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Wild, connected, and diverse: building a more resilient system of protected areas

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RH: Building a resilient system of reserves

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Abstract

Current systems of conservation reserves may be insufficient to sustain biodiversity in the face of climate change and habitat losses. Faced with these pressures, calls have been made to protect the Earth's remaining wildlands and complete the system of protected areas by establishing conservation reserves that (i) better represent ecosystems; (ii) increase connectivity to facilitate biota movement in response to stressors including climate change; and (iii) promote species persistence within intact landscapes. Using geospatial data, we conducted an assessment for expanding protected areas within the contiguous U.S. to include the least human-modified wildlands, establish a connected network, and better represent ecosystem diversity and hotspots of biodiversity. Our composite map highlights areas of high value to achieve goals in the western U.S., where existing protected areas and lands with high ecological integrity are concentrated. We identified important areas in the East rich in species and contain ecosystems that are poorly represented in the existing protected area system. Expanding protection to these priority areas is ultimately expected to create a more resilient system for protecting the nation's biological heritage. This expectation should be subject to rigorous testing prior to implementation, and regional monitoring will ensure areas and actions are adjusted over time.

Keywords: biodiversity, connectivity, conservation reserves, protected areas, wildlands

Introduction

For over 150 years, lands within the United States have been set aside as conservation reserves to protect scenic, geological, recreational, and ecological values. These lands form the foundation of our national protected area system and provide numerous benefits to nature and society (Naughton-Treves et al. 2005). Protected areas also serve as the cornerstones of global, national, and regional efforts to sustain biological diversity (Soulé and Terborgh 1999, Gaston et al. 2008). Historically, protected areas have been established in an *ad hoc* fashion (Pressey 1994) with little concern for representing the diversity of ecosystems (Aycrigg et al. 2013, Dietz et al. 2015) or species (Jenkins et al. 2015). Likewise, protected areas have not traditionally been intentionally connected (Belote et al. 2016), leaving many areas vulnerable to fragmentation by development (Radeloff et al. 2010, Hansen et al. 2014) and the ongoing impacts of human activities (Ordonez et al. 2014).

Many conservation scientists, therefore, recognize the need for additional protected areas that represent nature's diversity and are ecologically connected in a network, especially in the face of climate change (Secretariat of the Convention on Biological Diversity 2014). For instance, Aycrigg et al. (2016) recently called for "completing the system" of protected areas in the United States. Their recommendations include developing a national assessment of conservation priorities to identify important lands that fill gaps in the existing protected area system. At the same time, conservationists have documented the rapid decline in the Earth's remaining wildlands and have called for their protection (Martin et al. 2016, Watson et al. 2016).

Here, we build upon previous research and respond to these recent calls by conducting a spatial assessment of conservation values in the contiguous United States. We based our assessment on a number of widely accepted principles from conservation science that provide guidance on how to construct a system of protected areas to maintain biodiversity and ecological processes in the face of habitat fragmentation and climate change (Noss and Cooperrider 1994, Soulé and Terbough 1999, Mawdsley et al. 2009, Secretariat of the Convention on Biological Diversity 2014, Schmitz et al. 2015, Aycrigg et al. 2016). We refer to the capacity of a protected area system to sustain biodiversity and natural processes across a network, even as ecosystems change within individual protected areas, as "resilience" (*sensu* Anderson et al. 2012). While the term "resilience" may be defined various ways (Carpenter et al. 2001, Morecroft et al. 2012), the ability of populations and species to persist among a system of protected areas under changing environmental conditions likely requires that additional lands be protected. Lands that are relatively ecologically intact, connected to existing protected areas, and representative of ecosystem and species diversity may provide the greatest degree of adaptive capacity in the face of a global change (Dawson et al. 2011, Gillson et al. 2013, Schmitz et al. 2015, Martin and Watson 2016).

Methods

We used data on ecological integrity (Theobald 2013), connectivity (Belote et al. 2016), representation of ecosystems (Aycrigg et al. 2013), and a biodiversity priority index based on representation of range-limited species (Jenkins et al. 2015) to map wildland conservation values for a future protected area system in the contiguous United States. To identify intact areas of relatively high ecological integrity, we used Theobald's map of human modification (Theobald 2013). This is a composite map developed from spatial data representing land cover, human population density, roads, structures, and other stressors to ecosystems (Figure 1a). Lands that maintain a high degree of ecological integrity or low degree of human modification have been referred to as "wildlands" (Aplet 1999, Aplet et al. 2000), and protecting the remaining wildlands is considered by many to be among the highest of conservation priorities (Watson et al. 2009, 2016, Wuerthner et al. 2015, Martin et al. 2016).

