Received: 26 November 2019 | Revised: 5 February 2020 | Accepted: 21 February 2020
DOI: 10.1111/csp2.196

CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology
WILEY

Delineating greater ecosystems around protected areas to guide conservation

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Abstract

Protected areas represent a key strategy to conserve biodiversity. However, human land use and other impacts outside protected areas boundaries significantly influence species and ecosystems within protected areas. Therefore, identifying and delineating important lands surrounding protected areas may be critical to developing conservation strategies to sustain biodiversity. Here, we identify greater ecosystems of protected areas in the contiguous United States by delineating permeable wildlands located adjacent to protected area borders using the global human footprint map as the basis for estimating permeability. We evaluated how elevating the conservation status of greater ecosystems could help achieve aspirational targets for protecting additional terrestrial land area while better representing ecological diversity. We then assessed the feasibility of elevating conservation in greater ecosystems by quantifying the composition of land ownership and existing conservation status. Greater ecosystems of different protected areas often occur as large complexes that could be used to manage protected areas and monitor their status under regional conservation strategies. Elevating the conservation status of greater ecosystems could aid in achieving international targets while increasing the representation of vegetative types within conservation reserves. The most connected and permeable lands surrounding protected areas are dominated by public land (managed by the U.S. federal and state governments), though the amount of public land within greater ecosystems decreased with distance from protected areas. Public lands may provide opportunities to elevate the conservation status of greater ecosystems surrounding protected areas through policy and management changes. We focused on the contiguous United States, but our methods could be applied globally (which we demonstrate). To achieve bold international conservation goals, identifying the greater ecosystems

This paper is intended for conservation planners, NGOs, federal agencies, and other scientists interested in developing landscape conservation plans that include core protected areas and their surrounding lands.

around protected areas and developing conservation strategies of their landscape context will ultimately benefit species and ecosystems in protected areas.

KEYWORDS

connectivity, half-earth, national parks, permeability, protected area, protected area centered ecosystems, wilderness

1 | INTRODUCTION

Protected areas form the foundation of international strategies to conserve biodiversity (Gaston, Jackson, Cantú-Salazar, & Cruz-Piñón, 2008). However, conservation scientists increasingly recognize that isolated protected areas unconnected to a network may be limited in their ability to maintain biodiversity and ecological functions, especially under mounting pressures of land use and climate change (Belote et al., 2017; McGuire, Lawler, McRae, Nuñez, & Theobald, 2016; Ordonez, Martinuzzi, & Radelo, 2014). Protected areas have typically not been strategically connected (Saura, Bastin, Battistella, Mandrici, & Dubois, 2017), nor have they been located in areas that fully represent ecological diversity (Aycrigg et al., 2013). Acknowledging these limitations, international goals of conservation include protecting additional lands in "ecologically representative and well-connected systems of protected areas" (Convention on Biological Diversity, 2014) while expanding the amount of land protected to as much as 50% of the terrestrial land area (i.e., "Half-Earth" of Wilson, 2016, Dinerstein et al., 2019).

Maintaining species and ecological processes within protected areas require that their landscape context be considered in management and monitoring plans (DeFries, Hansen, Turner, Reid, & Liu, 2007; Hansen & DeFries, 2007). Yellowstone National Park, for example, is considered the core of the Greater Yellowstone Ecosystem (GYE) that includes lands adjacent to the park boundary (Noss, Carroll, Vance-borland, Wuerthner, & Vance-borland, 2002). Efforts to conserve the greater ecosystem of Yellowstone have been under way for over three decades (Clark, Amato, Whittermore, & Harvey, 1991). Acknowledging the value of the greater ecosystem concept, Hansen et al. (2011) proposed a framework and analysis to identify "protected area centered ecosystems" for guiding such management and monitoring strategies of protected areas and their surrounding lands. They used hydrological connectivity as determined through watersheds, home ranges of select species, and species area calculations to create ecologically based buffers around national parks. These buffers form the basis of delineating their proposed protected area centered ecosystems. Here, we build on their framework and developed a method to identify lands relatively ecologically connected to protected areas.

Identifying lands that are ecologically connected to protected areas may be a critical step in sustaining biodiversity and ecological processes (Hansen & DeFries, 2007). Efforts to monitor and manage Yellowstone National Park has benefited from considerations of the greater ecosystem concept. Assessing threats within and adjacent to Yellowstone National Park has allowed for recovery plans of species of conservation concern, evaluate threats emerging outside of park boundaries, and develop monitoring programs assessing ecological vital signs at ecologically meaningful spatial scales. Other parks and protected areas may benefit from identification of their respective greater ecosystems.

