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Quantifying the contribution of conservation easements to large-landscape conservation

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ABSTRACT

Private lands are critical for conservation of ecosystem diversity and sustaining large-scale ecological processes. Increasingly, conservation easements (CE) are used as a tool to protect private land from future development; yet, few studies have examined whether contemporary patterns of CE effectively contribute to landscape-scale biodiversity and ecosystem conservation goals. We analyzed the distribution of 1223 CE established between 1970 and 2016 in the High Divide, a region dominated by public lands and of national conservation importance in the Rocky Mountains of the United States, with respect to ecosystem representation and landscape connectivity, two common large-scale conservation goals. We found that CE were frequently located closer to water and to other land protected for biodiversity (e.g., GAP 1 and 2 status) than were private lands more generally. CE provided increased representation within the protected areas network for 10% of the ecosystems within the region, particularly for mesic and riparian areas. Despite the addition of CE to the protected areas network, we found insufficient representation for 43 out of 87 ecosystems (< 5% representation on land managed for biodiversity). Protection of priority ecosystems varied across CE and illustrated potential mismatches between regional and national scale conservation goals. Furthermore, while public lands contributed the most toward conserving important areas for connectivity, CE protected potential landscape connectivity only slightly more effectively than randomly allocated areas. CE provide important complements to public lands in terms of ecosystem diversity and landscape connectivity. However, conservation planners and land managers could increase conservation benefits from CE by prioritizing under-represented ecosystems and more explicitly targeting lands to maintain landscape permeability.

1. Introduction

Protected areas, including public lands and reserves, are crucial for persistence of species and ecosystems threatened by land-use change and habitat loss (Butchart et al., 2015; Woodley et al., 2012). In the United States, growth of the public land system has stagnated (USGS-GAP, 2016) and the current pattern of public lands and reserves does not provide sufficient ecosystem representation or protections for numerous species (Groves et al., 2000; Jenkins et al., 2015; Joppa and Pfaff, 2009; Rodrigues et al., 2004; Scott et al., 2001; Watson et al., 2014). Moreover, the current pattern of public lands and reserves may not be adequate to maintain the dynamic, multi-scale ecological patterns and processes (e.g., disturbance regimes, organism movement) needed to sustain biodiversity (Aycrigg et al., 2016; Belote et al., 2017; DeFries et al., 2007; Poiani et al., 2000; Schloss et al., 2011; Theobald et al., 2016).

Private land conservation provides a critical tool for biodiversity conservation (Drescher and Brenner, 2018; Heller and Zavaleta, 2009; Morrisette, 2001). Half of federally listed species rely on private lands for at least 80% of their habitat (Groves et al., 2000; Turner et al., 2006) and private lands interspersed between larger public lands are critical for species movement (Shafer, 2015). If conservation strategies relied only on public land, many biodiversity conservation goals including the 2020 targets established by the Convention on Biological Diversity (CBD) would not be achievable (Woodley et al., 2012). Private land conservation includes many different methods such as incentives for enrollment in short-term management agreements, land protection through fee simple acquisition, or protection by conservation easements (Kamal et al., 2015).

Conservation easements are voluntary conveyances of non-possessory property rights and, in contrast to public lands, their establishment has increased exponentially since the 1970s (Merenlender et al., 2004; Stolton et al., 2014). Most conservation easements are held by local and state land trusts, though government agencies are also commonly holders of easements (Fishburn et al., 2009). In the United States, the amount of land held in conservation easements has increased to 7 million hectares in 2015 (LTA, 2015) and studies suggest that CE have significantly limited habitat loss in some regions (Braza, 2017; Rissman and Merenlender, 2008). Recent analyses of conservation easements have focused on, among other things, landowners' motivations

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for conveying easements (Brenner et al., 2013; Farmer et al., 2011, 2015; Vizek and Nielsen-Pincus, 2017), easement policy and legal permanence (Gerber and Rissman, 2012), evolution of easement language, goals, and restrictions (Owley and Rissman, 2016), drivers of the spatial configuration of easements (Baldwin and Leonard, 2015; Lawley and Yang, 2015), and fine-scale differences between ecological outcomes on easements and other private lands (Pocewicz et al., 2011). However, the contribution of conservation easements in their current distribution to landscape-scale conservation goals is not well-studied (Fishburn et al., 2009; Rissman et al., 2007).

Conservation easements are held by a diverse suite of organizations in a variety of socio-economic and political settings (Merenlender et al., 2004) and can be established for a variety of purposes (e.g., open space, farmland preservation, biodiversity habitat, cultural heritage) (NCCUSL, 2007; Rissman et al., 2007). While considerable research effort and resource expenditure has been aimed at developing landscape- and regional-scale plans intended to guide land conservation actions (Bottrill and Pressey, 2012; Groves et al., 2002), relatively few plans are fully implemented (Fisher and Dills, 2012; Knight et al., 2008; McIntosh et al., 2016). Instead, conservation organizations rely on a broad combination of factors such as local and regional conservation goals (Carter et al., 2015; Crossman et al., 2011), cost and return on investment (Armsworth et al., 2017; Naidoo and Ricketts, 2006), landowner willingness and local community priorities (Bastian et al., 2017), as well as opportunism (Gerber and Rissman, 2012) to make actual land protection decisions (Perhans et al., 2008). Local conservation plans, when implemented, often include proximity to ecological or anthropogenic features as a surrogate for ecological values or threats to biodiversity (Groves and Game, 2016; Hanson et al., 2017) and land trusts may, due to logistical constraints, target lands for conservation that are closer to land trust offices or municipalities than other private lands. Thus, on-the-ground conservation implementation is a local- to regional-scale process dependent on social, economic, and political conditions with varied spatial and ecological outcomes (Carter et al., 2015).