To identify lands important for maintaining or establishing connections between protected areas, we used a mapped connectivity index from Belote et al. (2016) (Figure 1b). The index was developed to identify the least human-modified corridors between large existing protected areas, which were defined as all wilderness areas regardless of size and all other Gap Analysis Program (GAP) status 1 and 2 lands ≥ 4046.9 hectares (10,000 acres). GAP 1 and 2 areas are defined as lands for which laws, policies, or management plans mandate that biodiversity be a central conservation goal and that land conversion, commercial development, and resource extraction is prohibited or limited (USGS Gap Analysis Program 2016). Lands with a high connectivity index receive a higher wildland conservation value, as they may help to maintain ecological linkages between protected areas (Belote et al. 2016).

To identify ecosystems currently under-represented in the existing protected area system, we used an assessment of ecological representation in highly-protected lands (Figure 1c). Ecosystem representation has recently been calculated a number of ways, including based on the proportion of ecosystem area within different GAP status lands (Aycrigg et al. 2013), wilderness areas (Dietz et al. 2015), and roadless lands (Aycrigg et al. 2015). Our assessment of ecological representation is based on the proportion of an ecosystem's total area that occurs in lands identified in the Protected Areas Database (PAD) v 1.4 as GAP status 1 or 2 (U.S. Geological Survey Gap Analysis Program 2016). Ecosystem classifications are based on National Vegetation Classification System in GAP land cover data (USGS 2011). We recalculated analyses of Aycrigg et al. (2013) using the latest PAD to map the percentage of total area of each ecosystem occurring in GAP status 1 or 2 areas (i.e., $\frac{area\ of\ each\ ecosystem\ in\ GAP\ 1\ or\ 2\ units}{total\ area\ of\ each\ ecosystem} \times 100$). Lands composed of ecosystems that are less well-represented in protected areas are assigned a higher value than lands with ecosystems that are already highly protected.

To identify regions of under-represented species, we used a biodiversity priority index of Jenkins et al. (2015) (Figure 1d). This index was developed by overlaying maps of mammal, bird, reptile, amphibian, freshwater fish, and tree species distributions and weighting the rarity of species (calculated based on the size of each species' geographic distribution) and the proportion of its distribution that is protected based on International Union for Conservation of Nature (IUCN) categories I to VI (Jenkins et al. 2015). Lands classified in categories I to VI include similar land management goals to those of GAP 1 and 2 (http://gapanalysis.usgs.gov/blog/iucn-definitions) and most units with IUCN categories I-VI are also classified as GAP 1 or 2. Areas rich in endemic species with limited geographic distributions that are currently not well-represented in protected areas received a higher value in our index than areas with few such species.

To evaluate jointly all four conservation criteria, we normalized each mapped index using: $(x_i - x_{min})/(x_{max} - x_{min})$, where x_i is the value at each grid cell location, and x_{min} and x_{max} are the minimum and maximum values across the contiguous U.S. for each mapped criterion (Zuur et al. 2007; Appendix S1, Fig. S1). Developed lands, including urban, agricultural, or high-intensity land uses (e.g., mines) were assigned an ecosystem representation score of 0, so that they were not unintentionally prioritized for inclusion in a future protected area system even though they are not well represented in protected areas. Because of the highly right-skewed distribution of the Jenkins et al. (2015) biodiversity priority index, we log-transformed values before normalizing. The resulting distribution remained highly right-skewed, which was driven by a few species with very small geographic distributions. Because this index is ordinal, we chose to truncate the right tail of the distribution by collapsing outlying grid cells with very high values into one bin and re-normalized the index (Appendix S1, Fig. S2). Theobald's (2013) ecological integrity index was already scaled from 0 to 1 but represents a gradient of human modification where 1 is the most modified (the lowest ecological integrity). Therefore, we reversed the order so that the data ranged from 0 (lowest ecological integrity) to 1 (maximum integrity).

Following normalization, we summed the indices to produce a composite wildland conservation value map (Figure 2). Other mapping efforts overlaying multiple values have used different calculations, such as principal components scores (Dickson et al. 2014). We chose to use the simple method of summing the normalized indices (Sanderson et al. 2002, Leu et al. 2013), because it is easy to interpret the output (e.g., mapped grid values approaching 4 are locations where the highest values of each index overlap) and qualitatively similar to output from a principle components analysis (not shown). However, recognizing limitations to overlay summation (e.g., not adequately reflecting value conflicts or complementarity, Eastman et al. 1995, Brown et al. 2015), we also produced six bivariate maps to evaluate the four values in pairwise combinations (Figure 3). For bivariate maps, ecological integrity and ecosystem representation data were resampled from a 270-meter and 30-meter resolution, respectively, to a 1-km resolution using bilinear interpolation prior to producing bivariate maps. This step was necessary for aligning raster grids of all data. We then classified the continuous indices into four bins using Jenks' natural breaks algorithm to minimize variance within bins and maximize variance among bins (Jenks 1967). Four bins were used for bivariate maps to ensure the occurrence of all combinations of both values.