Such greater ecosystems may represent conservation priorities in service of maintaining biodiversity within existing protected areas. Elevating the level of conservation designations of lands surrounding core protected areas may also help achieve targets for protecting lands at various proposed levels from 17% (CBD, 2014), 30% (Dinerstein et al., 2019) to 50% (Dinerstein et al., 2017). However, the extent to which a focus on greater ecosystems directly adjacent to protected areas would meet ecosystem representation conservation goals is unknown.

We propose an approach to identify greater ecosystems of protected areas based on the permeability of lands adjacent to protected area boundaries. This approach, which we call the greater ecosystem model (GEM), allows us to delineate the least human modified landscapes (i.e., most wild) within which protected areas are embedded. We use estimates of landscape permeability (the opposite of resistance) to evaluate how conserving these greater ecosystems could achieve national targets of protecting land and better represent ecological diversity. We consider permeability as the ability for terrestrial ecological processes, including animal movement, seed dispersal, disturbance processes, and ecological flows to proceed unencumbered by human development. Finally, we assess feasibility of better conserving these greater ecosystems based on the current ownership and management status of lands. Federal and state lands could provide more feasible opportunities for enacting policies that conserve the greater ecosystems of protected areas.

2 | METHODS

2.1 | Selecting protected areas

To select core protected areas for our analysis, we used the Gap Analysis Program's (GAP) Protected Areas Database supplemented with data on wilderness areas from the University of Montana's Wilderness Institute. We selected protected areas similar to those outlined in Belote et al. (2016). Specifically, we included all wilderness areas irrespective of size, because these lands are consistently managed via the U.S. federal Wilderness Act and provide a high degree of protection from commercial development of natural resources and other potential threats to ecosystems. We also included all national parks intended to protect natural lands (i.e., we did not consider historical or battlefield parks), as well as national monuments, wildlife refuges, and highly protected state parks classified under GAP Status 1 or 2 over 202 km^2 (50,000 acres). We chose these units to reflect a relatively consistent degree of strict conservation protection and size of protected areas. Our final pool of protected areas consisted of 1,629 units.

2.2 | Modeling permeability via cost-weighted distance

To delineate greater ecosystems, we first assessed permeability away from the edge of all protected areas using the 2009 human footprint map of Venter et al. (2016). The human footprint represents a composite map of roads, land use, human population density, and other features representing impacts of humans on ecosystems. Maps of human modification and the human footprint have been used as inputs to connectivity modeling, assuming that higher human impacts are associated with greater mortality risk of moving organisms, behavioral avoidance, or more disrupted ecological flows (Belote et al., 2016; Dickson et al., 2016; Theobald, Reed, Fields, & Soulé, 2012). The human footprint has also been associated with altered movements of mammals around the globe (Tucker et al., 2018).

We assume that higher human footprint is associated with more resistant and less permeable lands. However, the shape of the relationship between the human footprint and permeability is less clear and may depend on individual species' sensitivity to human presence and development (Keeley, Beier, & Gagnon, 2016; Zeller, McGarigal, & Whiteley, 2012). We assumed that the relationship between gradients in the human footprint and permeability could take many forms, but we chose to model three alternatives (Figure 1). Borrowing transformation functions from Keeley et al. (2016), we created three different permeability layers based on the three alternative ways the human footprint could influence permeability. Specifically, we modeled permeability as the function $-(100 - 99 \times ((1 - exp[-c \times Human\ footprint])/(1 - exp[-c])))$ where we varied c to be either 1, 16, or −16 (Figure 1). These alternatives represent different ways in which terrestrial ecological processes and animal movement could respond to gradients in the human footprint. For instance, permeability where $c = 1$ represents situations or animals that respond relatively linearly to gradients in the human footprint. Models where $c = 16$ represent species or processes that are relatively unaffected by increasing human footprint up to a threshold where small changes in relatively developed lands would result in large influences on permeability (e.g., individual movement). The model where $c = -16$ is the opposite situation where species or processes are highly sensitive to small amounts of human footprint in relatively undeveloped lands and permeability is disrupted across most of the gradient of the human footprint. We calculated the least accumulated cost-distance away from protected areas with the COST DISTANCE tool in ArcMap 10.6 (ESRI ArcGIS®, Redlands, CA) using each of the three permeability layers (i.e., three levels of *c*) as an estimate of resistance. We focused our attention on identifying greater ecosystems of the contiguous United States, but we calculated cost distance using the footprint into Canada and Mexico.