Effective conservation depends on knowing where lands of conservation value occur across landscapes and how well current patterns of protected areas align with those locations. Increasingly, spatial data and sophisticated models are available to assess the degree to which protected areas contribute to landscape-scale goals. The "representation" approach to conservation is commonly used to assess the extent to which protected areas networks effectively conserve genetic, species, and community diversity (Aycrigg et al., 2013; Dietz et al., 2015; Gallo et al., 2009). Representation assumes that by conserving "some of everything", e.g., including the full diversity of ecosystem types (Margules and Pressey, 2000; Olson and Dinerstein, 1998), protected areas will better support the species and ecological processes characteristic of those ecological communities (Bunce et al., 2013; Rodrigues et al., 2004; Woodley et al., 2012). Simultaneously, maintaining landscape connectivity, e.g., the ability for a landscape to support movement for wide-ranging species between resources patches or protected areas (Taylor et al., 1993), has been identified as an important conservation target (Chetkiewicz et al., 2006; Heller and Zavaleta, 2009; Hilty et al., 2006; Rouget et al., 2006; Worboys et al., 2010).

Given the known and persistent bias in the spatial distribution of public protected areas (Joppa and Pfaff, 2009), the potential for small conservation areas such as easement to contribute landscape-scale conservation goals is an important and understudied research area (Baldwin and Fouch, 2018). In landscapes dominated by public lands, such as the American West, conservation easements may 'punch above their weight' and contribute disproportionately to the protection of ecosystems and biodiversity; conversely, conservation easements may be more likely to fulfill local conservation goals and contribute little additional value to a large-scale conservation portfolio (Baldwin and Fouch, 2018). Given the substantial and widespread investment in conservation easements, it is crucial to assess the outcomes of these local easements in the broader landscape context. Studies that have examined the contribution of conservation easements and public lands seldom compare the two distinct conservation types, nor are they compared to the potential contribution of areas outside of conserved lands (Baldwin and Fouch, 2018; Rissman and Merenlender, 2008). Here, we analyzed the distribution of 1223 conservation easements in the High Divide, a region of national conservation importance in Idaho and Montana, with respect to ecosystem representation and landscape connectivity, two common large-scale conservation goals (Heller and Zavaleta, 2009). We compared the contributions of conservation easements to those of public lands as well as randomly selected areas on private land. By assessing the cumulative and relative contribution from conservation easements, our study contributes to the on-going conversation of how to achieve large-landscape conservation goals. Specifically, we asked:

(1) How does the spatial distribution of conservation easements compare to public land and other private lands with respect to biophysical (e.g., distance to water) and anthropogenic (e.g., distance to roads) variables?
(2) How well does the current pattern of conservation easements contribute to ecosystem representation and conservation of priority ecosystems at regional and national scales? How does it compare to choosing areas at random and to public lands?
(3) How well does the current pattern of conservation easements contribute to conservation of lands important for landscape connectivity? How does it compare to choosing areas at random and to public lands?

2. Methods

2.1. Study area

The High Divide region of eastern Idaho and western Montana covers approximately 138,000 km^2 and contains the headwaters of the Missouri and Columbia watersheds. Elevation ranges between 750 m and 3860 m, with strong topographic gradients leading to corresponding diversity in vegetation communities. Lower elevations are dominated by sagebrush-steppe communities, while higher elevations are characterized by subalpine forests (Comer et al., 2003, Fig. S1). The High Divide region is vital for maintaining current and potential connectivity in the Rocky Mountains (Carroll et al., 2011; Shafer, 2015), protecting and sustaining irreplaceable ecosystems (Belote et al., 2015; Noss et al., 2002), providing spawning habitat for anadromous fish from the Pacific Ocean (McClure et al., 2008), and providing outstanding opportunities for outdoor recreation (Rasker and Hansen, 2000). With the exception of a few larger communities (e.g., Bozeman, MT, Idaho Falls, ID), most of the private land is sparsely populated though increasing exurban development has led to habitat loss and increased fragmentation (Brown et al., 2010; Gude et al., 2006). Public lands comprise ~60% (80,000 km^2) of the total land area in the High Divide, with the remainder of the landscape in private ownership (Fig. 1). As such, the High Divide exemplifies the potential importance of private land conservation for achieving broad-scale conservation objectives in mixed-ownership landscapes.

2.2. Conservation easement, public land, and non-conserved private land delineation

To delineate conservation easements and public land boundaries, we used the National Conservation Easement Database (NCED) and the US Geological Survey GAP (USGS-GAP) Protected Areas Database of the US (PAD-US 1.4). The NCED consists of voluntarily reported conservation easement boundaries, and also includes information on the protection status of the easements. Because the NCED is known to be incomplete (NCED, 2016), we supplemented the NCED data by