Results

Our composite map of wildland conservation value (Figure 2) reveals high-value areas concentrated throughout the western U.S., where lands tend to be less modified by humans and where large concentrations of protected areas exist. However, several high-value regions are also distributed throughout the eastern U.S., including the Southern Appalachian Mountains and Cumberland Plateau, the Allegheny Plateau of Pennsylvania, the Southeastern Coastal Plain (recently recognized as a global biodiversity hotspot, Noss et al. 2015), the

Sand Hills of Nebraska, the Ozark and Ouachita Mountains, east Texas and central Louisiana, Northern Minnesota and Wisconsin, and the Northern Appalachians of New England.

The bivariate maps (Figure 3) illustrate lands where component priorities align. Areas where high ecological integrity, connectivity, and under-represented ecosystems align are common and dominate the West (Figures 3a-c) but also occur in other areas throughout the country. Many lands located between protected areas in the West maintain a relatively high degree of ecological integrity, providing for high connectivity value (Figure 3a). Large regions of high integrity in the West are also composed of ecosystems not currently well-protected (Figure 3b). These areas (Figure 3c) may provide important opportunities for organisms to disperse as climate changes (McGuire et al. 2016). Many of these lands of the West are managed by the federal government (Appendix S1, Fig. S3) and provide opportunities for expanding protected areas through conservation designations (e.g., wilderness or national monuments) and agency management plans. Other ecosystems with limited levels of protection that are important for connectivity occur in the mid-Atlantic, southeastern, and northeastern states (Figure 3c). In these regions, most of the ecosystems have less than 5% of their distribution in protected areas. These areas may be relatively intact and important for maintaining a regional network of protected areas.

In contrast to the common co-occurrence of lands with high ecological integrity, connectivity, and ecosystem representation priorities, lands rich in range-limited species with a high degree of ecological integrity are infrequent and concentrated in California and Southwestern Oregon, as well as smaller patches located in the Southeastern U.S. (Figure 3d). These patterns suggest that hotspots of range-limited species tend to be more impacted by human development, a pattern observed globally (Venter et al. 2016). Areas rich in range-limited species occurring in under-represented ecosystems important for connectivity are also concentrated in California, Oregon, and the Southeast (Figure 3e-f). Appendix S1, Fig. S4 shows scatterplots between pairwise combinations of variables and describes a number of additional insights into relationships among the four metrics.

Discussion

Our assessment is designed to identify and map wildlands connecting existing protected areas that are composed of ecosystems and range-limited species not well protected in conservation reserves. Under our evaluation, these high-value areas are nationally significant and reveal several regional networks that hold promise in protecting relatively intact lands important for connectivity and representative of ecosystems and species. It is important to acknowledge, however, that our proposal be treated as an initial guide for where to focus conservation efforts given the data currently available. As such, prior to implementation any design should be subject to some form of initial evaluation and scrutiny to ensure that our guiding principals have empirical support. Critical to this initial evaluation is the determination of how robust any proposed conservation design is to data covering a broader set of taxa (e.g., invertebrates and herbaceous plants) and data on actual species occurrence (as opposed to the range maps used here). Even during implementation, monitoring and adaptive management will be required in the longer term to provide the evidence-based adjustments to the conservation strategies designed to maintain a resilient system of protected areas (Aycrigg et al. 2016). Regional conservation planning and monitoring coordination (e.g., through Landscape Conservation Cooperatives [Jacobson and Robertson 2012]) may be an important means to sustain these regional connected networks of protected areas.

Our work is not intended to prescribe specific actions necessary to protect individual high value lands. In practice, conservation is a complex process, involving many players using diverse tools. In some places, conservation may require the purchase of private property or easements. In other places, protection may involve the transfer of public land between agencies or the designation of a protective land class, such as wilderness. When decisions to allocate scarce resources are made by individual actors, information about costs, threats, marginal returns on investments, and other social factors are important for prioritizing conservation actions (Carwardine et al. 2008, Knight et al. 2011, Withey et al. 2012, Game et al. 2013), but determining such actions is not our intent here. Rather, we offer our assessment to guide where to take those actions, focusing on a subset of the landscape where safeguards should increase the diversity and representation of protected wildlands and facilitate movement among them.