This approach essentially measures the accumulated cost-weighted distance away from the edge of protected areas, and is the first step in identifying least cost corridors between core areas (Belote et al., 2016). However, in our model we did not attempt to identify the least cost corridor between protected areas, but rather measure the relative permeability (i.e., the opposite of cost-weighted distance) of lands surrounding—and connected to—each protected area. This method is similar to those outlined in Compton, McGarigal, Cushman, and Gamble (2007) and used in Cushman and Landguth (2012), but these efforts use known dispersal distances and probabilities in their models of connected core areas or populations. Our method is a simplified version of this approach and assumes that connectivity away from protected areas depends on distance and permeability (modeled as a function of the human footprint).

After mapping cost-weighted distance away from protected areas using the three alternative permeability models (Figure 1), we created a composite map by normalizing values from each output so that they scaled from 0 to 1 and summed the normalized values. We binned the composite layer into 5% quantiles to evaluate the permeable lands connected to protected areas in

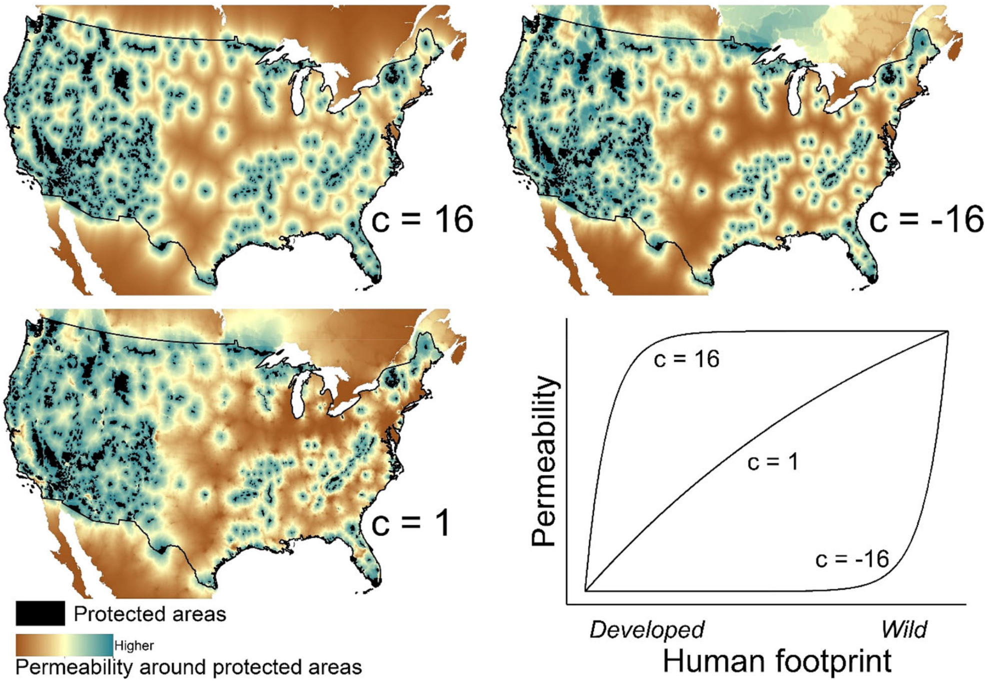

FIGURE 1 Permeability of ecological processes or animal movement likely varies along gradients of the human footprint, but the form of this relationship may depend on species or context. We used three alternative forms of relationships between the human footprint and landscape permeability by varying *c* in Permeability = −(100 − 99 × ((1 − exp(−*c* × Human footprint))/(1 × exp(−*c*)))) following a modified approach of Keeley et al. (2016). Each map shows the permeability away from protected area boundaries (color gradients are relative to values within each map)

concentric increments. The top 30 percentiles (5, 10, 15, 20, 25, 30%) of permeable lands around each protected area were mapped. Each bin was used to delineate greater ecosystems at varying levels of permeability and connectedness to protected areas. We refer to these as greater ecosystem bins.

2.3 | Assessing total size, ecological representation, and ownership

Using the 5% greater ecosystem bins from the composite map, we assessed the total area (as a proportion of the contiguous United States), degree of ecosystem representation within existing protected areas, and the ownership and management status across greater ecosystem bins. Specifically, we calculated the area of land in protected areas, as well as the total land area within the 5% greater ecosystem bins to evaluate how protecting greater ecosystems might sum to meet benchmarks of conserving land from various targets (e.g., 17, 30, or 50%; Dinerstein et al., 2017, 2019).