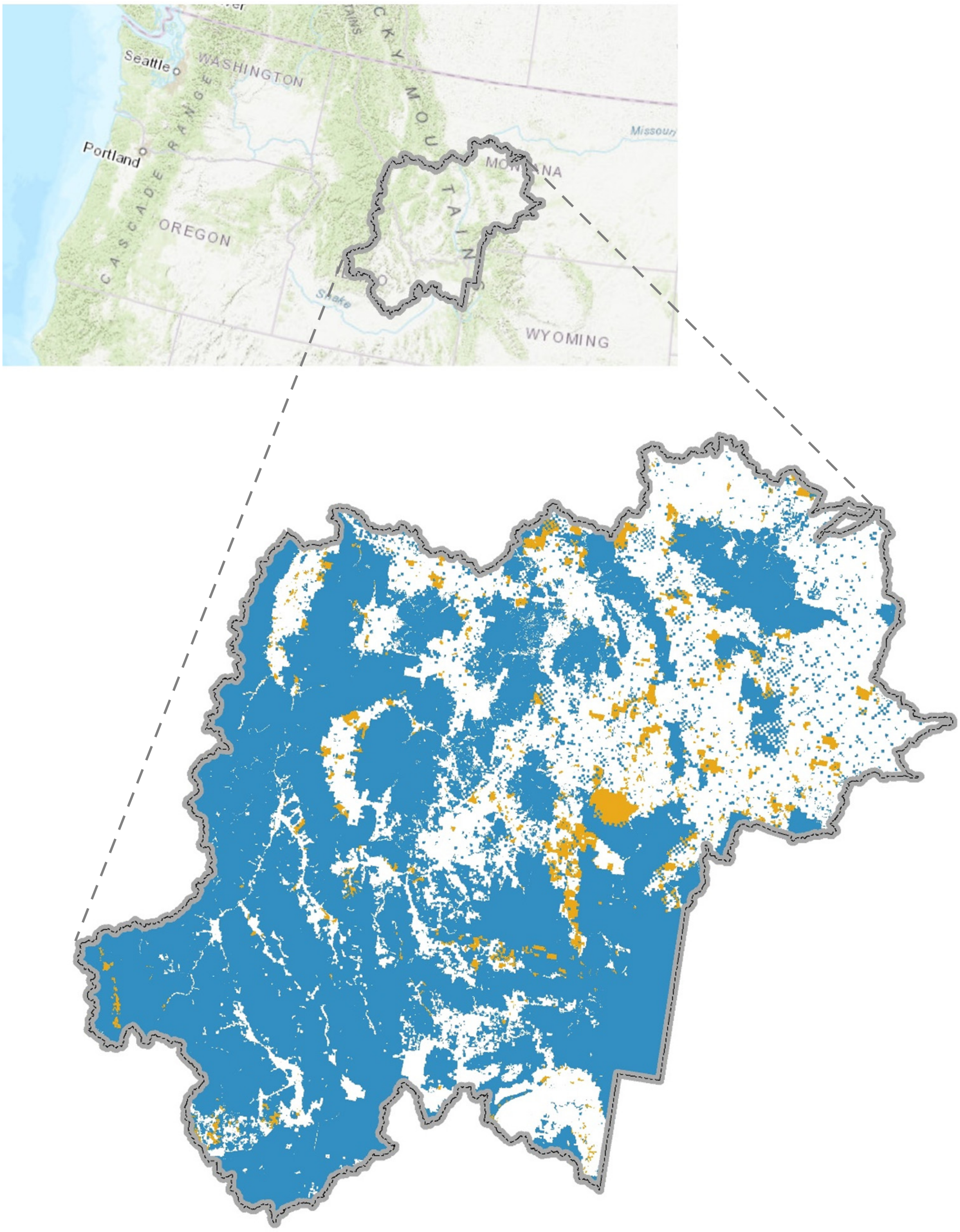

Fig. 1. Map of the High Divide, located in the Northern Rocky Mountains along the continental divide in the United States (inset). Public lands (blue) comprise the majority of the land area, with conservation easements (orange) and non-conserved private lands (white) interspersed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

identifying land trusts within the area that were not reported in the NCED and requesting spatial data for their easements, allowing us to compile a more complete picture of land conservation in the region. PAD-US consists of federal, state, and voluntarily provided protected area boundaries as well as information on the protection status of these areas (USGS-GAP, 2016). For the purposes of our analysis, we defined public lands as land owned and managed by any public entity as well as reserves owned by NGOs with public access. This led to the inclusion of 14 “NGO reserve” parcels in our ‘public lands’ dataset, all of which were directly adjacent to existing public lands (Table S1). All land not mapped as a conservation easement or designated as public land was considered non-conserved private land.

Conservation easements and public lands vary in their management status from lands managed with the intent to maintain biodiversity to lands with few or no mandated biodiversity protections. In this study, we differentiate conservation status into 3 categories based on their reported GAP conservation status (Table 1). Conservation status for land is determined by the perceived permanence of biodiversity protection, the type of management (e.g., limiting natural disturbances, extractive uses, etc.), and whether or not that management is mandated (USGS-GAP, 2016). We tallied the area of conservation easements and public land within each conservation status. Because the management status for non-conserved private lands is not reported in publicly available data, all non-conserved private lands were assumed to have no known management (or GAP 4 status).

2.3. Q1: Biophysical and anthropogenic settings of conservation easements, public lands, and non-conserved private lands

We evaluated whether differences existed in the current spatial distribution of conservation easements, public lands, and non-conserved private lands in the High Divide by comparing the biophysical

Table 1
Description of the protection status of lands within the High Divide, based on the conservation status (i.e., GAP) categories in the US Protected Areas Database (PAD-US). Modified from Aycrigg et al., 2013.