Our analysis will serve as a resource for local conservation biologists and land managers in evaluating the national significance of local or regional lands. Of course, national gradients in values shown in Figure 2 may not reflect some locally important areas, and regional and local assessments should complement this national evaluation. For regional and local assessments, we recommend including data not available in a national assessment such as ours (e.g., priorities for protecting herbaceous plant species or habitat used by species of conservation concern). Indeed, even when values in our composite map are rescaled to a state-wide or regional level, local areas of high value emerge (Appendix S1, Fig. S5). Many conservation decisions take place at the local or regional scales, and our assessment can place the value of local lands into a national context.

We recognize that the history of conservation science suggests that we may never be able to "complete the system," even armed with the most comprehensive assessments. A protected area system may be built that samples all known ecosystem types and even all known species, but determining the area necessary to sustain those ecosystems and species has proven difficult. The largest national park in the contiguous United States is known to depend on the surrounding lands to maintain its components (Hansen et al. 2011), and sustaining its ecosystems into the future may require connecting "Yellowstone to Yukon" (Chester et al. 2012). Building a resilient protected area system of the future is likely to be a continuing project, growing and improving as we learn more about species, ecosystems, threats, and the nature of future change through coordinated monitoring programs. It is our hope that assessments such as we provide here can offer a "guiding star" for the construction of that future system.

In a provocative new book, eminent biologist Edward O. Wilson calls for half of the terrestrial surface of Earth to be protected to maintain biodiversity (Wilson 2016). Wilson and others' vision (Noss et al. 2012, Locke 2015) is aspirational. The U.S. has been setting aside lands as conservation reserves for over 150 years. As we look to the future it is imperative that we ask ourselves, what kind of system of protected areas should we pass down to future generations?

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References cited

Anderson, M. G., A. Barnett, M. Clark, C. Ferree, A. O. Sheldon, and J. Prince. 2012. Resilient Sites for Terrestrial Conservation in the Northeast and Mid-Atlantic Region.

The Nature Conservancy, Eastern Conservation Science.

Aplet, G. H. 1999. On the nature of wildness: exploring what wilderness really protects. Denver Law Review 76:347–367.

Aplet, G., J. Thomson, and M. Wilbert. 2000. Indicators of wildness: Using attributes of the land to assess the context of wilderness. Pages 89–98*in* S. F. McCool, D. N. Cole, W. T. Borrie, and J. O'Laughlin, editors.Proceedings: Wilderness science in a time of change.

Aycrigg, J. L., A. Davidson, L. K. Svancara, K. J. Gergely, A. McKerrow, and J. M. Scott. 2013. Representation of ecological systems within the protected areas network of the continental United States. PLoS ONE 8:e54689.

Aycrigg, J. L., C. Groves, J. A. Hilty, J. M. Scott, P. Beier, D. A. Boyce, D. Figg, H. Hamilton, G. Machlis, K. Muller, K. V. Rosenberg, R. M. Sauvajot, M. Shaffer, and R. Wentworth. 2016. Completing the system: opportunities and challenges for a national habitat conservation system. BioScience 66:774–784.

Aycrigg, J. L., J. Tricker, R. T. Belote, M. S. Dietz, L. Duarte, and G. H. Aplet. 2015. The next 50 years: opportunities for diversifying the ecological representation of the National Wilderness Preservation System within the contiguous United States. Journal of Forestry 114:1–9.

Belote, R. T., M. S. Dietz, B. H. McRae, D. M. Theobald, M. L. McClure, G. H. Irwin, P. S. McKinley, J. A. Gage, and G. H. Aplet. 2016. Identifying corridors among large protected areas in the United States. PLoS ONE 11:e0154223.

Brown, C. J., M. Bode, O. Venter, M. D. Barnesd, J. McGowanc, C. Runge, J. E. M. Watson, and H. P. Possingham. 2015. Effective conservation requires clear objectives and prioritising actions, not places or species. Proceedings of the National Academy of Sciences USA 112:4342.

Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From Metaphor to

Measurement: Resilience of What to What? Ecosystems 4:765–781.

Carwardine, J., K. A. Wilson, M. Watts, A. Etter, C. J. Klein, and H. P. Possingham. 2008. Avoiding costly conservation mistakes: The importance of defining actions and costs in spatial priority settings. PLoS ONE 3:e2586.