We also asked how the representation of ecosystems might be improved if lands within the greater ecosystem bins were conserved. We started with assessing the percent of area that each macrogroup (National Vegetation Classification level 5) from the GAP land cover data was represented in protected areas, and then assessed potential changes for each macrogroup if lands within the greater ecosystem bins were added to the national system of protected areas. Our work could include finer taxonomic resolutions from the NVC system, but we focus on macrogroups as a balance between minimizing the number of different ecological groups to consider ($N = 52$ different macrogroups after removing agricultural and developed groups) while still assessing distinct vegetation types below more broad classification levels.

The feasibility of achieving bold conservation targets such as protecting 30 or 50% of land area is likely influenced by existing ownership and the management status of lands within these greater ecosystems. Therefore, we used the PAD-US to assess the composition of lands within each 5% greater ecosystem bin. We assessed whether lands within greater ecosystems surrounding protected areas were federal, state, or other and which GAP Status those lands were assigned. GAP Status is a classification of the conservation protection where GAP Status 1 and 2 are lands where biodiversity protection is mandated, land cover conversion is prevented, and commercial activities like mining and logging are limited. GAP Status 3 lands are managed to protected biodiversity and limit land cover conversion, but allow commercial

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extractive activities. GAP Status 4 lands are managed by federal agencies, but typically have unknown conservation mandates and policies. GAP Status 3 lands are largely dominated by lands managed by federal agencies (e.g., the U.S. Forest Service or Bureau of Land Management) but without formal protection (e.g., wilderness designation). We assume that federal and state land (publicly-managed lands) and lands with a higher GAP Status would provide greater feasibility and opportunities for elevating the level of conservation protection of lands within delineated greater ecosystem bins. In some cases, greater ecosystems that are not part of our pool of protected areas include lands already protected (i.e., classified as GAP Status 1 or 2), but these protected units may not share a boundary or otherwise meet the criteria for inclusion in our pool of protected areas.

3 | RESULTS

Our selected 1,629 protected areas made up 367,172 km^2 or 4.2% of the contiguous United States. Geographic patterns of relative permeability from protected areas varied by the function we used to estimate permeability based on the human footprint. When permeability varied little across the majority of the human footprint gradient ($c = 16$) cost distance was more similar to simple Euclidean distances away from protected area boundaries. Alternatively, when the human footprint varied semi-linearly ($c = 1$) as a function whereby large increases in resistance only occurred at the highest degrees of human footprint, permeability tended to be more driven by patterns in the human footprint (Figure 1).

From the composite map used to delineate greater ecosystems (Figure 2), we found that the most permeable connected 5% of lands combined with the protected areas to cover 667,873 km^2 or 12.7% of the contiguous United States. Increasing the area to the top 10% of greater ecosystem bins covered 1.57 million km^2 or 20.2% of the contiguous United States. The top 30% of greater ecosystem bins covered 3.69 million km^2 or 47.6% of the contiguous United States (Figure 2).

On average 15.8% (ranging from 0 to 81.2%) of the geographic distribution of each macrogroup vegetation class was represented in existing protected areas. If these macrogroups were protected in conservation lands within the top 5, 10, and 15% greater ecosystem bins, average representation would increase to 30.4% (ranging from 0 to 93.6% among different land cover macrogroups), 41.3% (ranging from 0 to 96.2%), and 49.8% (ranging from 0 to 96.6%), respectively (Figure 3). The number of macrogroups represented in protected areas at the 17% level would increase from 12 to 38 if the top 15% greater ecosystem bins were fully protected. The number of macrogroups represented at the 30% level would increase

