deviation σ (cm)
Ambient	0.0154 (0.011–0.019)	26.8 (23.9–30.0)	10.36 (6.7–14.7)
Elevated	0.023 (0.019–0.028)	21.0 (19.6–22.7)	7.7 (5.76–10.7)
Deviance	122.54	16.6	0.029
P value (df)	<0.0001 (1)	0.00026 (1)	0.865 (1)

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Ecological Degradation in Protected Areas: The Case of Wolong Nature Reserve for Giant Pandas

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It is generally perceived that biodiversity is better protected from human activities after an area is designated as a protected area. However, we found that this common perception was not true in Wolong Nature Reserve (southwestern China), which was established in 1975 as a "flagship" protected area for the world-renowned endangered giant pandas. Analyses of remote sensing data from pre- and post-establishment periods indicate that the reserve has become more fragmented and less suitable for giant panda habitation. The rate of loss of high-quality habitat after the reserve's establishment was much higher than before the reserve was created, and the fragmentation of high-quality habitat became far more severe. After the creation of the reserve, rates of habitat loss and fragmentation inside the reserve unexpectedly increased to levels that were similar to or higher than those outside the reserve, in contrast to the situation before the reserve was created.

More than 12,700 protected areas have been established around the world, accounting for 13.2 million km² (an area greater than the United States or China), or 8.81% of Earth's land surface (*1*). Although protected areas are generally believed to be the cornerstones of biodiversity conservation (*2–4*) and the safest strongholds of wilderness (*2, 5, 6*), human encroachments and threats are still very common in many protected areas (*7, 8*). The problems of mismanagement and conservation politics have been widely publicized (*7, 9*), but quantitative information about the deterioration of protected areas is scant (*10*). It is not clear whether all protected areas are effectively protected because there is little research comparing ecological degradation before and after the protected areas were established.

Is the rate of ecological degradation lower after the establishment of a protected area? To answer this question, we performed a case study of Wolong Nature Reserve, Sichuan Province, southwestern China (102°52' to 103°24'E, 30°45' to 31°25'N). We chose Wolong for three main reasons. First, it is the largest protected area designated for conserving the endangered giant pandas [*Ailuropoda melanoleuca* (*11*)] and contains approximately 10% of the wild panda population (*12*); created in 1975, the reserve covers an area of approximately 200,000 ha (*12*). Second, as in many other protected areas, there are local people residing in Wolong. Third, Wolong is a "flagship" nature reserve and has received exceptional financial and technical support from the Chinese government and many international organizations, such as the World Wildlife Fund (WWF) (*9*). To a large extent, Wolong's ecological fate represents the success or failure of tremendous conservation efforts made by the Chinese government and many international organizations (*9*).

We assessed the rates of change in forest cover and giant panda habitat before and after Wolong was established as a nature reserve. Forest cover, slope, and elevation are important factors affecting pandas (*11, 12*). We incorporated these factors to estimate habitat suitability for pandas. In a process similar to hurricane damage assessment examining pre- and post-hurricane conditions (*13, 14*), we quantified forest cover before and after the reserve's establishment, using remotely sensed data obtained at three different time points (*15*). The different sources of data used in our study are typical of many studies of land use and land cover change (*16–18*), because it is unrealistic to obtain remote sensing data on the same characteristics over a long period of time because of changes in the sensors. Neither aerial photography nor multispectral data were available for the entire time span of this study. Although cloud-free images with consistent phenology were not available, leaf-off [Corona data and Landsat Multispectral Scanner (MSS) data] versus leaf-on [Landsat Thematic Mapper (TM) data] conditions did not contribute significantly to the forest and panda habitat analyses

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