PLANT ECOLOGY

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

Ellen I. Damschen[1]*, Lars A. Brudvig[2], Melissa A. Burt[3]†, Robert J. Fletcher Jr.[4], Nick M. Haddad[3], Douglas J. Levey[5], John L. Orrock[1], Julian Resasco[6], Joshua J. Tewksbury[7,8,9]

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).

[1]Department of Integrative Biology, University of Wisconsin–Madison, Madison, WI 53706, USA. [2]Department of Plant Biology and Program in Ecology, Evolutionary Biology, and Behavior, Michigan State University, East Lansing, MI 48824, USA. [3]Kellogg Biological Station and Department of Integrative Biology, Michigan State University, Hickory Corners, MI 49060, USA. [4]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA. [5]Division of Environmental Biology, National Science Foundation, Alexandria, VA 22314, USA. [6]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA. [7]Future Earth, Sustainability Innovation Lab at Colorado and Department of Environmental Studies, University of Colorado, Boulder, CO 80309, USA. [8]Future Earth, School of Global Environmental Sustainability, Colorado State University, Fort Collins, CO 80523, USA. [9]Department of Environmental Science and Policy, George Mason University, Fairfax, VA 22030, USA.
***Corresponding author. Email: damschen@wisc.edu**
†Present address: Department of Biological Sciences, Virginia Tech University, Blacksburg, VA 24061, USA.

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

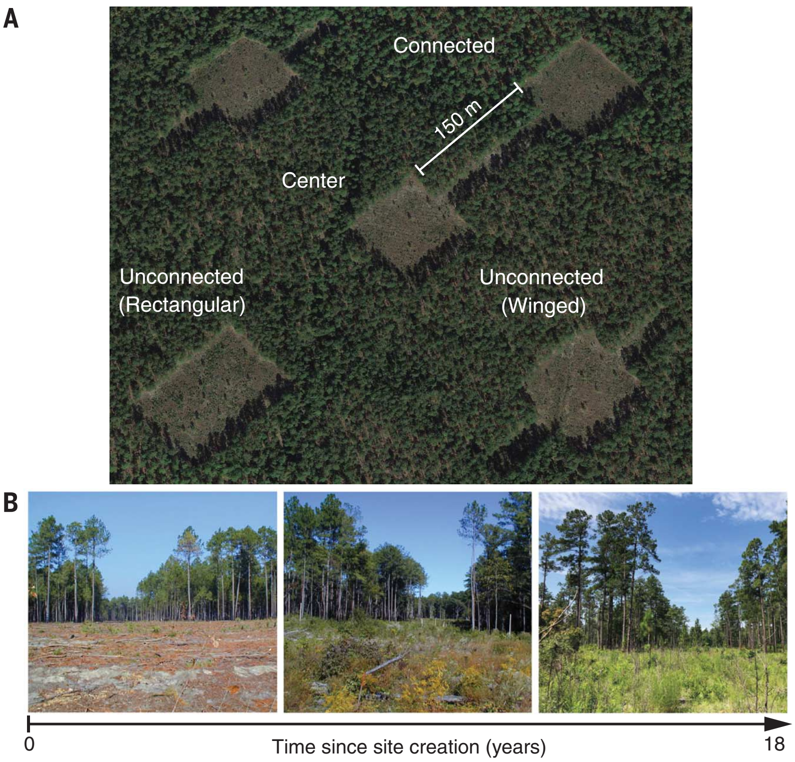

Fig. 1. A long-term habitat connectivity experiment. (**A**) One of 10 experimental landscapes (N = 10), each containing a center fragment that is connected or unconnected (winged and rectangular) to peripheral fragments of open longleaf pine savanna surrounded by dense pine plantations [additional details 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]

