duction in early Eocene nascent arcs of the western Pacific.

A key remaining question concerns the cause of forced convergence that modeling indicates was needed to kick-start IBM subduction (*21*). The straight track of the Hawaiian-Emperor chain from Suiko (60.9 ± 0.3 Ma) to Koko's southern summit (50.4 ± 0.1 Ma) does not record changes in the direction of Pacific plate motion; therefore, motion change in the Eurasian or Australian plates adjoining to the west may be indicated. Possible triggers for such change are the lockup of the India-Eurasia collision zone (*4*, *27*), which is approximately dated by the onset of major crustal shortening in that region at ~50 Ma (*28*), and rifting of Australia from Antarctica, leading to convergence between the Australian and Pacific plates (*23*).

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Corridors Increase Plant Species Richness at Large Scales

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Habitat fragmentation is one of the largest threats to biodiversity. Landscape corridors, which are hypothesized to reduce the negative consequences of fragmentation, have become common features of ecological management plans worldwide. Despite their popularity, there is little evidence documenting the effectiveness of corridors in preserving biodiversity at large scales. Using a large-scale replicated experiment, we showed that habitat patches connected by corridors retain more native plant species than do isolated patches, that this difference increases over time, and that corridors do not promote invasion by exotic species. Our results support the use of corridors in biodiversity conservation.

Loss of biological diversity is a leading threat to the sustainability of the biosphere (*1*) and is largely caused by habitat loss and fragmentation (*2*). Landscape corridors (strips of habitat connecting otherwise isolated habitat patches) are hypothesized to reduce the negative effects of fragmentation by facilitating gene flow and the movement of organisms, thereby preventing local extinctions and increasing species diversity (*3*). Corridors have become a central feature of ecological management plans worldwide, but evidence of their effectiveness has lagged behind the push for their implementation (*4*).

Although a number of experimental studies have demonstrated positive corridor effects on single species (*5–7*), few have examined corridor effects on entire communities. All of these studies were conducted at very small spatial scales (10 cm^2 to 10 m^2), and taken together they have yielded equivocal results (*8–11*).

We examined the long-term effect of corridors on plant species diversity by studying six ~50-ha experimental landscapes at the Savannah River Site in South Carolina, containing both isolated and connected habitat patches (Fig. 1A). Each landscape consisted of a central patch measuring 100 m by 100 m, four surrounding patches 150 m away, and a buffer area extending >150 m from these surrounding patches' furthest edges (Fig. 1A). One of the four surrounding patches was connected to the central patch by a corridor 150 m by 25 m (the "connected" patch). The other three surrounding patches were equal in area to the connected patch plus its corridor, but were unconnected. These unconnected patches were of two types: winged and rectangular. Rectangular patches were 100 m by 137.5 m; the additional 37.5 m relative to the 100-m–by–100-m central patch controlled for the increased area provided by the connected patch's corridor. Winged patches were 100 m by 100 m, with two 25-m–by–75-m projections off of opposite patch sides to control for the area of the connected patch's corridor and to allow examination of the elongation in patch shape associated with corridors. Winged and connected patches had equal edge-to-area ratios. Patch and corridor dimensions were chosen because they are within the range of typical U.S. Forest Service (USFS) management activities. Further explanation of the experimental design is provided elsewhere and in the supporting online material (*6*, *12*).

All plant species were surveyed in each patch from 2000 to 2005, except in 2004, when patches were burned by the USFS as part of restoration management (*12*). Our patches were open habitats with young longleaf pines

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(*Pinus palustris*) surrounded by dense pine plantations. There was a sharp contrast between the patch habitat, which had a rich herbaceous understory, and the surrounding pine plantation matrix, which was relatively depauperate. Longleaf pine forests historically dominated this region, covering >37 million ha (Fig. 1B) (*13*). Over 97% of these forests have been lost to agriculture, pine plantations, and the interruption of historical fire regimes (*13, 14*). Native longleaf pine forests are characterized by an open, productive, and diverse understory, with a sparse canopy overhead (*13, 14*). They are maintained by fre-

quent low-intensity fires (*13, 14*). Many species native to longleaf pine forests persisted inside our patch openings but were absent from the surrounding pine plantation matrix.

