PLANT ECOLOGY

Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

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Deleterious effects of habitat fragmentation and benefits of connecting fragments could be significantly underestimated because changes in colonization and extinction rates that drive changes in biodiversity can take decades to accrue. In a large and well-replicated habitat fragmentation experiment, we find that annual colonization rates for 239 plant species in connected fragments are 5% higher and annual extinction rates 2% lower than in unconnected fragments. This has resulted in a steady, nonasymptotic increase in diversity, with nearly 14% more species in connected fragments after almost two decades. Our results show that the full biodiversity value of connectivity is much greater than previously estimated, cannot be effectively evaluated at short time scales, and can be maximized by connecting habitat sooner rather than later.

Habitat loss and fragmentation are leading threats to biodiversity in ecosystems across the globe (*1*–*4*). In a world replete with small, isolated fragments, where 70% of the world's forest area is within just 1 km of an edge, biodiversity loss is mounting (*1*). Increasing habitat connectivity is a key conservation strategy to minimize biodiversity losses by facilitating dispersal and rescuing declining populations from extinction (*5*). However, it is not known if restoring connectivity among habitat fragments will increase biodiversity by promoting the colonization of new species.

A well-established body of ecological theory predicts the importance of connectivity for biodiversity. Metapopulation theory (*6*, *7*) illustrates how increasing connectivity is predicted to lead to greater regional population persistence by promoting colonization of new habitats, increasing recolonization of habitats where extinction has occurred (recolonization rescue), and buffering existing populations against extinction via increased immigration (demographic rescue). Metacommunity theory (*8*, *9*) and island biogeography theory (*10*) integrate these population-level effects of connectivity to yield predictions regarding biodiversity. These developments provide strong theoretical reasons to expect that modifying connectivity can increase biodiversity by increasing colonization and decreasing extinction, but they also caution that nonintuitive effects (e.g., synchronization of population dynamics or modification of interactions) are possible (*8*, *11*).

Despite the presumed importance of connectivity for community diversity in both basic and applied ecology (*12*, *13*), empirical evidence for predictions from theory has been mixed (*14*–*16*). A primary challenge in evaluating these predictions in empirical systems is that ecological processes vary greatly in space and time: The dynamic nature of colonization and extinction processes necessitates well-replicated, large-scale, and long-term studies to draw meaningful inference about the ultimate role of connectivity in affecting diversity. For example, changes in biodiversity due to either lost or restored connectivity do not occur instantaneously. In fragmented habitats, species can continue to persist for years before eventually going extinct (*17*), resulting in an "extinction debt" paid over decades or even centuries (*18*, *19*). Similarly, "colonization credits" can accrue when habitat connectivity is restored among species-impoverished habitats, catalyzing the potential for biodiversity gains (*20*–*23*). Species may not colonize immediately because of low dispersal rates, which are difficult to measure, making the extent of colonization credits unknown (*20*, *23*). This lack of information is important because colonization credits could forestall or even reverse extinction debt.

We tested the long-term effects of habitat connectivity on plant colonization and extinction dynamics and their resulting impacts on species richness over nearly two decades in a habitat fragmentation experiment at the Savannah River Site in South Carolina, USA. This experiment manipulates connectivity through the creation of habitat corridors—thin strips of habitat that connect otherwise isolated habitat fragments (*24*). Ten experimental landscapes each contain four 1.375-ha fragments of equal area that are either unconnected or connected to a central 1-ha fragment by a 150 m–by–25 m corridor (Fig. 1). Fragments and corridors are being restored to longleaf pine savanna, a threatened ecosystem within a global biodiversity hotspot (*25*), and are surrounded by dense pine plantations that limit herbaceous plant growth. For 18 years, we censused occupancy of all plant species as communities assembled after each restored fragment's creation. Connected and unconnected fragments were randomly assigned and did not differ in species richness at the start of the experiment [fig. S1; see also supplementary materials and methods (*26*)].

Habitat connectivity has increased rates of colonization and decreased rates of extinction. As communities assembled, connectivity increased the average annual species colonization rate by 5% and decreased the average annual extinction rate by 2% beyond expected successional dynamics (Fig. 2A and fig. S2). These apparently small differences in annual rates are persistent and have compounded over time, generating large increases in species richness in fragments connected by corridors, magnifying colonization credits (Fig. 2B and fig. S3). These impacts occur across 239 plant species with diverse life histories, including species of conservation and restoration concern from the longleaf pine ecosystem (fig. S6) and species that vary in their dispersal ability (fig. S7).

Higher colonization rates and lower extinction rates have shortened the average time for a species to colonize a fragment (Fig. 3) and have driven a large increase in plant species richness (Fig. 2B and figs. S3 and S5). Corridor-connected fragments now support, on average, 24 additional plant species compared with unconnected fragments (200 versus 176 in connected versus unconnected fragments, respectively; fig. S3), an increase of 14%. Notably, connectivity's effects on species richness continue to accumulate; our best-fit models of species richness differences over time show no asymptote. Moreover, connectivity's impacts on colonization and extinction rates remain consistent across the 18 years of this study (Fig. 2 and figs. S4 and S5) (*26*).