Chester, C. C., J. A. Hilty, and W. L. Francis. 2012. Yellowstone to Yukon, North America. Pages 240–252*in* J. A. Hilty, C. C. Chester, and M. S. Cross, editors.Climate and Conservation: Landscape and Seascape Science, Planning, and Action. Island Press, Washington, D.C.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science (New York, N.Y.) 332:53–8.

Dickson, B. G., L. J. Zachmann, and C. M. Albano. 2014. Systematic identification of potential conservation priority areas on roadless Bureau of Land Management lands in the western United States. Biological Conservation 178:117–127.

Dietz, M. S., R. T. Belote, G. H. Aplet, and J. L. Aycrigg. 2015. The world's largest wilderness protection network after 50 years: An assessment of ecological system representation in the U.S. National Wilderness Preservation System. Biological Conservation 184:431–438.

Eastman, R., W. Jin, P. A. K. Kyem, and J. Toledano. 1995. Raster procedures for multi-criteria/multi-objective decisions. Photogrammetric Engineering and Remote Sensing 61:539–547.

Game, E. T., P. Kareiva, and H. P. Possingham. 2013. Six common mistakes in conservation priority setting. Conservation Biology 27:480–485.

Gaston, K. J., S. F. Jackson, L. Cantú-Salazar, and G. Cruz-Piñón. 2008. The ecological performance of protected areas. Annual Review of Ecology, Evolution, and Systematics

39:93–113.

Gillson, L., T. P. Dawson, S. Jack, and M. A. McGeoch. 2013. Accommodating climate change contingencies in conservation strategy. Trends in Ecology and Evolution 28:135–142.

Hansen, A. J., C. R. Davis, N. Piekielek, J. Gross, D. M. Theobald, S. Goetz, F. Melton, and R. DeFries. 2011. Delineating the Ecosystems Containing Protected Areas for Monitoring and Management. BioScience 61:363–373.

Hansen, A. J., N. Piekielek, C. Davis, J. Haas, D. M. Theobald, J. E. Gross, W. B. Monahan, T. Olliff, and S. W. Running. 2014. Exposure of U. S. National Parks to land use and climate change 1900-2100. Ecological Applications 24:484–502.

Jacobson, C., and A. L. Robertson. 2012. Landscape Conservation Cooperatives: bridging entities to facilitate adaptive co-governance of social–ecological systems. Human Dimensions of Wildlife 17:333–343.

Jenkins, C. N., K. S. Van Houtan, S. L. Pimm, and J. O. Sexton. 2015. US protected lands mismatch biodiversity priorities. Proceedings of the National Academy of Sciences of the United States of America 112:5081–5086.

Jenks, G. F. 1967. The data model concept in statistical mapping. International Yearbook of Cartography 7:186–190.

Knight, A. T., S. Sarkar, R. J. Smith, N. Strange, and K. A. Wilson. 2011. Engage the hodgepodge: Management factors are essential when prioritizing areas for restoration and conservation action. Diversity and Distributions 17:1234–1238.

Leu, M., S. E. Hanser, S. T. Knick, S. E. Applications, and N. Jul. 2013. The Human Footprint in the West : A Large-Scale Analysis of Anthropogenic Impacts. Ecological Applications 18:1119–1139.

Locke, H. 2015. Nature needs (at least) half: a necessary new agenda for protected areas.

Pages 3–15Protecting the Wild: Parks and Wilderness, the Foundation for Conservation.

Martin, J.-L., V. Maris, and D. S. Simberloff. 2016. The need to respect nature and its limits challenges society and conservation science. Proceedings of the National Academy of Sciences 113:6105–6112.

Martin, T. G., and J. E. M. Watson. 2016. Intact ecosystems provide best defence against climate change. Nature Climate Change 6:122–124.

Mawdsley, J. R., R. O'Malley, and D. S. Ojima. 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conservation Biology 23:1080–1089.

McGuire, J. L., J. J. Lawler, B. H. McRae, T. Nuñez, and D. M. Theobald. 2016. Achieving climate connectivity in a fragmented landscape. Proceedings of the National Academy of Sciences of the United States of America 113:7195–7200.

Morecroft, M. D., H. Q. P. Crick, S. J. Duffield, and N. A. Macgregor. 2012. Resilience to climate change: Translating principles into practice. Journal of Applied Ecology 49:547–551.

Naughton-Treves, L., M. B. Holland, and K. Brandon. 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annual Review of Environment and Resources 30:219–252.

Noss, R. F., and A. Cooperrider. 1994. Saving Nature's Legacy: protecting and restoring biodiversity. Island Press, Washington, D.C.