We detected no difference in the number of plant species in connected and unconnected patches immediately after the creation of our experimental landscapes (Fig. 2A). Over time, connected patches became more species-rich, containing 20% more plant species than unconnected patches by the end of the study (Fig. 2, A and B).

Our experimental design allowed us to link the beneficial effects of corridors on spe-

cies richness directly to the connectivity provided by corridors. Specifically, it allowed us to reject four alternative hypotheses about what generated the higher species richness in connected patches. First, higher species richness was not caused by increased patch area or elongation, because connected patches had greater numbers of species than did unconnected patches (rectangular or winged) of equal area or equal patch elongation (winged patches). These results did not change when we removed species found in the corridor, wings, or the extra area of the rectangle and compared only the central areas (100 m by

Fig. 1. (**A**) One of the six experimental study sites at the Savannah River Site, South Carolina, USA. Patches are connected or unconnected by a corridor. Unconnected patches are either rectangular or winged. (**B**) The location of the Savannah River Site relative to the historical distribution of native longleaf pine forest [after Outcalt and Sheffield (*25*)].
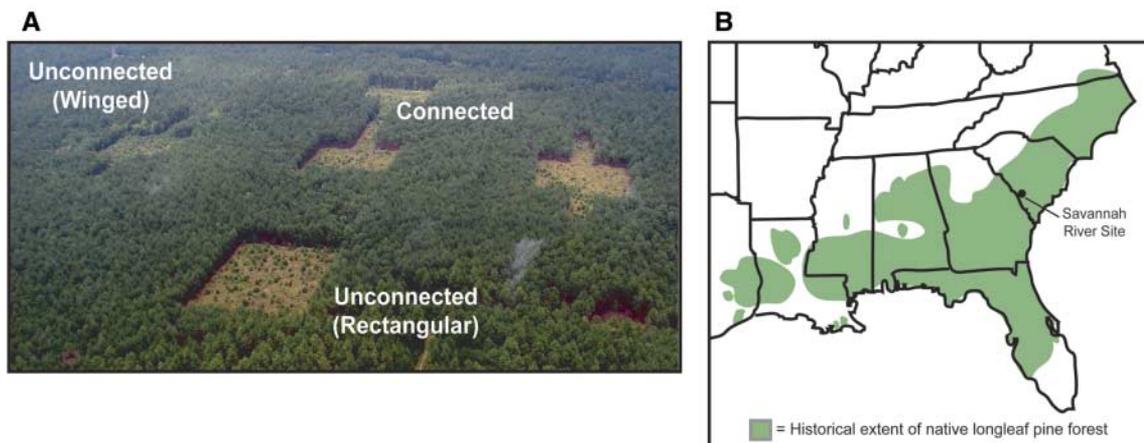

Fig. 2. (**A**) Plant species richness over time. In 2000, the first growing season after site creation, plant species richness did not differ between connected and unconnected patches (ANCOVA, $F_{1,9.4}$ = 0.36, P = 0.56), indicating that subsequent changes were due to the experimental manipulation [species richness in 2000 is not directly comparable to 2001–2005, indicated with breaks on the x axis, because es-