Our results underscore that typical experiments of 1 to 5 years in duration (*1*, *27*) likely underestimate the impact of long-term connectivity restoration on community diversity. Connectivity's impacts are not fully realized until the ongoing, lagged assembly processes and responses equilibrate. Theory from spatial ecology and community assembly predicts that connectivity's effect on diversity will eventually reach an asymptote because of local ecological processes constraining species richness (e.g., competition) and because local communities draw from a finite number of species in the region (*10*, *28*). Long-term empirical investigations of how landscape configuration alters colonization

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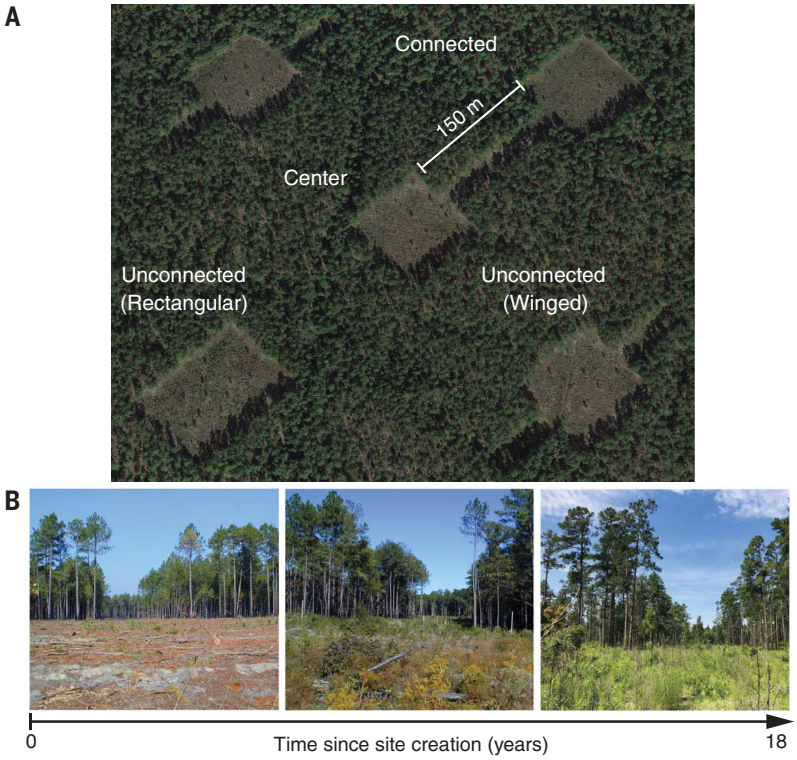

Fig. 1. A long-term habitat connectivity experiment. (**A**) One of 10 experimental landscapes (N = 10), each containing a center fragment that is connected or unconnected (winged and rectangular) to peripheral fragments of open longleaf pine savanna surrounded by dense pine plantations [additional details in (*26*)]. [Credit: Google Earth 2019] (**B**) Plant communities within fragments have assembled over nearly two decades and are being restored to native longleaf pine savanna using frequent, low-intensity fires that mimic the historic fire regime. See (*26*) for further information on the study design. [Credits (left to right): M. A. Burt, N. M. Haddad, and E. I. Damschen]

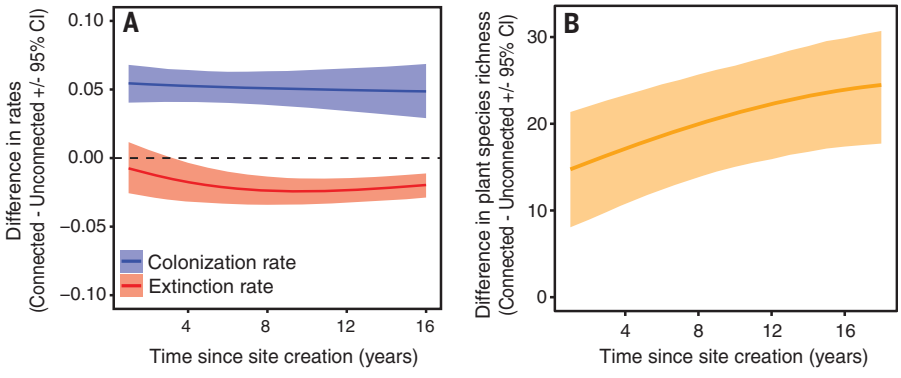

Fig. 2. Connectivity reduces extinction and increases colonization rates over two decades, resulting in accruals of species in connected fragments. (**A**) Average colonization rates are 5% greater and extinction rates are 2% lower for species in connected fragments than rates for those in unconnected fragments. These rates are constant over time. The net accrual of colonization credits increases biodiversity in connected fragments. (**B**) Plant species richness in connected fragments has increased at a greater rate than in unconnected fragments. Shown is the difference in estimated species richness over time, illustrating greater increases in richness in connected versus unconnected fragments. This rate increase has been consistent for nearly two decades and has resulted in connected fragments having 24 more plant species than unconnected fragments (fig. S3). A linear model (on the logit scale) is the best fit for the difference in species richness between connected and unconnected fragments over time (*26*). Shaded regions represent 95% confidence intervals.

and extinction rates are critical for determining and predicting human-induced changes to the environment; communities will almost never exhibit instantaneous responses or equilibrial dynamics (*29*).

We show that connectivity directly alters colonization and extinction dynamics among fragments, providing mechanisms for observed landscape-level biodiversity patterns (*30*). Our

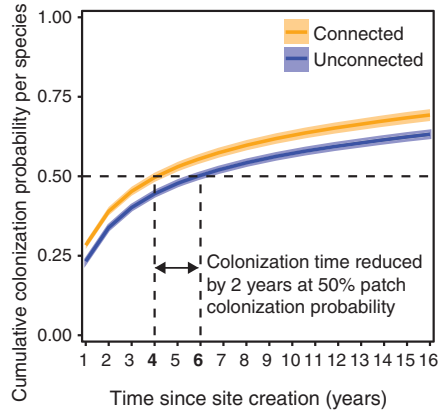

Fig. 3. Connectivity reduces colonization timing, resulting in colonization credits. The average cumulative probability of each individual species colonizing connected fragments is 1 to 6 years earlier than in unconnected fragments, resulting in reduced colonization lags and increased colonization credits. For example, the point at which a single species has a 50% likelihood of colonizing a habitat fragment (dotted lines) occurs a full 2 years earlier in connected versus unconnected fragments. Shaded regions represent 95% confidence intervals.

results contrast with hypotheses that attribute biodiversity change to habitat area alone and those that do not attempt to isolate underlying mechanisms (*14*). In our study system, connectivity leads to wholesale temporal shifts in community assembly, driven by lags in colonization that generate colonization credits, regardless of whether an equilibrium is achieved. Connecting fragments with corridors results in a 1- to 6-year reduction in the time it takes an individual species to colonize new habitat fragments, relative to the time needed for colonization of unconnected fragments (Fig. 3). For example, the 50% likelihood of a single species colonizing a fragment (dotted lines in Fig. 3) occurs a full 2 years earlier in connected fragments than for that same species in unconnected fragments (Fig. 3). These temporal shifts in the speed of colonization (Fig. 3 and fig. S8) have unexplored and potentially important ramifications for time-dependent ecological processes (e.g., priority effects). Although less explored, our results also suggest that corridor-mediated changes in the movement of individuals and alleles may affect evolutionary processes by altering effective population size and gene flow (*31*). Our results raise the need for theory to better integrate temporal duration in conservation and management.