Conservation status	Description	GAP status equivalents	Area in study area (km^2)		
Biodiversity management (i.e., highest protections)	Permanent protection from conversion of natural cover; managed to maintain biodiversity; natural disturbance events may or may not be allowed to proceed or be mimicked by management.	GAP 1 or GAP 2	12,108	Public land	11,029
				Conservation easements	1080
				Non-conserved private lands	na
Multiple-use management (i.e., protected from conversion)	Permanent protection from conversion of natural cover over the majority of the land area; subject to extractive uses which can include low-intensity (e.g., logging) or localized high-intensity (e.g., mining) disturbances.	GAP 3	68,539	Public land	67,012
				Conservation easements	1526
				Non-conserved private lands	na
No known management (i.e., unknown protections)	Management intent is unknown, but may be managed for conservation.	GAP 4	57,459	Public land	1960
				Conservation easements	2249
				Non-conserved private lands	53,250

Table 2
Summary statistics highlight differences in the centers (median) and dispersion (interquartile range, i.e., IQR) of landscape variables among public areas, conservation easements, and non-conserved private lands within the High Divide region of Idaho and Montana. Central tendency and IQR were calculated based on the entire landscape distribution, grouped by land type, of each variable. The full range for each variable across the entire study region is reported.

	Elevation (m)	Soil productivity (non-irrigated capability class[a])	Dist. to water (km)	Dist. to roads (km)	Dist. to town (km)	Dist. to land trust office (km)	Dist. to GAP 1 or GAP 2 status lands (km)	Dist. to any public lands (km)
Median (IQR)								
Non-conserved private lands	1559 (1381–1770)	6 (4–7)	8.2 (3.2–16.9)	4.8 (1.9–9.9)	26.6 (15.7–42.7)	72.7 (48.5–105.3)	16.9 (9.1–29.7)	10.6 (4.2–20.3)
Conservation easements	1669 (1479–1891)	6 (4.5–7)	6.8 (2.6–12.7)	6.0 (2.7–10.3)	27.3 (18.7–40.3)	60.2 (38.4–83.2)	11.3 (5.3–24.0)	9.6 (3.8–19.1)
Public lands	2093 (1816–2369)	6 (4–7)	10.5 (5.3–17.8)	10.2 (5.3–16.4)	31.9 (21.4–43.5)	72.3 (48.3–93.5)	6.9 (1.7–13.5)	na
Landscape range (Min–Max)								
High Divide study region				0–249.8		0–303.0	0–48.6	0–191.2

[a] Non-irrigated capability class ranges from 3 to 8 within the study area. Class 3 soils have low productivity and severe limitations, while class 8 soils have extremely low productivity and extreme limitations which make them unsuitable for production (USDA, 2000).

and anthropogenic setting of each using a suite of variables (Table 2). In all cases, we compared the entire landscape distribution for conservation easements, public land, and non-conserved private lands. We followed the method described by Aycrigg et al. (2013) wherein maps of each variable (i.e., elevation, soil) were intersected with land type designations and then full distribution of values within each a given land type were tabulated and used to calculate frequency distributions.

To evaluate whether conservation easements follow published trends of protected areas occurring more frequently at high elevation and low productivity areas, we evaluated the distribution of conservation easements, public lands, and non-conserved private lands with respect to soils and elevation by calculating the cross-tabulated proportion of each land type comprised of different elevation and soil productivity classes. We used elevation data mapped at 30-m resolution from the National Elevation Dataset (NED; https://nationalmap.gov/elevation) and soil productivity data extracted from the STATSGO2 dataset (https://datagateway.nrcs.usda.gov/). Elevation data were reclassified into 10 classes ranging from 750 m to > 3000 m at 250-meter intervals. Soil productivity classes were determined by the non-irrigated land capability class from the STATSGO data and, nationally, can range from very low to very high (http://soils.usda.gov/technical/handbook). However, soils within the study area classified relatively poor and the classification ranges from limited productivity to extremely limited productivity.

We examined cumulative frequency distributions to compare the distribution of the remainder of biophysical and anthropogenic variables within conservation easements, public lands, and non-conserved lands (Gardner and Urban, 2007). Proximity to anthropogenic and biophysical features was calculated as Euclidean distance on a 30-m grid using ArcMap 10.4. Locations of rivers and waterbodies were extracted from the National Hydrography Dataset (NHD; https://nhd.usgs.gov). Roads were extracted from the USGS Transportation data (https://nationalmap.gov/transport) and based on the TIGER/Line data provided by the U.S. Census Bureau. The location of city centers was also extracted from the U.S. Census data (https://www.census.gov/geo/maps-data/data/tiger-line). Land trust office locations were determined using zipcode or physical address data, depending on availability, obtained from the National Land Trust Census conducted by the Land Trust Alliance census (https://www.landtrustalliance.org/about/national-land-trust-census). Distance to protected areas was based on Euclidean distance to the nearest public land with a GAP conservation status of 1 or 2.

2.4. Q2: Conservation easement contribution to ecosystem representation and protection of priority ecosystems

We assessed the contribution from conservation easements to representation of ecosystems at both regional and national scales. Ecosystems were delineated using GAP land cover data (USGS-GAP, 2011) to map ecological systems at the finest information resolution (i.e., Level 6, hereafter “ecosystems”) within the study region (sensu Dietz et al., 2015). We excluded 6 highly-human-modified ecosystem types: developed, high, medium, and low intensity; developed, open space; orchards and vineyards; quarries, mines, and oil wells. Open water was also excluded from analysis.