Noss, R. F., A. P. Dobson, R. Baldwin, P. Beier, C. R. Davis, D. A. Dellasala, J. Francis, H. Locke, K. Nowak, R. Lopez, C. Reining, S. C. Trombulak, and G. Tabor. 2012. Bolder thinking for conservation. Conservation Biology 26:1–4.

Noss, R. F., W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, and R. K. Peet. 2015. How global biodiversity hotspots may go unrecognized: Lessons from the

North American Coastal Plain. Diversity and Distributions 21:236–244.

Ordonez, A., S. Martinuzzi, and V. C. Radelo. 2014. Combined speeds of climate and land-use change of the conterminous US until 2050. Nature Climate Change 4:1–6.

Pressey, R. L. 1994. Ad hoc reservations: forward or backward steps in developing representative reserve systems. Conservation Biology 8:662–668.

Radeloff, V. C., S. I. Stewart, T. J. Hawbaker, U. Gimmi, A. M. Pidgeon, C. H. Flather, R. B. Hammer, and D. P. Helmers. 2010. Housing growth in and near United States protected areas limits their conservation value. Proceedings of the National Academy of Sciences of the United States of America 107:940–945.

Sanderson, E. W., M. Jaiteh, M. a. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. BioScience 52:891–904.

Schmitz, O. J., J. J. Lawler, P. Beier, C. Groves, G. Knight, A. B. J. Douglas, J. Bullock, K. M. Johnston, M. L. Klein, K. Muller, D. J. Pierce, W. R. Singleton, J. R. Strittholt, D. M. Theobald, S. C. Trombulak, and A. Trainor. 2015. Conserving biodiversity: practical guidance about climate change adaptation approaches in support of land-use planning. Natural Areas Journal 35:190–203.

Secretariat of the Convention on Biological Diversity. 2014. Global biodiversity outlook 4.

Soulé, M. E., and J. Terbough. 1999. Conserving nature at regional and continental scales: a scientific program for North America. BioScience 49:809–817.

Theobald, D. M. 2013. A general model to quantify ecological integrity for landscape assessments and US application. Landscape Ecology 28:1859–1874.

U.S. Geological Survey Gap Analysis Program. 2016. Protected Areas Database of the United States (PAD-US), version 1.4.

US Geological Survey, G. A. P. (GAP). 2011. National Land Cover, Version 2.

Venter, O., E. W. Sanderson, A. Magrach, J. R. Allan, J. Beher, K. R. Jones, H. P.

Possingham, W. F. Laurance, P. Wood, B. M. Fekete, M. A. Levy, and J. E. M. Watson. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nature Communications 7:1–11.

Watson, J. E. M., R. A. Fuller, A. W. T. Watson, B. G. MacKey, K. A. Wilson, H. S. Grantham, M. Turner, C. J. Klein, J. Carwardine, L. N. Joseph, and H. P. Possingham. 2009. Wilderness and future conservation priorities in Australia. Diversity and Distributions 15:1028–1036.

Watson, J. E. M., D. F. Shanahan, M. Di Marco, E. W. Sanderson, and B. Mackey. 2016. Catastrophic declines in wilderness areas undermine global environment targets. Current Biology 26:1–6.

Wilson, E. O. 2016. Half Earth: Our Planet's Fight for Life. Liveright Publishing, New York.

Withey, J. C., J. J. Lawler, S. Polasky, A. J. Plantinga, E. J. Nelson, P. Kareiva, C. B. Wilsey, C. A. Schloss, T. M. Nogeire, A. Ruesch, J. Ramos, and W. Reid. 2012. Maximising return on conservation investment in the conterminous USA. Ecology Letters 15:1249–1256.

Wuerthner, G., E. Crist, and T. Butler. 2015. Protecting the wild. Island Press, Washington, D.C.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. Analysing Ecological Data. Springer, New York.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data associated with this paper have been deposited in Data Basin