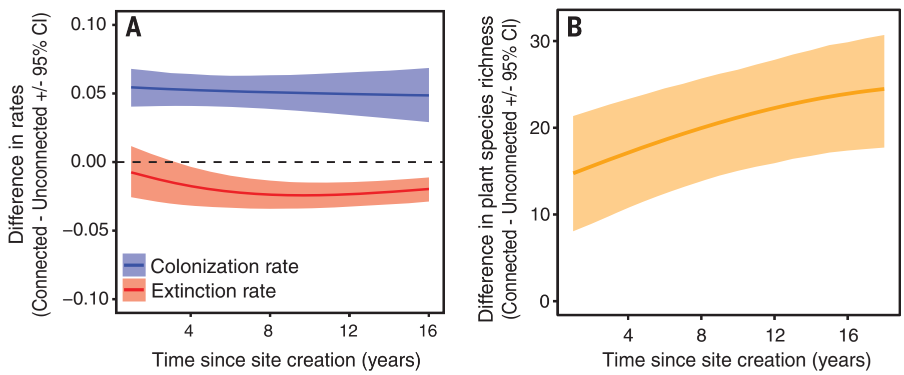

Fig. 2. Connectivity reduces extinction and increases colonization rates over two decades, resulting in accruals of species in connected fragments. (**A**) Average colonization rates are 5% greater and extinction rates are 2% lower for species in connected fragments than rates for those in unconnected 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 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.

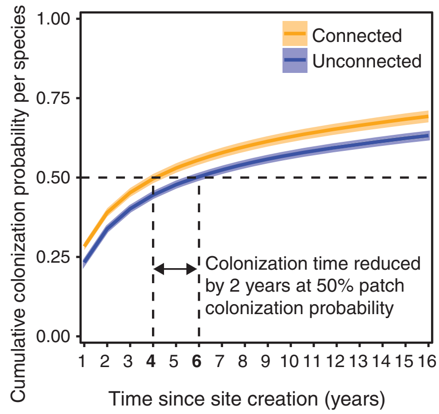

Fig. 3. Connectivity reduces colonization timing, resulting in colonization credits. The average cumulative probability of each individual species colonizing connected fragments is 1 to 6 years earlier than in unconnected fragments, resulting in reduced colonization lags and increased colonization credits. 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.

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*).