We analyzed the relative contribution of conservation easements to regional ecosystem representation (hereafter “regional representation” or RR) by overlaying conservation easement and public land boundaries with GAP ecosystems data. For each ecosystem, we calculated the total area within land conservation type (e.g., conservation easements vs. public land) and by conservation status (e.g., biodiversity management, multiple-use management, unknown management, Table 1). RR was calculated for each ecosystem using Eq. (1), where i = land conservation type and j = conservation status:

$$\frac{\sum_{i,j} \textit{area of the ecosystem}}{\textit{total area of the ecosystem within the High Divide region}} \times 100 \tag{1}$$

For example, a regional representation of 20% for an ecosystem means that of all land within the study area of ecosystem type, 20% is conserved at some level on conservation easements or public lands. Regional representation was also calculated for each ecosystem by conservation status (Table 1). For example, regional representation of an ecosystem on land managed for biodiversity ($\text{RR}_{\text{Biodiversity}}$) provides an estimate of the percent of an ecosystem within the study area that is conserved with the highest protection status (GAP 1 or 2).

2.4.1. Cumulative contribution of CE to ecosystem representation

Following Dietz et al., 2015, we analyzed how conservation easements change the total area and diversity of ecosystems accumulated on protected lands within the High Divide. Using the species accumulation function in the vegan package for the R statistical environment (Oksanen et al., 2018; R Core Team, 2017), we calculated ecosystem accumulation curves for protected land. Accumulation curves plot the cumulative number of ecosystems as a function of sampling effort (i.e., the number or area of conserved areas sampled). We evaluated accumulation of new ecosystems into the conserved area network based on presence (i.e., any portion of that ecosystem is represented on conserved land) as well as based on achieving 5% and 20% thresholds (i.e., at least 5% or 20% regional ecosystem representation). We chose those thresholds in order to evaluate a wide range of potential landscape conservation goals (sensu Dietz et al., 2015). We used the “collector” method to accumulate ecosystems, which allowed us to add protected areas in pre-determined order. Specifically, sites were added based on the protected status and site type: (1) public lands managed for biodiversity, (2) conservation easements managed for biodiversity, (3) public lands managed for multiple uses, (4) conservation easements managed for multiple uses, (5) public lands with unknown management, (6) conservation easements with unknown management. Adding sites in this order allowed us to determine how many new ecosystems were added to the protected areas network, at what protection level, and over a wide range of representation “thresholds”.

2.4.2. Contribution of CE to conservation of priority ecosystems

To identify the extent to which conservation easements contribute toward regional- and national-scale ecosystem representation priorities, we mapped the ecosystems in the High Divide in terms of their relative regional and national priority scores, as calculated below. Calculated scores were mapped back to the 30-m USGS-GAP land cover ecosystem dataset.

The regional priority index incorporates regional geographic rarity of ecosystems, endemism, and the current protection level at regional scale, all of which are factors that have commonly been used for informing conservation prioritization (Jenkins et al., 2015; Rabinowitz, 1981; Sifleet et al., 2015) and provide effective prioritizations to increase or maximize representation of species and ecosystems (Albuquerque and Beier, 2015; Gauthier et al., 2010). Specifically, the regional priority score was calculated for each ecosystem using Eq. (2) where the relative regional geographic rarity (RGR) and endemism value (A_R/A_N) of an ecosystem are weighted by the regional representation of that ecosystem on lands managed for biodiversity ($\text{RR}_{\text{Biodiversity}}$). Relative geographic rarity (RGR) is a simple ranking of ecosystems by their area within the High Divide region, rescaled to 0–1 so that the least common ecosystem has an RGR = 1 (Sifleet et al., 2015). Endemism is the relative proportion of an ecosystem that occurs within study region compared to its national extent, i.e., the regional area occupied by the ecosystem (A_R) divided by the national area occupied by the ecosystem (A_N). Ecosystems that are unique to the study region have higher values (i.e., as A_R approaches A_N and a smaller portion of that ecosystem is found outside of the region) (Noss et al., 2002; Pressey et al., 1994). Endemism, which has been termed "regional responsibility", is included in prioritization because it allows allocation of conservation effort based the extent to which an ecosystem is associated with a particular region (Potter, 2018; Schmeller et al., 2008). By including both regional geographic rarity and endemism, our regional priority index accounts for the effect of setting conservation priorities at different geographic scales (Gauthier et al., 2010). The calculated endemism and RGR of each ecosystem is available in Table S1.

$$\textit{Regional Priority} = \left(\frac{A_R}{A_N} + RGR\right) \times (1 - RR_{Biodiversity}) \tag{2}$$

National priority was adapted from Belote et al. (2017) wherein ecosystems with lower representation on lands with GAP 1 or 2 conservation status are assigned higher priority values then those that are already highly protected. We calculated the national priority score using Eq. (3), which weighted national representation ($\mathrm{NR_{biodiversity}}$) by endemism to account for regional responsibility at the national scale. $\mathrm{NR_{biodiversity}}$ was determined using data tables from Belote et al., 2017. National priority is highest for ecosystems which have low national representation and are highly endemic to the region.

$$\textit{National Priority} = \frac{A_R}{A_N} \times (1 - NR_{Biodiversity}) \tag{3}$$

After mapping regional and national priority, we overlaid locations of conservation easements onto the regional and national priority maps and calculated the area-weighted ecosystem priority score for each conservation easement. A higher ecosystem priority score indicates that an easement contains ecosystems that are of high conservation priority at regional or national scales. We plotted the regional ecosystem priority scores against the national ecosystem priority scores and used a comparison index line (i.e., 1:1 line) to investigate whether conservation easements are more likely contributing to regional or national conservation goals. We also compared the regional and national priority scores of conservation easements to public lands using Welch's unpaired *t*-tests.