timates were obtained using different data collection methods (*12*)]. Over time, plant species richness in connected patches increased relative to that in unconnected patches (repeated measures ANCOVA, $F_{1,12.5}$ = 11.57, P < 0.01). Unconnected winged and rectangular patches did not differ in species richness, so they are combined (2000, ANCOVA, $F_{1,9.4}$ = 1.12, P = 0.32; 2000–2005, repeated measures ANCOVA, $F_{1,12.4}$ = 1.13, P = 0.31, with soil moisture as covariate). All error bars indicate standard errors. (**B**) The difference in species richness between connected and unconnected patches for all species increased from 2001 to 2005 [linear regression, R^2 = 0.97, df = 3, P = 0.02 (*12*)]. (**C**) This difference in species richness grew over time in connected versus unconnected patches for native longleaf pine forest species (R^2 = 0.89, df = 3, P = 0.05) but not for exotic species (R^2 = 0.07, df = 3, P = 0.74). Species were classified with the use of regional floras, vegetation classifications, primary literature, and online plant databases (*12*).
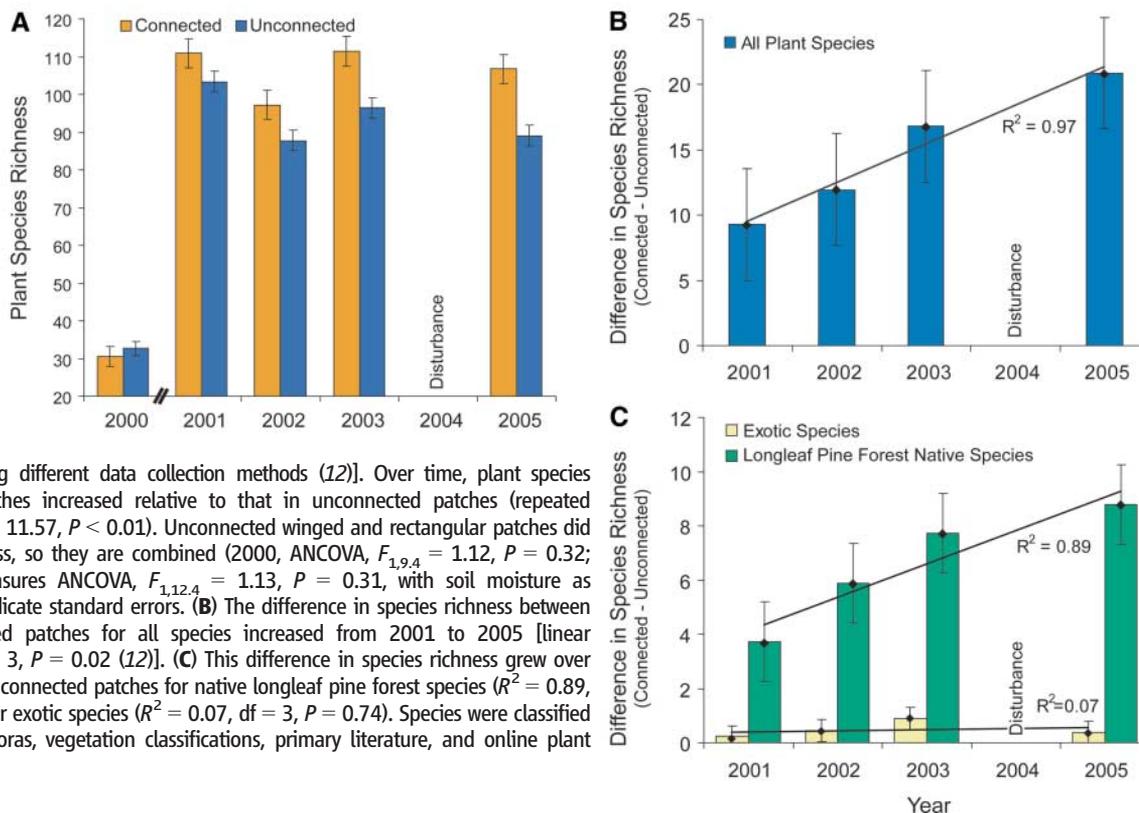
100 m) of each patch [analysis of covariance (ANCOVA), $F_{1,13.3} = 10.66$, $P < 0.01$ (*12*) (fig. S1 and table S1)], confirming that the area of the corridor was not driving the pattern.

Second, the increased species richness in connected patches was not generated by differences in patch shape that are independent of connectivity (such as variation in the proportion of edge, altering within-patch heterogeneity). Permanent vegetation plots distributed across all parts of all patches (fig. S1) did not differ in species richness (repeated measures ANCOVA, $F_{6,21.6} = 0.64$, $P = 0.70$) or evenness (repeated measures ANCOVA, $F_{6,34.5} = 1.32$, $P = 0.28$, table S2), and the degree of similarity among plots was not affected by patch shape [multi-variate analysis of variance (MANOVA), Pillai's trace, $F_{6,28} = 0.81$, $P = 0.57$, Bray-Curtis distance; MANOVA, Pillai's trace, $F_{6,28} = 1.14$, $P = 0.37$, Sorenson distance (*12*)].