REFERENCES AND NOTES

1. N. M. Haddad *et al*., *Sci. Adv.* **1**, e1500052 (2015).
2. M. Pfeifer *et al*., *Nature* **551**, 187–191 (2017).
3. T. Newbold *et al*., *Nature* **520**, 45–50 (2015).
4. IPBES, "The IPBES assessment report on land degradation and restoration" [Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2018].
5. J. H. Brown, A. Kodric-Brown, *Ecology* **58**, 445–449 (1977).
6. R. Levins, *Bull. Entomol. Soc. Am.* **15**, 237–240 (1969).
7. I. Hanski, *Metapopulation Ecology* (Oxford Univ. Press, 1999).
8. M. Holyoak, M. A. Leibold, R. D. Holt, *Metacommunities: Spatial Dynamics and Ecological Communities* (Univ. of Chicago Press, 2005).
9. M. A. Leibold, J. M. Chase, *Metacommunity Ecology* (Princeton Univ. Press, 2018), vol. 59.
10. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, 1967).
11. D. J. Earn, S. A. Levin, P. Rohani, *Science* **290**, 1360–1364 (2000).
12. E. O. Wilson, E. O. Willis, in *Ecology and Evolution of Communities*, M. L. Cody, J. M. Diamond, Eds. (Belknap Press, 1975), vol. 522, pp. 522–534.
13. R. K. Didham, V. Kapos, R. M. Ewers, *Oikos* **121**, 161–170 (2012).
14. L. Fahrig, *Annu. Rev. Ecol. Evol. Syst.* **48**, 1–23 (2017).
15. J. Åström, T. Pärt, *Ecology* **94**, 72–82 (2013).
16. N. M. Haddad *et al*., *Ecography* **40**, 48–55 (2017).
17. M. L. Rosenzweig, *Science* **284**, 276–277 (1999).
18. D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, *Nature* **371**, 65–66 (1994).
19. M. Kuussaari *et al*., *Trends Ecol. Evol.* **24**, 564–571 (2009).
20. S. T. Jackson, D. F. Sax, *Trends Ecol. Evol.* **25**, 153–160 (2010).
21. T. Naaf, J. Kolk, *Biol. Conserv.* **182**, 155–163 (2015).
22. J. Kolk, T. Naaf, M. Wulf, *Biol. Conserv.* **26**, 735–755 (2017).
23. I. Hanski, *Ann. Zool. Fenn.* **37**, 271–280 (2000).
24. K. R. Crooks, M. Sanjayan, Eds., *Connectivity Conservation: Maintaining Connections for Nature* (Cambridge Univ. Press, 2006).
25. R. F. Noss *et al*., *Divers. Distrib.* **21**, 236–244 (2014).
26. See supplementary materials.
27. E. I. Damschen, N. M. Haddad, J. L. Orrock, J. J. Tewksbury, D. J. Levey, *Science* **313**, 1284–1286 (2006).
28. H. V. Cornell, S. P. Harrison, *Annu. Rev. Ecol. Evol. Syst.* **45**, 45–67 (2014).
29. A. J. Miller-Rushing *et al*., *Biol. Conserv.* **232**, 271–273 (2019).
30. N. M. Haddad, R. D. Holt, R. J. Fletcher Jr., M. Loreau, J. Clobert, *Ecography* **40**, 1–8 (2017).
31. T. Lenormand, *Trends Ecol. Evol.* **17**, 183–189 (2002).
32. R. J. Fletcher Jr. *et al*., *Biol. Conserv.* **226**, 9–15 (2018).
33. E. I. Damschen *et al*., SRS Corridor Experiment Annual Plant Occurrence Dataset, South Carolina, USA, 2000 - current, Environmental Data Initiative (2019); https://doi.org/10.6073/pasta/ea07f86ced76a28f8cb843f517959e0b.

ACKNOWLEDGMENTS

We thank J. Blake, A. Horcher, D. Clark, E. Olson, K. Wright, T. Thomas, C. Hobson, J. Segar, J. Brown, P. Varnedoe, and the USDA Forest Service–Savannah River for helping to create and maintain the experimental landscapes; Q. Sorenson, C. Warneke, S. Breland, and the Corridor Research Group for site maintenance, data management, and conversations about the ideas in this paper; and A. Gonzalez, S. Harrison, and B. Holt for comments on the manuscript. **Funding:** This work was supported by the National Science Foundation (DEB-1354085, DEB-1354101, DEB-1354218, DEB-1912729, and DEB-1913501). Support was provided by the Department of Energy–Savannah River Operations Office through the U.S. Forest Service–Savannah River under Interagency Agreement DE-EM0003622. The views expressed in this paper do not necessarily reflect those of the National Science Foundation or the United States government. **Author contributions:** Authorship was determined by the sequence-determines-credit approach, with all authors after the first two contributing equally and listed alphabetically. All authors contributed to idea generation. E.I.D., L.A.B., and M.A.B. collected the data. R.J.F. conducted analyses. D.J.L. and N.M.H. created and E.I.D., D.J.L., J.L.O., J.J.T., J.R., L.A.B., M.A.B., and N.M.H. maintained the experimental landscapes. E.I.D. led the manuscript writing, with contributions from all other authors. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** Data are available from the Environmental Data Initiative (*33*) and DataOne.

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

2 May 2019; accepted 4 September 2019
10.1126/science.aax8992

Science

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

Ellen I. Damschen, Lars A. Brudvig, Melissa A. Burt, Robert J. Fletcher Jr., Nick M. Haddad, Douglas J. Levey, John L. Orrock, Julian Resasco and Joshua J. Tewksbury

Science **365** (6460), 1478-1480.
DOI: 10.1126/science.aax8992

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.

Science, this issue p. 1478