Conservation strategies to mitigate biodiversity losses due to habitat fragmentation and loss are urgently needed, and habitat corridors feature prominently in global conservation plans (*4*). Our study shows that efforts to increase connectivity will pay off over the long term. Conservation plans that ignore connectivity, such as plans that focus solely on habitat area, will

leave unrealized the substantial, complementary, and persistent gains in biodiversity attributable specifically to landscape connectivity (*30*, *32*).

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/365/6460/1478/suppl/DC1
Materials and Methods
Supplementary Results
Figs. S1 to S8
Table S1
References (*34*–*61*)
Supplementary Code

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Habitat connectivity enhances diversity

Fragmentation of ecosystems leads to loss of biodiversity in the remaining habitat patches, but retaining connecting corridors can reduce these losses. Using long-term data from a large, replicated experiment, Damschen *et al.* show quantitatively how these losses are reduced. In their pine savanna system, corridors reduced the likelihood of plant extinction in patches by about 2% per year and increased the likelihood of patch colonization by about 5% per year. These benefits continued to accrue over the course of the 18-year experiment. By the end of monitoring, connected patches had 14% more species than unconnected patches. Restoring habitat connectivity may thus be a powerful technique for conserving biodiversity, and investment in connections can be expected to magnify conservation benefit.

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Supplementary Materials for

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This PDF file includes:

Materials and Methods
Supplementary Results
Figs. S1 to S8
Table S1
Caption for Supplementary Code
References

Other Supplementary Material for this manuscript includes the following:
(available at science.sciencemag.org/content/365/6460/1478/suppl/DC1)

Supplementary Code (.pdf)

Materials and Methods

Landscape experiment

In 2000, we initiated a landscape experiment to test whether habitat corridors promote connectivity and impact community diversity. The experiment is at the Savannah River Site, a National Environmental Research Park in Aiken and Barnwell Counties, South Carolina, USA. Established by the U.S. Department of Energy, the site is managed by the US Forest Service under agreement with the Department of Energy.

The experiment consists of 10 replicate landscapes (experimental blocks), each comprised of five open-habitat fragments created by clearing mature pine plantation forest and restoring fragments to native longleaf pine savanna. There is a strong contrast between the open fragments and the surrounding closed-canopy pine plantation matrix. Eight landscapes were created prior to the 2000 growing season (i.e., before April) and two additional landscapes were created prior to the 2007 growing season. Two of the original eight landscapes were discontinued following the 2007 growing season due to management constraints and one was destroyed by a wind event following the 2015 growing season. The remaining five landscapes initiated in 2000 and the two landscapes initiated in 2007 continue through the end of this study. When examining patterns over time, landscapes are evaluated based on the number of years since that landscape was created. All available replicate landscapes (blocks) are used for each time point in this study. This staggered initiation of replicate landscapes also provides a benefit by separating connectivity effects due to time since replicate initiation from annual effects attributable to specific years.

Each landscape contains a center fragment (100 × 100 m, 1 ha) surrounded by four peripheral fragments that are each 150 m from the center fragment (Fig. 1). The center fragment is connected to one peripheral fragment by a 150 × 25 m corridor and the other three peripheral fragments are isolated from the center fragment by dense, mature loblolly (*Pinus taeda*) or longleaf pine (*Pinus palustris*) plantation forest. Unconnected fragments are equal in area to the connected peripheral fragment plus its corridor (1.375 ha) and are either rectangular (100 × 137.5 m) or winged. Winged fragments have two 75 × 25 m projections, each with the dimensions of half of a corridor, extending from each side of a 100 × 100 m fragment (Fig. 1). The identity of peripheral fragments (connected, rectangle, winged) was randomly assigned within each landscape, with one duplicate winged or rectangle fragment in each landscape. This study design allows us to separate influences of corridors mediated through connectivity from those mediated through differences in edge-to-area ratio. Specifically, impacts of connectivity are assessed by comparing response variables in winged and connected fragments (comparable edge-to-area ratio, different connectivity). Impacts of edge-to-area ratio are assessed by comparing the same variables in winged and rectangle fragments (comparable connectivity, different edge-to-area ratio). Because analyses used in this study showed no differences among unconnected fragment types (Table S1), response variables were averaged for those fragment types. The center fragment is not included in analyses comparing fragment types, therefore comparisons are always made for fragments of equal area. This approach is directly comparable to an earlier analysis of species richness in these fragments (*27*).

Through periodic prescribed fire and removal of establishing hardwood trees, we have restored fragments to their historical ecosystem type: open-canopy longleaf pine savanna. We used standard management practices in this ecosystem (*34*) and applied them consistently across experimental treatments (i.e., we managed all fragment types in the same way). Prescribed fires

are implemented and controlled by our partners at the USDA Forest Service-Savannah River consistent with the historic fire regime and with fire management in longleaf pine savanna conservation today (*35*). Low-intensity surface fires are ignited every two to three years during the dormant season (November - April) and are allowed to burn across large burn areas that include all experimental fragments for a given experimental landscape (block). Longleaf pine savanna species are fire-adapted and many species readily re-sprout after fire. Thus, ecological communities in our experimental landscapes recover quickly following fire, yet fire results in both mortality of resident species and recruitment opportunities for new species (*36*). Consistent with restoration practices in this ecosystem (*34*), we have also reduced woody encroachment in our fragments by cutting hardwood tree species with brush saws every three-to-four years and applying targeted herbicide to cut stumps and/or the base of individual stems. These management practices allow the fragments to undergo succession toward mature longleaf pine savanna, characterized by low density overstory longleaf pine trees and an understory dominated by highly diverse perennial herbs and grasses (*36*), while maintaining the contrast between our experimental fragments and surrounding matrix over the duration of the study.