2.4.3. Comparison of easements to public lands and randomly chosen areas on private land

To determine how conservation easements performed in their current distribution in comparison to a random set of areas of equivalent size, we generated 1000 permutations of random "pseudo-easement" datasets to compare to the actual observed easement dataset (sensu Araújo et al., 2011). This method allows us to analyze whether conservation easements provide different conservation outcomes than simply choosing areas at random. Using R packages *sp* (Pebesma and Bivand, 2005) and *rgeos* (Bivand and Rundel, 2017), we distributed 1223 circular polygons randomly across the non-conserved private land in the High Divide. In each permutation, polygon sizes approximately matched the area of the 1223 observed easements. We then compared mean regional and national priority scores from the observed conservation easements to the distribution of regional and national priority scores from the random permutations. We also plotted the distribution of regional and national priority scores for public lands for comparison.

2.5. Q3: Landscape connectivity

We used regional-scale connectivity models to quantify the degree to which conservation easements contribute to maintaining the potential flow of species across the landscape. Connectivity models based on the naturalness of a landscape (i.e., the degree of human modification) are likely to represent the potential permeability of the landscape to a variety of species, especially those that are sensitive to human disturbances (Krosby et al., 2015), and have been used to assess potential connectivity across the Western US (Dickson et al., 2017; Littlefield et al., 2017) as well as across the entire United States (Belote et al., 2016; Theobald et al., 2012). We modeled potential flow across the region using Circuitscape 4.0.5 (McRae et al., 2013), which couples random-walk theory with analogies to electrical circuit theory to determine where animals are likely to move across a landscape (McRae et al., 2008). Patterns of electrical current (in amperes [Amps]) are used to predict potential movement patterns, where organisms are more likely to move through low-resistance cells than high-resistance cells (McRae et al., 2008; Littlefield et al., 2017). We chose circuit theory because of its ability to integrate variable probabilities of connectivity across an entire surface, as well as its common application to prioritizing areas important for maintaining landscape permeability.

Delineation of patches to connect (e.g., core habitats, nodes) can be challenging and researchers have defined nodes as, among others, core protected areas (Belote et al., 2016), centroids of public land (Dickson et al., 2017), and 'highly natural' areas (Theobald et al., 2012). Connectivity models can be highly sensitive to the locations of nodes (Belote et al., 2016; Butts, 2009; Carroll et al., 2011; Koen et al., 2014). Thus, rather than predetermining a set of nodes to connect which forces assumptions about habitat and species requirements, we chose to model overall landscape flow using a wall-to-wall approach (Anderson et al., 2012, 2014; Pelletier et al., 2014).

The wall-to-wall method, modified from Anderson et al. (2012, 2014), establishes a buffer area around the focal region and then passes current from a source on one edge of the buffer to a ground on the opposite edge (Fig. S2). This is repeated for each of the four cardinal directions (e.g., east-west, west-east, north-south, south-north) and the resulting current maps are summed to create a continuous omnidirectional cumulative current map. For our study, we first created a rectangular envelope around the study area, buffered the study area by 100 km to avoid artifacts created by study area edge. We used a human modification index (Theobald, 2013) to represent landscape resistance in the connectivity models. This resistance surface is based on the degree of human modification via altered land cover, roads, and other qualities that alter landscape permeability and has been used as the basis of resistance surfaces in other connectivity models (Belote et al., 2016; Dickson et al., 2017). Scaling resistance surfaces for connectivity models based on degree of human modification assumes that human altered features on landscapes will increase the resistance (e.g., behavioral avoidance, risk of mortality, movement barriers). Some researchers have assumed a non-linear relationship between human modification and connectivity resistance (Belote et al., 2016; Keeley et al., 2017). Here, we assume a linear relationship between human modification and resistance.

Using Circuitscape, we injected 1-Amp of current into each pixel within 5-km wide linear source region (Fig. S2). The current then flowed from source to ground nodes across the resistance surface in each cardinal direction, the results of which were then summed to provide a final landscape connectivity map.

2.5.1. Comparison of conservation easements to public lands and randomly chosen areas on private land

For each conservation easement, we calculated the area-weighted current flow by calculating the total current flow across each easement and public land unit and dividing it by its area (e.g., average current flow centrality sensu Dickson et al., 2017; Newman, 2005). Easements and public lands $< 1\ \mathrm{km}^2$ in area were calculated as the total current flow divided by 1, due to the minimum mapping resolution of the connectivity model ($1\ \mathrm{km}^2$). We compared the current flow protected by conservation easements to current flow protected by public lands using Welch's unpaired t-tests. Following the methods above, we calculated the area-weighted current flow for randomly chosen areas. To compare the contribution of conservation easements to public land and randomly chosen areas, we plotted the distribution of area-weighted current flow for conservation easements, public land, and randomly chosen areas.