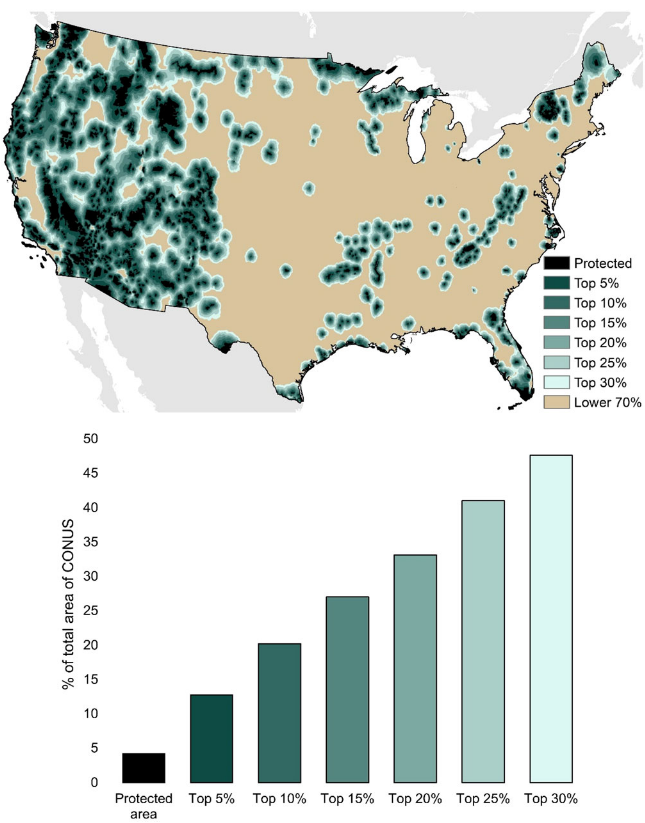

FIGURE 2 Greater ecosystems based on bins of permeability away from protected areas (top) and the total area (shown as a proportion of the contiguous United States) represented by protected areas and across greater ecosystem bins (bottom)

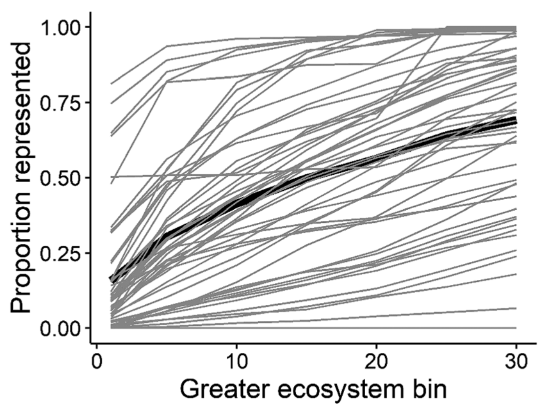

FIGURE 3 The representation of 52 different macrogroup vegetation types within protected areas (starting values at 1 along the *x*-axis) and increasing in 5% bins of greater ecosystems. As the total area increases with increasing greater ecosystem bins, the representation of macrogroup vegetation types increases. Each grey line represents a different macrogroup vegetation type, and the bold black line is the average among all types

TABLE 1 Percent area managed by federal, state, or other entities summarized by the Gap Analysis Program status for permeable lands surrounding protected areas in the contiguous United States

		Greater ecosystem bin					
Owner	**GAP status**	**Top 5%**	**Top 10%**	**Top 15%**	**Top 20%**	**Top 25%**	**Top 30%**
Federal	1 or 2	15.47	6.10	4.03	3.39	2.56	1.41
	3	43.04	34.21	27.60	23.92	19.38	14.76
	4	3.24	2.86	2.52	1.98	1.40	1.27
State	1 or 2	1.26	0.62	0.51	0.54	0.57	0.45
	3	3.48	3.73	3.82	4.08	3.77	3.70
	4	1.39	2.45	2.22	2.00	1.43	0.81
Other	1 or 2	1.08	0.83	0.59	0.70	0.86	0.63
	3	0.23	0.43	0.35	0.31	0.27	0.24
	4	30.81	48.78	58.36	63.08	69.77	76.74

Notes: Each bin of permeable lands represents a concentric level of cost distance away from the edge of protected areas. For instance, the top 5% bin represents the most permeable lands adjacent to protected areas and represents a modest delineation of greater ecosystems centered on protected core areas. This analysis represents the opportunity for protect greater ecosystems based on existing ownership and degrees of conservation protection.

from 10 to 33, and macrogroups represented at 50% level would increase from 5 to 17 (Figure 3).

Ownership of greater ecosystems varied across greater ecosystem bins (Table 1). In general opportunities for elevating the levels of protection of land declined with increasing greater ecosystem bins away from protected areas. For example, the most connected land to protected areas (top 5% bin) was composed of 67.9% federal or state lands, but the proportion of federal or state lands declined with increasing cost-distance away from protected areas (Table 1). The relative amount of land within GAP Status 3 also declined with increasing greater ecosystem bins away from protected areas (65.6% of land in GAP Status 3 in the most connected bin to 21.2% in the furthest bin we evaluated).

4 | DISCUSSION

Land use and climate change continue to impact ecosystems in and surrounding protected areas (Hansen et al., 2014; Martinuzzi et al., 2015). Therefore, sustaining biodiversity and ecological processes within existing protected areas will require careful consideration of the lands surrounding protected areas. Our approach allowed us to map the most permeable lands connected to protected areas, which we consider a means of identifying greater ecosystems with protected areas at their core ("protected area centered ecosystems" of Hansen et al., 2011). Our assessment is similar to that of Hansen et al. (2011), but with an explicit assessment on terrestrial connectivity of surrounding lands to protected areas. These greater ecosystems may represent future conservation priorities to both secure the biodiversity within protected areas, expand conservation lands to meet international targets, and better represent ecosystems in conservation reserves.