Data collection

To quantify plant species richness and rates of extinction and colonization within our fragments, we annually survey each fragment for all plant species occurrences. We conduct surveys between May 15 and July 15, when most species in our system are visually identifiable. Here, we include data from 2001 through 2018 (except 2004 when active management prevented sampling). The goal of each survey is to census all species in each fragment by systematically walking the area of each fragment in a set pattern around permanent 3m-tall poles placed in a 12.5m grid. This grid consists of 88 small (12.5 × 12.5 m) sampling units in each fragment. For each census, we record all species in the first sampling unit and then record only new species in subsequent sampling units. This method allows us to consistently cover the entire area of each fragment and compile a list of all vascular plant species observed in each fragment as well as the order in which they were detected across the 88 sampling units. Over the entire 18-year time series, we have kept the number of observers to a minimum – three (Damschen, Brudvig, and Burt). These observers standardize sampling effort and taxonomic identification rules prior to each annual survey. Resulting estimates of species richness for each fragment are from equal areas (1.375 ha). Taxonomy follows (*38*) and (*39*). In rare cases where identification is not possible at the species level (2% of taxa), we combine species to the genus level.

We assigned each plant species one of three primary dispersal modes: wind, animal, or gravity. We chose these modes because they capture distinctive classes of seed movement. We determined dispersal modes by first searching the Kew Garden Seed Information Database (*40*). If species were not in that database, we searched the primary literature with ISI Web of Science for papers that described dispersal for the species and/or genus. In some cases, we also searched reliable plant natural history websites to cross-reference obtained information. All designations were independently reviewed by two plant ecologists within our plant ecology research team (E. Damschen, L. Brudvig, M. Burt, C. Warneke, Q. Sorenson). Any conflicting or missing designations were discussed and decided by this entire team and decided on based on morphological and field observations (11% of species). Wind dispersal included both wind and tumbling dispersal mechanisms. Animal dispersal included endozoochory and epizoochory by birds and mammals and myrmecochory by ants. Gravity dispersal included ballistic dispersal mechanisms and species lacking apparent morphology to assist dispersal.

We also determined whether each species was associated with longleaf pine savannas (i.e., "longleaf pine species"). We were interested in assessing the responses of these species because they are of particular conservation and restoration concern and could respond more strongly to the contrasting habitat differences between the fragments and matrix in our experimental landscapes. We classified species as longleaf pine indicator species if they met one or both of the following criteria: 1) designation as longleaf pine upland species in published species lists for the Savannah River Site (*41, 42*), or 2) designation as "indicator species" in previous analyses of longleaf pine savanna plant communities at the Savannah River Site (*43*).

Because soil moisture is an important determinant of plant diversity in longleaf pine savannas (*44, 45*), we quantified soil water holding capacity. We used the same methods as Damschen et al. (*27*) by collecting 96-136, 10-cm deep × 2.5-cm diameter soil cores, evenly distributed across each fragment. We then determined soil water holding capacity as (wet mass - dry mass)/dry mass for each sample (*46*) and used the average of all samples from a fragment in our analyses.

All data are available from the Environmental Data Initiative and Data One (*33*).

Analyses

We modeled changes in plant communities using multi-species occupancy models and their extensions to capture both changes in species richness and colonization-extinction dynamics (*47, 48*). Occupancy modeling provides two major benefits. First, it can account for species-specific imperfect detection (observation errors). Second, it estimates species directly rather than modeling summary statistics of communities (e.g., species richness), such that species identity is honored and tracked in the modeling process. The latter benefit also allows for understanding how species-specific characteristics (e.g., dispersal mode) may impact communities while also providing a means to derive community-level parameters (e.g., species richness). This general approach uses a hierarchical framework. To ensure that results were robust to the modeling framework we used, we used a negative binomial regression to contrast results to those from modeling species richness without accounting for imperfect detection.

As part of our occupancy modeling, we estimated imperfect detection using detection histories for each species in each fragment for each year. We used spatial replicates based on the long-term sampling design to create those detection histories. For each fragment, we pooled 88 samples that covered the entire fragment into $J = 8$ replicates. This sampling strategy is best viewed as a 'removal' design (*49*), where once a species is detected, it is no longer tracked in fragment *i*. For example, a detection history for species *k* at fragment *i* in year *t* could be [0 0 0 0 1 NA NA NA], where NA refers to no data, given the 'removal' design. For most analyses, we focus on comparing communities in connected (corridor) versus unconnected (rectangular and winged) fragments and did not include the center fragment in modeling (but see below for interpreting if colonization of corridor fragments arose from center fragments).

We first modeled the entire plant community ($K = 309$ species) to estimate potential effects of corridors over time on species richness. To model species richness over time, we used an 'implicit dynamics' formulation of the multi-species occupancy model (*50*). In this context, we modeled the probability of occurrence ψ for species *k* in time *t* at fragment *i* as:

$$z_{k,i,t} \sim \text{Bernoulli}\left(\psi_{k,i,t}\right) \quad (1)$$

where *z* is the latent occupancy state (0,1). We modeled ψ as:

$$logit\left(\psi_{k,i,t}\right) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (2)$$

such that each species *k* had a different, treatment-specific intercept and slope over time (i.e., an interaction of treatment*species*time). Note that in this model, we initially considered site as a random effect to account for within-site repeated measures over time, which provided similar results. We removed this effect in the final model to simplify model structure given the large number of latent parameters (e.g,. species-specific effects).