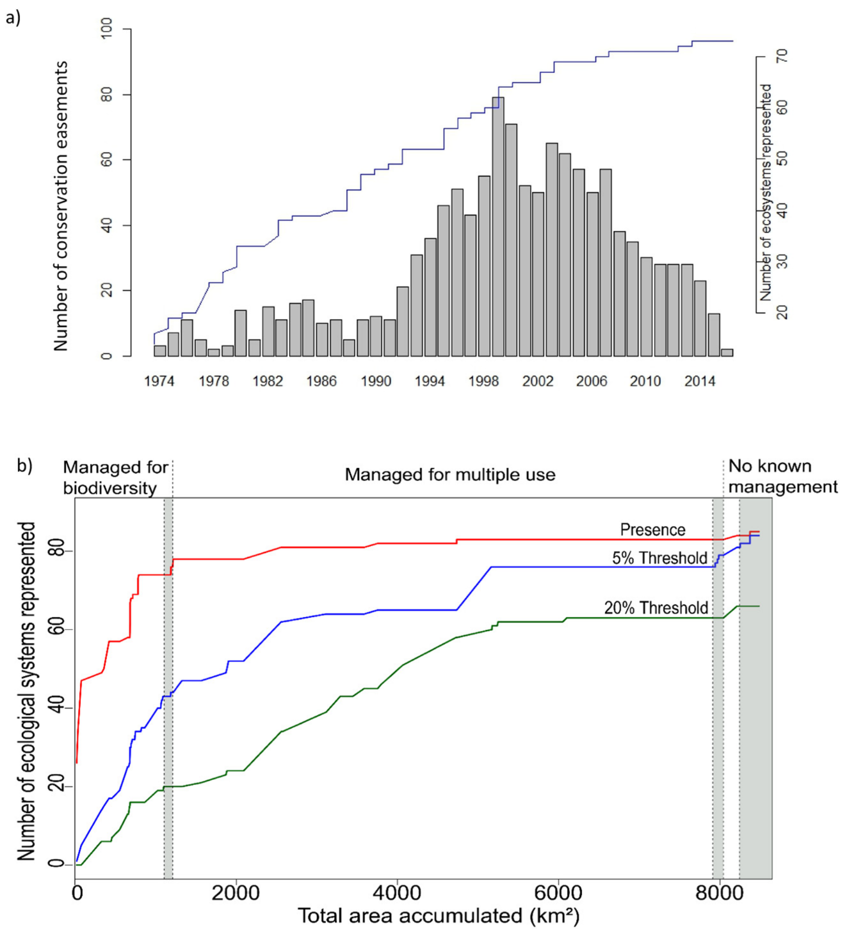

Fig. 2. Ecosystem accumulation curves for conservation easements and public land in the High Divide. (a) The number of ecosystems represented on conservation easements over time, left axis shows the number of easements established during each time period, right axis indicates the number of ecosystems represented on easements. (b) The number of unique ecological systems represented on public lands (no shading) and conservation easements (gray shading) as a function of area accumulated and protection status. The red line represents presence of an ecological system on protected lands in the High Divide. The blue and green lines indicate ecological systems with at least 5% and 20% regional representation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

Conservation easements (n = 1223) cover 9.1% (4855 km^2) of the private land area and 3.6% of the total land area in the High Divide (Fig. 1). Conservation easements range in size from 0.01 km^2 to over 460 km^2 (mean = 3.9 km^2, SD = 15.5). The majority of conservation easements have protection status that emphasizes multiple uses (i.e., GAP 3, 42%, 1526 km^2) or unknown management (i.e. GAP 4, 45% of CEs resulting in 2249 km^2). Only 13% of reported CEs prioritized management for biodiversity protection (GAP 1 or 2, 1080 km^2). Public lands comprise ~60% (80,000 km^2) of the total land area in the High Divide, of which 84% is managed for multiple use, 14% for biodiversity, and 2% with no known management mandate (Fig. S3). Mapped public land areas ranged in size from 0.01 km^2 to 6560 km^2 (mean = 110.5 km^2, SD = 478.9).

3.1. *Spatial distribution and biophysical assessment of conservation easements, public land, and non-conserved private lands*

The distribution of biophysical and anthropogenic characteristics among public lands, conservation easements, and non-conserved private lands suggest spatial patterns of land conservation within the High Divide (Table 2, Fig. S4 & S5). Conservation easements tended to be at mid-elevations and occur at the upper ends of elevations occupied by private lands; public lands tended to occur at higher elevations as compared conservation easements and non-conserved private lands (Table 2). Soil productivity (i.e., non-irrigated capability) is low throughout the High Divide, with all soils ranging between Class 3 (e.g., severe limitations) to Class 8 (e.g., plant production very low; uses limited to recreation, wildlife, water supply, or aesthetic purposes). Conservation easements are more frequently located on lower productivity soils as compared to non-conserved private lands (Fig. S4).

Examination of the frequency distributions indicated that conservation easements and non-protected private lands tend to both be relatively close to public lands. Conservation easements tend to be closer to water and closer to land trust offices than either public lands or non-conserved private lands (Fig. S5). Conservation easements also are closer to lands protected for biodiversity (e.g., GAP 1 and 2 status) as compared to non-conserved private lands. Both conservation easements and non-conserved land are closer to major roads than are public lands within the High Divide. Frequency distributions describing the distance to towns and distance to public lands were similar between conservation easements and the other land types.