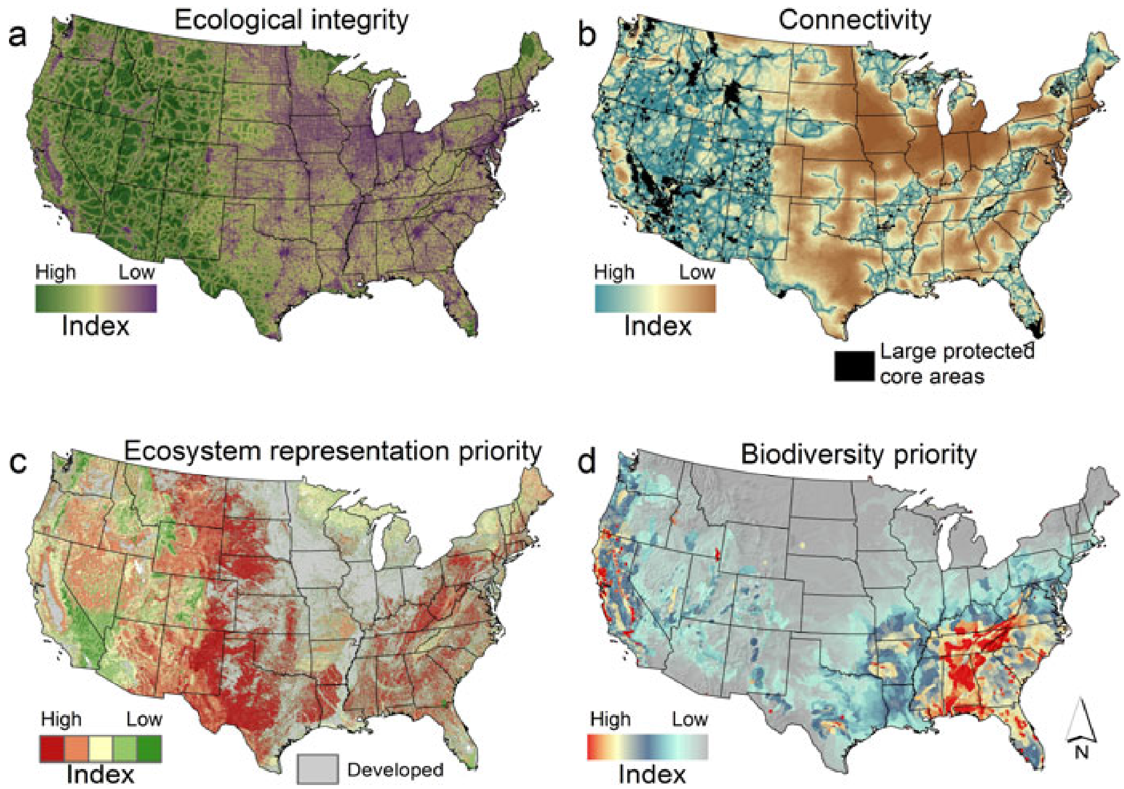
http://adaptwest.databasin.org/pages/wildland-conservation-value

Figure Legends

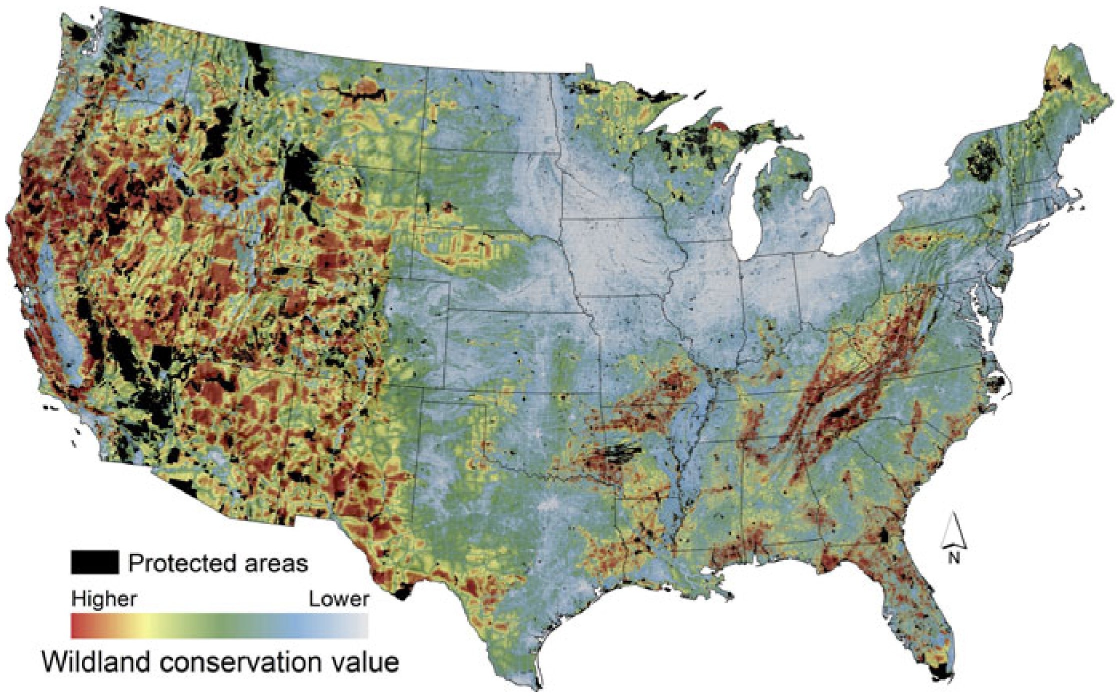
Figure 1. Indices of conservation values used to prioritize completing the system of protected areas: ecological integrity (a), connectivity (b), ecosystem representation priority (c), and biodiversity priority (d).