Our observation model was described as:

$$y_{k,i,t,j} \sim \text{Bernoulli}\left(z_{k,i,t} p_k\right) \quad (3)$$

Where $y_{k,i,t,j}$ is the detection of species *k* in fragment *i* at year *t* for replicate observation *j* and p_k is the probability of detection of species *k*, conditional on presence. We allowed detection to vary by species.

This model formulation assumes a linear effect of time since corridor creation (on the logit scale) on species-specific occurrence; however, this effect can appear non-linear on the probability (and species richness) scale, as in logistic regression. We also considered two types of non-linear functions (considering the log of time or adding a quadratic term of time), neither of which were supported by the data based on the Deviance Information Criterion, DIC (lower values indicate better fit; linear time: 93634; log time: 93840; quadratic time: 94352). We also initially considered the potential effects of soil moisture in this model, but found no support for its effect based on DIC (soils ignored: 93634; soils included: 99562). Thus, we did not include soil moisture in final models. We contrasted these results to modeling raw species richness with non-linear effects over time using a negative binomial regression, finding similar support for a linear effect of time and qualitatively similar patterns of changes in species richness as found in the multi-species occupancy model (Figs. S4, S5).

For a subset of the community (i.e., those species with > 10 detections over time; $K = 239$ species of the possible 309 species), we explicitly modeled colonization-extinction dynamics. While the entire community could be modeled to interpret colonization-extinction dynamics, little information is available for rare species to interpret treatment effects and how they change over time. Thus, such an approach would make the implicit assumption that rare species, which contribute a comparatively small amount of data on extinction and colonization, respond similarly to treatments as more common species, such that rare species dynamics do not have a large impact on conclusions (*48*). Because of this effect, we use the 239 species subset of more common species to make conclusions on colonization-extinction dynamics. We note, however, that modeling colonization-extinction dynamics of all species showed similar patterns.

We followed methods of Dorazio et al. (*48*), who extended the multi-species occupancy framework for capturing colonization-extinction dynamics. The dynamics of species occurrence can be described and estimated with time-series data by assuming a first-order Markov process, where $z_{k,i}$ at time *t* is contingent on $z_{k,i}$ at time *t* - 1, as well as local colonization, γ, and local extinction, ε, processes. If we define $\phi = 1 - \varepsilon$, then:

$$z_{k,i,t} = \text{Bernoulli}\left(z_{k,i,t-1}\phi_{k,i,t-1} + \left(1 - z_{k,i,t-1}\right)\gamma_{k,i,t-1}\right). \quad (4)$$

This framework requires estimating occupancy at time 1, and then colonization-extinction dynamics in subsequent time steps. We also considered an alternative parameterization that accounts for potential rescue effects ("pseudo-rescue effects" sensu Hanski 1999) replacing $\phi_{k,i,t-1}$ in equation 4 as (*51*):

$$\phi^*_{k,i,t-1} = \left(1 - \left(1 - \phi_{k,i,t-1}\right)\right)\left(1 - \gamma_{k,i,t-1}\right). \quad (5)$$

To further interpret support of rescue effects, we contrasted similar models as described in equations 4-5 but fit to single species (i.e., 'dynamic occupancy models'; *52*). We also note that

rescue effects are also often interpreted as occurring when connectivity (e.g., corridors) decrease local extinction rates, although it can be unclear if such patterns are driven by rescue effect mechanisms (*53*).

We allowed for ψ to vary by species (we also initially considered that ψ could vary by treatment; however, there was no support for this added complexity so we do not consider it further, See Fig. S1). We also allowed for γ and ε to vary by treatment over time for each species as:

$$logit(\gamma_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (6)$$

$$logit(\phi_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (7)$$

From this model, we then summarized the average ε and γ across species and associated 95% credible intervals for each treatment over time based on the species-specific posterior distributions of model parameters. We averaged unconnected treatments (winged, rectangular) because the rates of change for these treatments were similar (Table S1).

To determine if the results are consistent for species of conservation and restoration concern and to determine whether movement ability of species influences our results, we also summarize colonization-extinction dynamics on two types of species traits: 1) longleaf indicator status; and 2) dispersal mode (see Data Collection for descriptions of these characteristics).

To better interpret if colonization was driven by corridors, we re-ran the colonization-extinction model (using equation 4) and included the center fragment (Fig. 1) into the model. Based on this model, we determined if connected fragments tended to be colonized sooner than unconnected fragments for species that occurred (i.e., $z_{k,i,t}$ =1) in center fragments prior to other fragments within each landscape.

We assumed vague priors for all parameters ($N \sim (0, 100)$), and used uniform hyperpriors for standard deviation parameters ($U \sim (0, 10)$). We ran all models in jags using the jagsUI package to call jags from R. We ran four chains for 37,500 Markov chain Monte Carlo (MCMC) iterations and thinned chains by 50 after a burn-in of 15000 and an adaptation phase of 15000, ultimately saving 3000 samples from the posteriors. We assessed model convergence using the Gelman-Rubin statistic R-hat, assuming that an R-hat > 1.05 indicated convergence problems (*50, 54*).

Supplementary Text

Supplementary Results

Plant species in may have arrived in fragments through three different pathways. First, seeds could have arrived in the area where we created our experimental fragments before our experiment was created and remained in the soil seed bank. In our study system, the soil seed bank is dominated by annual herbs and graminoids, a small subset of the total species in our study system, and whose composition did not differ by fragment type at the start of our study (*27*). Second, plants were present in the pine plantation understory before our experiment was created, and some regrew after forest harvest. Our assignment of treatments to fragments was randomized and we have previously confirmed that species richness and composition did not differ by fragment type at the start of our study (*27*) (Figure S1). Third, species may arrive from the regional species pool into one of the fragments within an experimental landscape. The increased colonization rates and decreased extinction rates in connected fragments suggests that

species are more likely to move to a connected fragment than unconnected fragments. Based on temporal changes in $z_{k,i,t}$ from the colonization-extinction model that include all five fragments in each experimental landscape, we found species that first arrived in the center fragment of an experimental landscape (block) were more likely to next colonize a connected fragment than an unconnected fragment (Fig. S8). Our analysis of the order of colonization events showed that connected fragments were colonized sooner than unconnected fragments in 60% of the species (out of 120 species for which this situation occurred), but the distribution was highly skewed (Fig. S8), providing evidence of corridors facilitating colonization of species from center fragments. This evidence is bolstered by studies of individual species' movement in our experiment that overwhelmingly show increased rates of movement between connected fragments when compared to unconnected fragments (*55*).