Third, inputs to the plant community from the soil seed bank cannot account for increased plant species richness in connected patches. The plant community arising from the seed bank after the sites were created in 2000 was unaffected by corridors (Fig. 2A and table S1). Additionally, 3 years later, the number of species of seeds emerging from over 12,000 soil cores collected from 960 plots where plant communities were measured remained unaffected by corridors [ANCOVA, $F_{2,16.4} = 0.72$, $P = 0.50$ (*12*)]. This suggests that species in the seed bank were not limited by dispersal, were unaffected by corridors, and were not responsible for the increase in species richness we observed.

Fourth, local differences in soil moisture, an important driver of plant species richness in longleaf pine forests (*15*), were not responsible for the increased species richness in connected patches. Soil moisture was often a predictor of species richness in analyses, but after controlling for these within-patch differences, connectivity effects remained (*12*).

Corridor effects were apparent across the 5 years of our study despite environmental variation in successional stages, annual precipitation, and disturbance events. The influences of these other effects were apparent in the annual fluctuations in species richness across both connected and unconnected patches (Fig. 2A). For example, unusually high rainfall at the study area in 2003 [35% higher than the mean from 2000 to 2005 and 57% higher than in the previous year (2002)] and the prescribed burn in 2004 are plausible explanations for the increased species richness in 2003 and 2005, respectively. Our study shows that despite other factors that influence the number of plant species in any given year, a consistent effect of connectivity emerges.

Corridors are often championed as tools to help preserve species of conservation concern, largely on the basis of the untested assumption that increased connectivity benefits native species more than it benefits common "weedy," exotic, or invasive species. Our results support this assumption. Our experimental sites harbored many species that are native to longleaf pine forests (*16*, *17*), including 29 species of locally rare or uncommon flowering herbs and grasses that are a part of restoration efforts by the USFS (*17*). The species richness (repeated measures ANCOVA, $F_{1,11} = 6.62$, $P = 0.03$, Fig. 2C) and abundance (repeated measures ANCOVA, $F_{1,9.3} = 6.12$, $P = 0.04$, table S3) of these native species increased over time in connected versus unconnected patches.

Conversely, one of the major and untested concerns about using corridors is that they will increase the spread of exotic species (*18*, *19*). In our experiment, corridors had no detectable effect on the number of exotic species [repeated measures ANCOVA, $F_{1,23.5} = 2.32$, $P = 0.14$; our definition of exotic species included invasive exotics (*12*) (Fig. 2C and table S4)]. Corridors similarly did not affect the abundance (repeated measures ANCOVA, $F_{1,9.1} = 0.76$, $P = 0.41$) or proportion (repeated measures ANCOVA, $F_{1,14.8} = 0.15$, $P = 0.70$, table S4) of exotic species in the total species pool. In addition, native early-successional weeds that are not associated with historical longleaf pine forests were also not responsible for the increase in species richness we observed. Our results did not change when these species were removed (repeated measures ANCOVA, connectivity, $F_{1,11.9} = 9.36$, $P = 0.01$, table S3).

The most parsimonious explanation for the increased plant species richness we observed in connected patches is that corridors alter the balance among three important processes and interactions in ways that promote diversity. Corridors promote colonization by increasing seed deposition (*6*, *20*), promote within-patch recruitment by increasing pollen movement (*6*, *21*), and alter foraging by seed predators that could benefit species otherwise more likely to be excluded by seedling competition (*22–24*). Although individual plant species and their interactions will differ in their response to corridors, the results reported here show that across ~300 plant species and their countless interactions, connecting patches with corridors leads to a positive net effect on native plant species richness. By providing experimental evidence that corridors increase the number of native plant species in large-scale communities over a wide range of environmental conditions, we show that corridors are not simply an intuitive conservation paradigm; they are a practical tool for preserving biodiversity.

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