The concept of greater ecosystems originated when Greater Yellowstone was identified as a means of protecting the isolated grizzly bear (*Ursus arctos* L.) populations located in and around Yellowstone National Park (Glick & Clark, 1998). Since then, the concept has evolved as a means of conserving large-scale ecological processes and seasonal animal migrations. Interestingly, our approach to identifying greater ecosystems around protected areas matches closely the current boundary of the Greater Yellowstone Ecosystem adopted and used by the Greater Yellowstone Coordinating Committee (GYCC, Figure 4). The GYCC brings together multiple federal agencies and partners to develop conservation strategies to maintain species and ecosystems within Yellowstone National Park. Other similar efforts exist around Glacier National Park and the Bob Marshall Wilderness (e.g., Prato & Fagre, 2007), Grand Canyon and the Colorado Plateau (e.g., Van Riper, Wakeling, & Sisk, 2010), and the Great Smoky Mountains National Parks and surrounding lands (Peine, 1999). Our approach could be used as a starting point for identifying greater ecosystems surrounding other protected areas.

The greater ecosystems we identified could be used to initiate greater ecosystem coordinating committees centered around core protected areas. For instance, our approach to delineating greater ecosystems can serve as a monitoring tool for a variety of factors outside protected areas such as land use changes (Martinuzzi et al., 2015), barriers to animal migration (e.g., Seidler, Long, Berger, Bergen, & Beckmann, 2015), the introduction of exotic

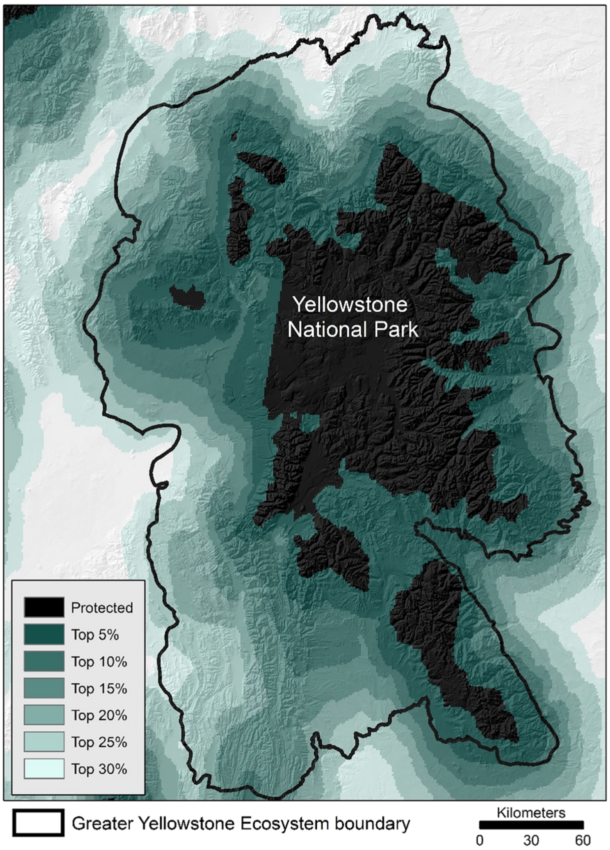

FIGURE 4 The Greater Yellowstone Ecosystem boundary as used by the Greater Yellowstone Coordinating Committee (black outline) compared to our greater ecosystem bins (shown as shades of green) based on permeability of lands surrounding protected areas

species, and other human impacts that could ultimately influence species and processes within protected areas (Hansen et al., 2014). Increased monitoring of greater ecosystems of protected areas will aid in identifying and quantifying the drivers of biodiversity losses within protected areas and mitigating these impacts (Hansen & DeFries, 2007; Hansen & Phillips, 2018).

Focusing conservation on lands surrounding existing protected areas could also serve as priorities for expanding protection of land to meet international and aspirational benchmarks for conserving terrestrial land (Dinerstein et al., 2019). We evaluated this possibility by calculating the percent of the contiguous United States in protected areas and in the permeable lands connected to protected areas as a series of greater ecosystem bins. Protecting greater ecosystem bins could achieve international targets of protecting 17% by 2020, 30% by 2030, or eventually half of terrestrial land under half-earth goals. In addition, elevating the conservation status of lands within the most connected greater ecosystem bins would increase the number of macrogroup vegetation types represented at the 17, 30, and 50% levels. For instance, the number of macrogroup vegetation types represented at the 17% level would more than triple and those represented at the 30 and 50% representation would double if the most connect greater ecosystem bin (i.e., top 5 percentile bin) were protected. Greater ecosystems, therefore, provide opportunities for representing total land area in a highly protected status while also increasing the level that specific macrogroup vegetation types are represented in protected areas. Focusing conservation efforts on these greater ecosystems could thus help achieve global conservation targets (Convention on Biological Diversity, 2014).