It is also possible that rescue effects – instances where immigration prevents extinction (*5*) – are responsible for the lower extinction rates in connected fragments. When we evaluated the potential for rescue effects for the entire community, the model parameterization that included rescue effects (Eq. 5) did not fit the data as well as when no rescue effects were assumed (based on DIC: assuming rescue effect, DIC = 194,151.7, assuming no rescue effect, DIC = 192,533.7). Thus, there was no strong support for rescue effects at the community level. When evaluating whether models that included rescue effects were important for individual species, there was support for rescue effects for 54% of the 239 species based on DIC (i.e., lower DIC for the rescue effects parameterization than assuming no rescue effects). This support did not explain variation in species responses to corridors (i.e., variation in DIC did not correlate with corridor effect sizes based on treatment parameters in Eq. 6-7; $r < |0.07|$). Thus, we focused on the non-rescue effect model parameterization above for all general results in the main text. However, it is important to note that while rescue effects do not generally explain the community-level patterns we report, they can and do occur for some species.

Finally, once species arrive within fragments, connectivity may alter species interactions in ways that minimize species extinctions or promote colonization. For example, we have documented higher pollination rates in connected than unconnected fragments (*56*, *57*), which may increase seed set and population size, thereby lowering the likelihood of extinction. Additionally, changes in seed predation caused by connectivity may create competition-free microsites that facilitate colonization (*58*). Corridors also increase the temperature at which prescribed fires burn, opening microsites for plant colonization and reducing dominance by woody species, which can increase persistence of subordinate herbs (*59*). Populations may also benefit from corridors by increasing gene flow and reducing impacts of inbreeding depression (*60*). Gene flow takes place through seed dispersal and pollination, both of which are facilitated by corridors in our study system (*56*, *57*, *61*).

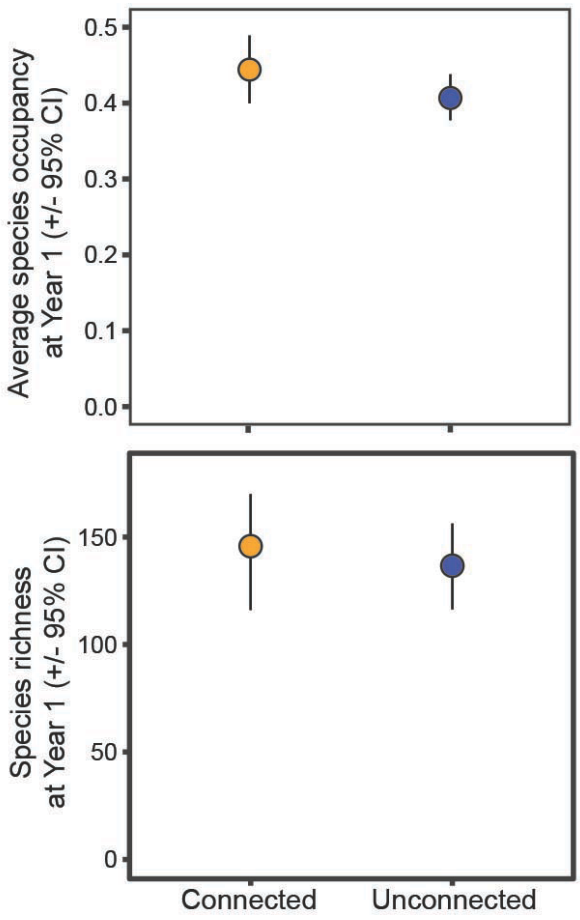

Fig. S1. Starting conditions did not vary by treatment. Initial probability of **(A)** species occurrence and **(B)** species richness did not differ by fragment type.

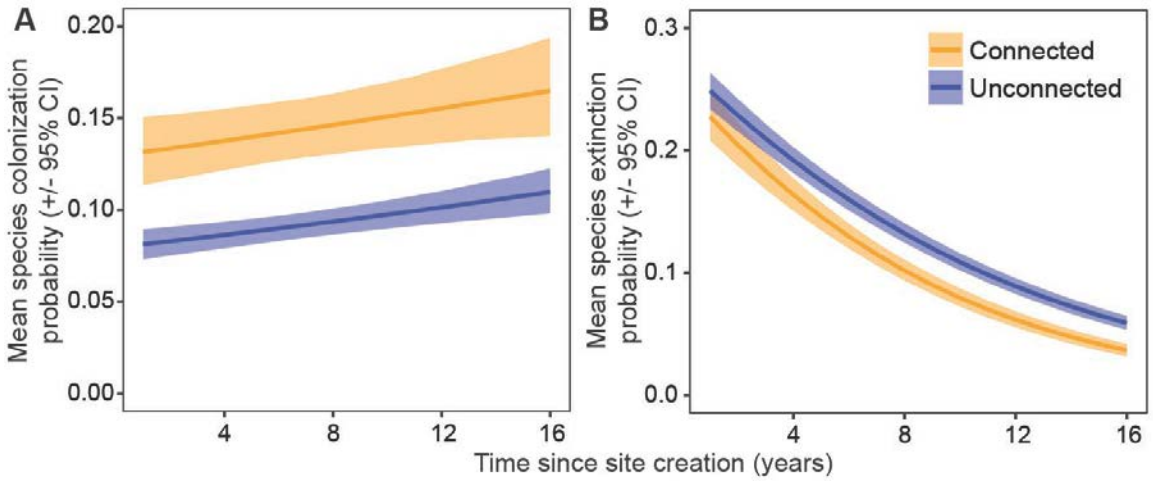

Fig. S2. (A) Colonization and (B) extinction rates over time for connected and unconnected fragments. The difference in these rates were used to produce Fig. 2A.