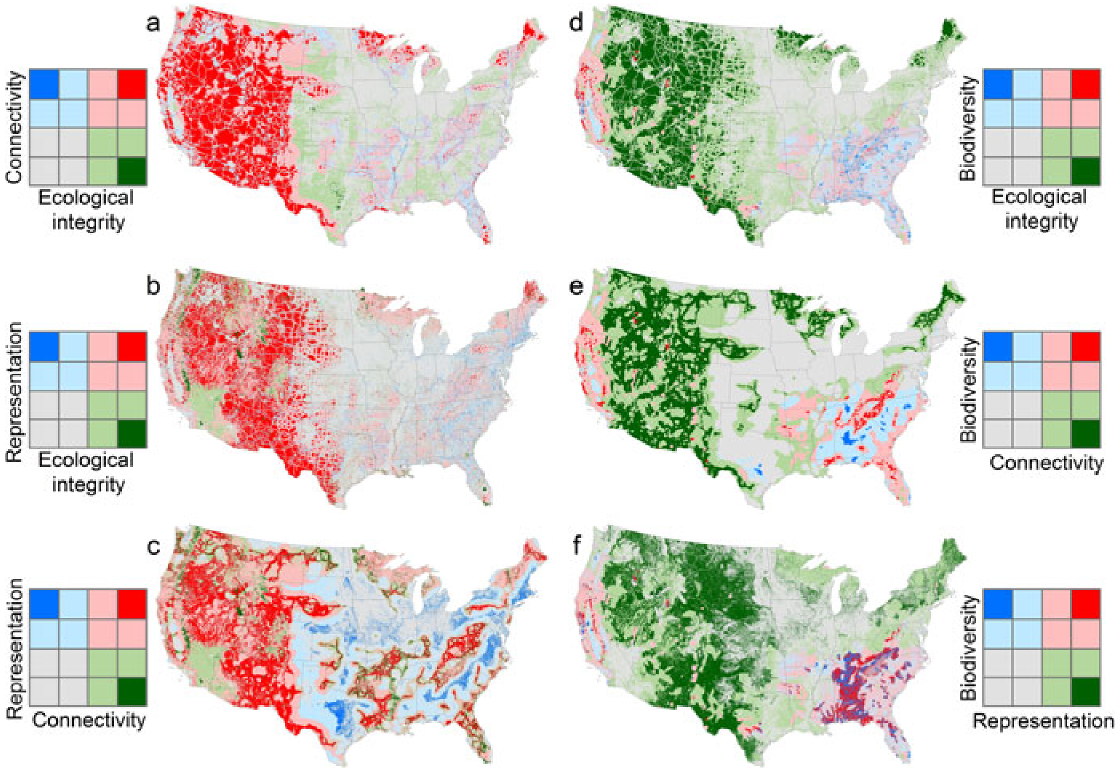
Figure 2. Composite map of wildland conservation value based on an overlay sum of qualities in Figure 1. Lands within existing protected areas (GAP status 1 and 2) are shown here as black (i.e., not a priority, because they are already highly protected).

Figure 3. Bivariate maps showing pairwise relationships between indices of (a) ecological integrity and connectivity; (b) ecological integrity and ecosystem representation priority; (c) connectivity and ecosystem representation priority; (d) ecological integrity and biodiversity priority; (e) connectivity and biodiversity; and (f) ecosystem representation priority and biodiversity. Values on each axis represent natural breaks in the index going from lower to higher from left to right along the x-axis and bottom to top on the y-axis. Therefore, in all six maps, red areas represent lands where both priorities align, blue and green areas where one priority is high and the other low.



a
Ecological integrity
High
Low
Index
b
Connectivity
High
Low
Index
Large protected
core areas
c
Ecosystem representation priority
High
Low
Index
Developed
d
Biodiversity priority
High
Low
Index
N


Protected areas
Higher
Lower
Wildland conservation value
N


a
b
c
d
e
f
Connectivity
Ecological integrity
Representation
Ecological integrity
Representation
Connectivity
Biodiversity
Ecological integrity
Biodiversity
Connectivity
Biodiversity
Representation