Of course, expanding protected areas to meet these aspirational targets depends on opportunities for elevating the conservation protections of lands within the greater ecosystems. The opportunity of elevating the degree of conservation of lands decreases with distance away from protected areas, based on the relative amount of public land. However, the greater ecosystems with the highest connectedness to protected areas tended to be dominated by public lands (state and federal lands). In fact, over 1 million km^2 of the top 10% of greater ecosystem bins are public. Adding these lands to better conserve biodiversity within existing protected areas could more than double the land area that is protected. Management plans, congressional legislation, or executive orders could elevate the degree of protection on the federal lands located in greater ecosystems. However, other land uses conflicting with biodiversity conservation exist and may continue within greater ecosystems around protected areas (DeFries et al., 2007; Martinuzzi et al., 2015). Our intent was not to assess these conflicts and describe policy recommendations associated with tradeoffs between conserving ecosystems and developing resources. Our proposed method for delineating greater ecosystems could be used as a means for defining buffers around protected areas where more detailed assessment of such tradeoffs will be needed. Coordinating committees made up of stakeholders and land management agencies charged with developing policy recommendations may benefit from such an objective means of defining greater ecosystems around existing protected areas (Hansen et al., 2011). We note that our approach could be added to the portfolio of approaches proposed by Hansen et al. (2011) for identifying protected area centered ecosystems.

Our approach focuses on connectivity of protected areas to their surrounding lands. We did not intentionally seek to identify corridors or linkages between protected areas (sensu Belote et al., 2016). However, our approach identified large regional complexes of protected areas that share greater ecosystem boundaries. In the western United States, the distance between protected areas and the low degree of human footprint results in large regions where protected areas share greater ecosystems. In the eastern United States, we identified a number of clusters of protected areas that were connected in this way: the upper Midwest, the Ozarks, Southern Appalachians, and Florida host opportunities for conserving regional complexes of relatively connected protected areas. Co-operative management and monitoring among agencies responsible for stewardship of the ecosystems in and around protected areas is needed (Baldwin et al., 2018), and delineation of greater ecosystems connected to protected areas may help develop regions to prioritize such efforts. The large connected complexes of protected areas could form the core of landscapes where co-operative management and monitoring would be focused.

One benefit of our approach is that it is based on a global dataset representing the human footprint's influence on landscape permeability. Therefore, national or global maps such as the one we produced could be easily replicated for any country or region. In fact, to demonstrate this, we produced a global map of greater ecosystems around protected areas based on the World Protected Areas Database IUCN categories Ia, Ib, and II using a linearly-scaled permeability layer calculated from the human footprint (Figure 5). Large areas with limited human footprint and connected to protected areas were clearly identified, as were regions where regional networks of protected areas emerge. The total area protected and within greater ecosystems shown here represents over 42% of total land area of the globe, near the bold targets of Half Earth (Noss et al., 2012; Wilson, 2016). Our intent with this global analysis is only meant as a demonstration of how our approach can be conducted across the globe. We conducted this global analysis on a desktop computer with using over 200,000 protected area polygons with the 1-km human footprint resolution. Future global analyses could refine the pool of protected areas based on specific objectives and use alternative forms of permeability as a function of the human footprint.

The ways in which the gradients in the human footprint creates barriers to movement of species or ecological process is likely context dependent. Different species likely respond in different ways to patterns and intensity of the human footprint. By quantifying cost-distance using three alternative functions, we acknowledge this variability. Future work could focus on understanding how different species or processes are influenced by the intensity of human footprint. As human infrastructure and land use intensifies, a better understanding of species ability to move through landscapes with varying degrees of the human footprint will be critical for allowing species to track changes in climate (Lawler, Ruesch, Olden, & McRae, 2013). Other datasets not available globally could be used to estimate permeability of lands surrounding protected areas. For instance, data on fences or features not mapped in the global human footprint may influence animal movement and could be incorporated where available. In addition, other methods for assessing connectivity away from protected areas (e.g., omnidirectional methods in Circuitscape; McRae et al., 2016) could be used as an alternative means for delineating greater ecosystems.