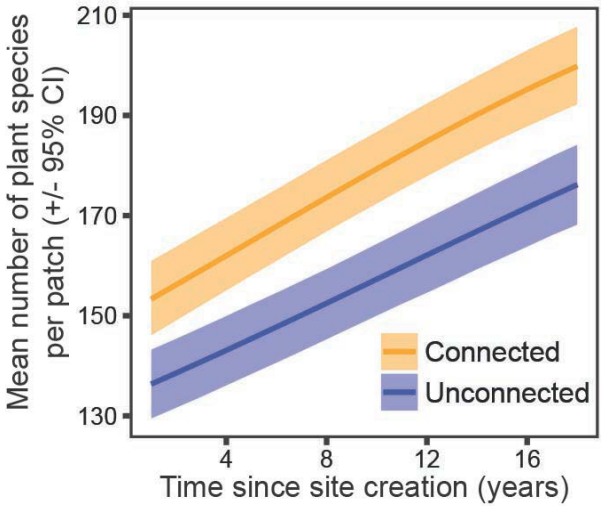

Fig. S3. Estimated species richness over time in connected and unconnected fragments. In the last time point (Year 18), on average there are 24 more species in connected than unconnected fragments (200 vs 176 species, respectively). The difference in these rates were used to produce Fig. 2B.

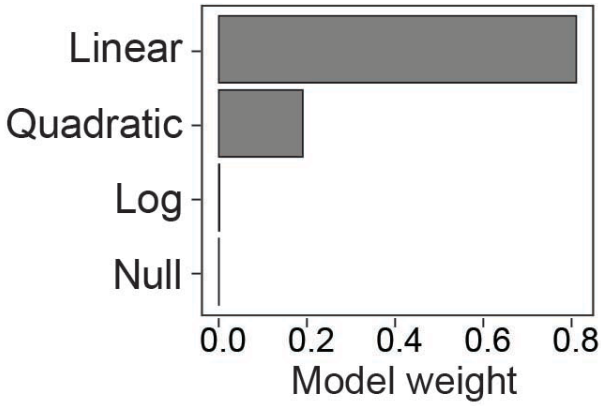

Fig. S4. A linear model is the best fit for the difference in species richness between connected and unconnected fragments over time. Model weights represent AIC model weights taken from negative binomial regressions that included the main and interactive effects of treatment and time since site creation (treated as either a linear, log-linear, or quadratic effect of time, in contrast to no effect of time represented as 'Null'. Higher model weight signifies greater support for a model relative to the other models considered, with a value of 1 indicating full support. Consequently, these weights suggest overwhelming support of a linear effect of treatments over time relative to potential non-linear (log time, quadratic time) effects of time.

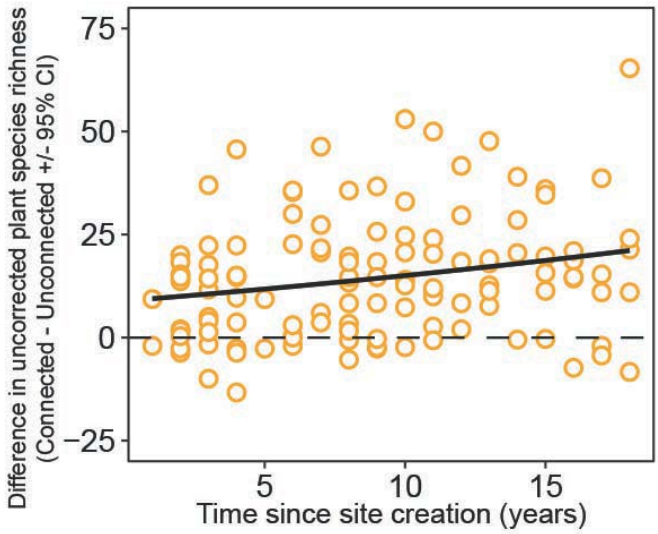

Fig. S5. The linear increase over time is evident in the difference in uncorrected, raw plant species richness over time between connected and unconnected fragments. Predicted line comes from the linear model (Fig. S4).

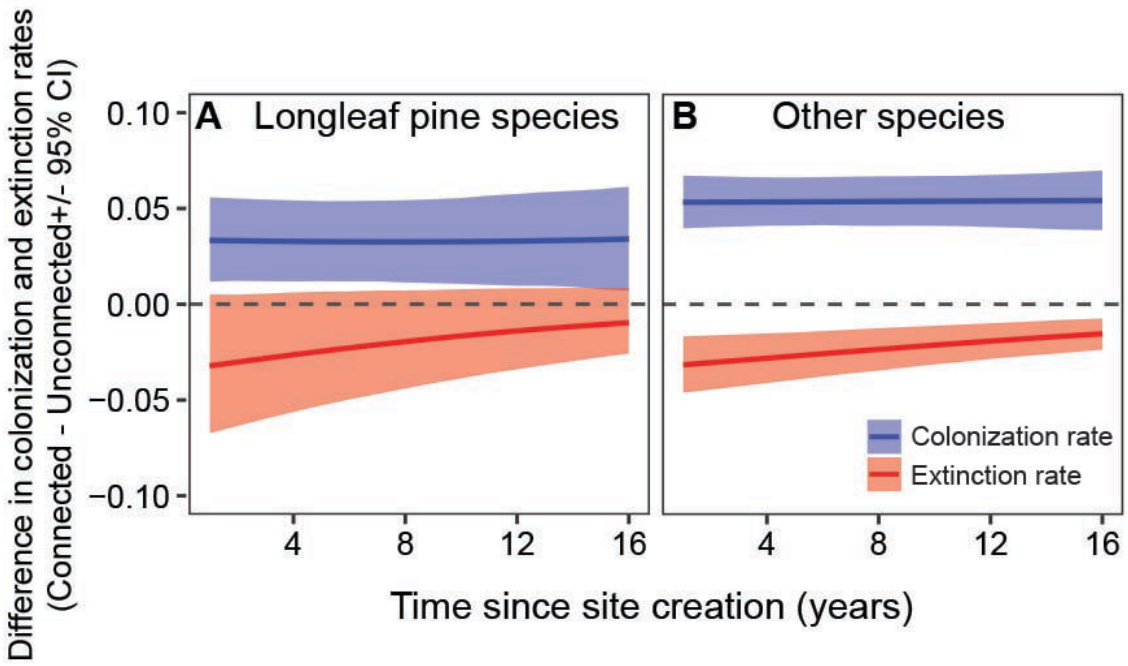

Fig. S6. Plant species (A) associated with longleaf pine habitat and (B) other species respond similarly to connectivity over time, although uncertainty is greater for species associated with longleaf pine habitat due to a smaller number of species**.** The difference between connected and unconnected fragments for colonization and extinction probabilities is shown for both groups.

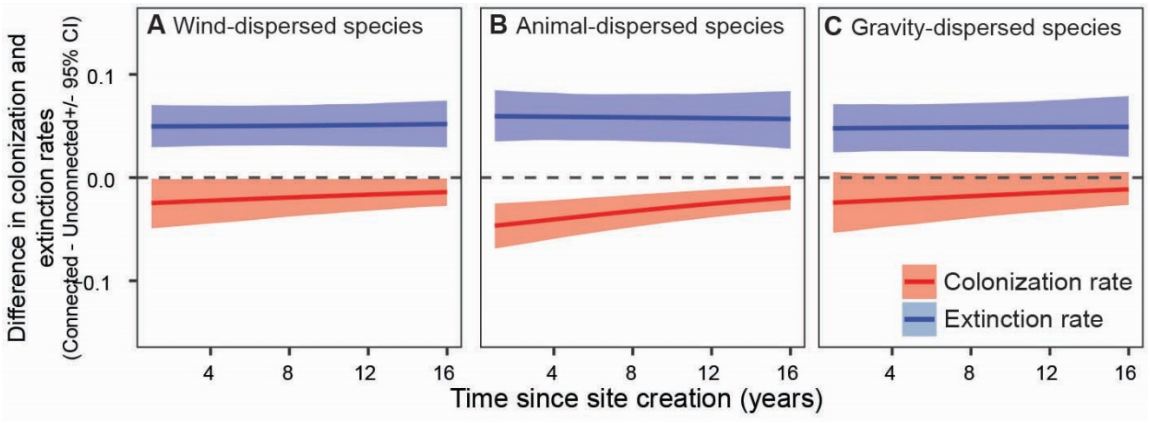

Fig. S7. Plant species respond similarly to connectivity over time across seed dispersal modes. The difference between connected and unconnected fragments for colonization and extinction probabilities of **(A)** wind-dispersed, **(B)** animal-dispersed, and **(C)** gravity-dispersed plant species over time.

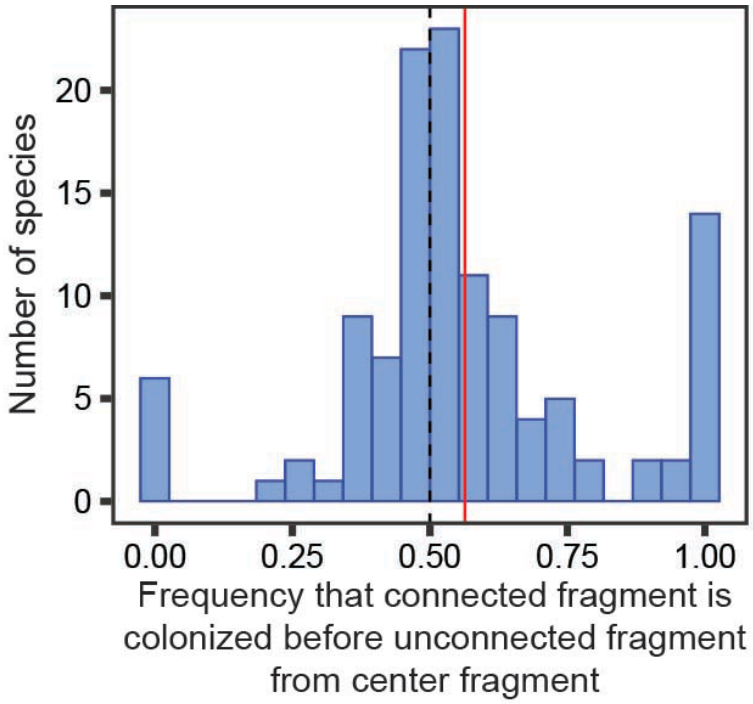

Fig. S8. Colonization events from the center fragment reach connected fragments sooner than unconnected fragments. When species arrived for the first time in an experimental block in the center fragment, connected fragments were colonized sooner than unconnected fragments for 60% of the species (out of 120 species for which this situation occurred; mean frequency = 0.56). The distribution was highly skewed providing some evidence of corridors facilitating colonization of species from center fragments.

Table S1. Summary of parameter estimates (on the logit scale) from multi-species occupancy model used to derive species richness over time. We show average estimates across species because this model estimates a parameter for each species (K = 309) regarding species detectability, treatment intercepts and rates of change over time. Estimates are provided for connected, unconnected rectangular, and unconnected winged fragments. LCL and UCL are lower and upper confidence limits, respectively.

Parameter	Estimate	95% LCL	95% UCL
Species mean detectability	-2.123	-2.466	-1.773
Species mean occupancy			
Connected intercept	0.447	0.294	0.607
Rectangular intercept	-0.220	-0.379	-0.065
Winged intercept	0.251	0.098	0.407
Connected time effect	0.672	0.574	0.768
Rectangular time effect	0.491	0.404	0.578
Winged time effect	0.553	0.467	0.672

Supplementary Code. The code used to estimate occupancy, species richness, and colonization-extinction dynamics over time is provided as a separate supplementary file.

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