While we investigated an approach for delineating greater ecosystems and assess their potential to contribute to conservation goals, we point out greater ecosystems identified here may fail to represent the important areas for protecting biodiversity (Belote et al., 2017; Jenkins, Van Houtan, Pimm, & Sexton, 2015; Pimm, Jenkins, & Li, 2018). Protected areas have not typically been located strategically to fully represent ecosystem or

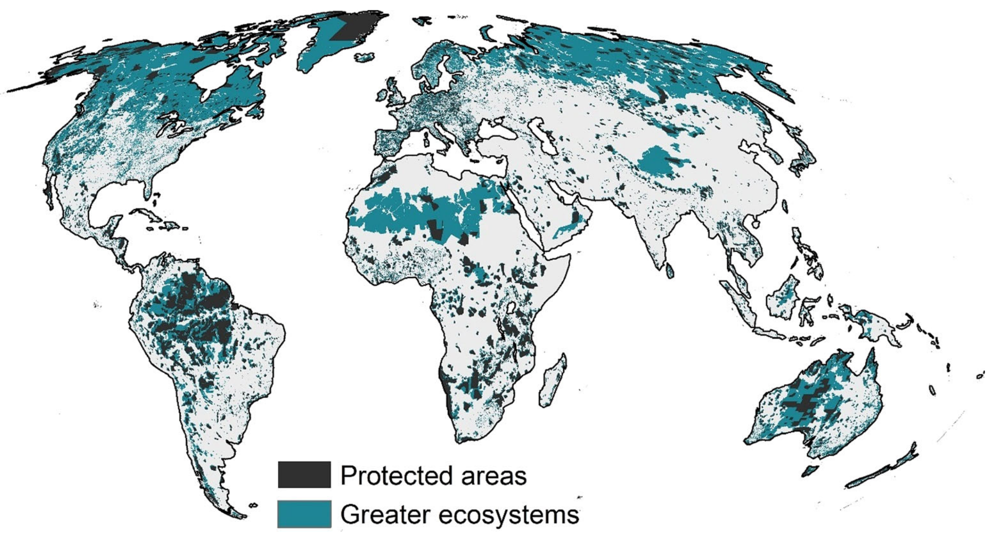

FIGURE 5 To demonstrate the generalizability of our approach, we used the World Database on Protected Areas to identify greater ecosystems around all protected areas classified as IUCN categories Ia, Ib, and II. Greater ecosystems in the top 10% of most permeable lands adjacent to protected areas are shown based on methods outlined in the text

species diversity (Scott et al., 2001). While we show that focusing conservation on greater ecosystems around protected areas may provide opportunities for increasing the ecosystem types represented in conservation reserves, other lands away from existing protected areas may be higher priorities for expanding conservation efforts to better protect all species and habitats. In fact, our global map of greater ecosystems has limited overlap with biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). About a quarter (24.7%) of global hotspots of biodiversity were considered greater ecosystems based on our global analysis. Our intent was to identify greater ecosystems around protected areas based on terrestrial connectivity of surrounding lands. These areas could be useful to guide investments in future conservation efforts focused on large landscapes or regions, but we acknowledge that areas outside these greater ecosystems also represent national or international conservation priorities based on the locations of range-limited and poorly protected species (Jenkins et al., 2015; Pimm et al., 2018). Future analyses should investigate how to protect wild lands connected to existing protected areas while also expanding conservation reserves to better represent national or global biodiversity (sensu Pimm et al., 2018).

5 | CONCLUSIONS

Protected areas may fail to sustain biodiversity without considerations for the greater ecosystems within which they are embedded. We provide a relatively simple method for identifying greater ecosystems around protected areas based on the permeability of lands adjacent to their boundaries. By identifying the relatively permeable lands surrounding protected areas, regional conservation efforts may better coordinate plans to reduce threats around protected areas, while also explicitly delineating lands for expanding monitoring efforts (Hansen et al., 2011). We show that these greater ecosystems could also be priorities for expanding conservation to meet international and bold aspirational targets for protecting additional lands and better represent vegetation types in protected areas.

ACKNOWLEDGMENTS

We thank Mark Leighton and Andy Hansen for discussions and inspiration to pursue these questions. Thanks to Oscar Venter for making the human footprint data publicly available.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

R.T.B. and M.B.W. conceived of the project, conducted analyses, and wrote the paper.

ETHICAL STATEMENT

No ethics approval was required for this research.

DATA AVAILABILITY STATEMENT

Greater ecosystem bin data are available on DataBasin at: https://databasin.org/datasets/0561b6f3b8be4fb484caf3b74b89518c.

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How to cite this article: Belote RT, Wilson MB. Delineating greater ecosystems around protected areas to guide conservation. *Conservation Science and Practice*. 2020;e196. https://doi.org/10.1111/csp2.196