3.2. *Contribution of CE to ecosystem representation and protection of priority ecosystems*

Conservation easements in the High Divide provide protection for 73 of the 87 ecosystems present in the High Divide, and that number has increased over time, even as the rate of easement establishment has slowed (Fig. 2a). In contrast, public land provides protection to 84 ecosystems (Table S1). In total, 85 of the 87 (98%) ecosystems present in the High Divide region are represented on conservation easements and public lands, one of which (Northern Rocky Mountain Wooded Vernal Pools) is conserved only on conservation easements (USGS-GAP, 2011). Conservation easements increased the level of representation (i.e., what percent of each ecosystem is protected and at what level) for nine of the 87 ecosystems present in the region (Fig. 2b). Specifically, easements led to seven ecosystems surpassing 5% representation overall and two ecosystems meeting the 5% representation threshold on lands managed for biodiversity (Table 3). For a full list of the 87 ecosystems analyzed within the High Divide, along with their levels of

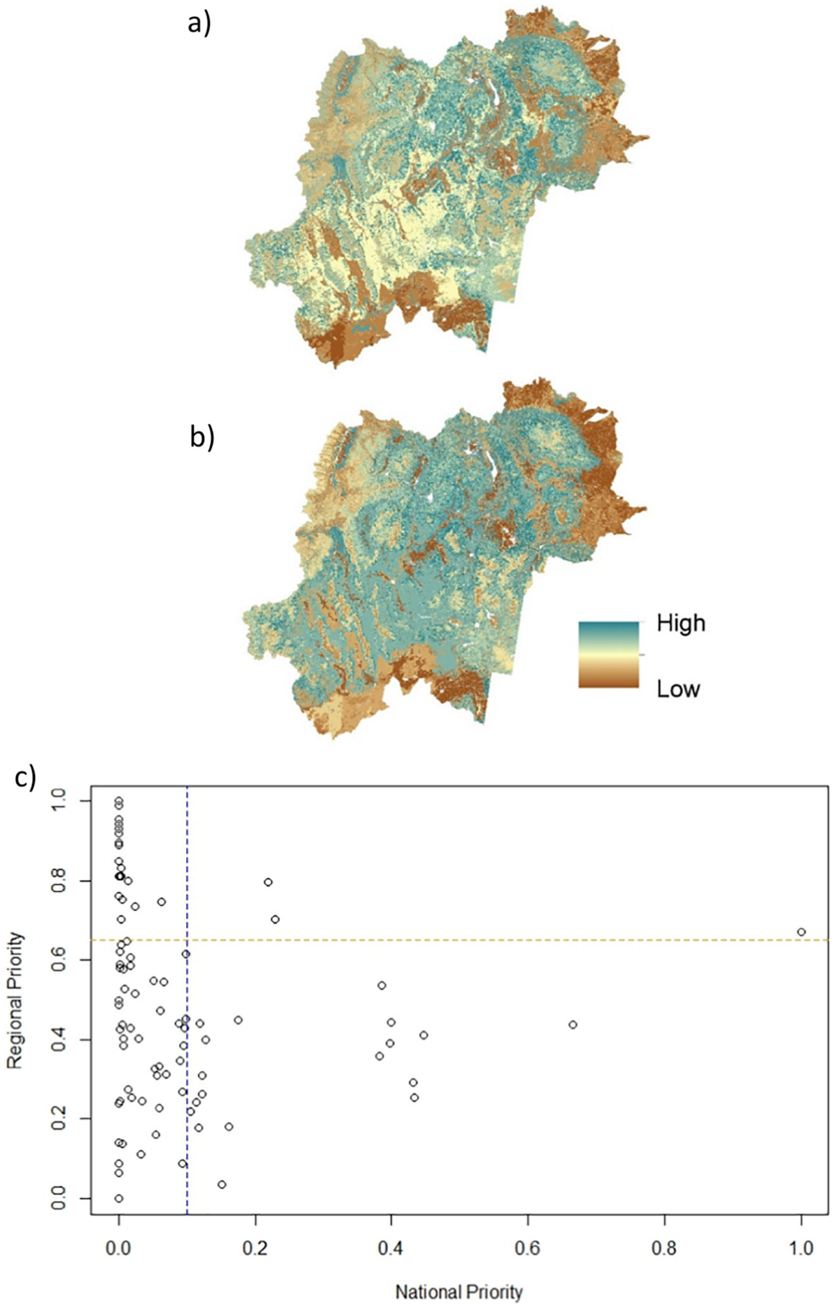

Fig. 3. Indices of ecosystem representation priority at (a) regional and (b) national scales; (c) bivariate plot of regional versus national priority for 87 ecosystems. Blue ($x = 0.10$) and orange ($y = 0.65$) lines represent the upper quantile for each index and highlight 19 ecological systems as high priority (> 0.65; upper quantile) regionally but lower priority (< 0.10) nationally. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

representation by land type and conservation status, refer to Table S1.

Ecosystem priority designation varied based on the regional and national priority indices (Fig. 3), with several high regional priority ecosystems having lower national priority scores. Endemism ranged from 0 to 0.69. The highest value was assigned to the Middle Rocky Mountain Montane Douglas-fir Forest and Woodland, indicating that 69% of that ecosystem's US geographic area is found within the High Divide Region (Table S1). Ecosystems with high endemism values tended to have low relative geographic rarity ($r = -0.49$, $p < 0.01$; Fig. S6) and endemism value was slightly correlated with regional representation ($r = 0.21$, $p = 0.05$; Fig. S6). There was no relationship between relative geographic rarity and regional representation (Fig. S6). Overall, ecosystems with less area on private land (e.g., high representation on public lands) had lower representation on conservation easements ($rho = 0.59$, $p < 0.01$). However, for ecosystems with > 20% of their area on private lands, there was no relationship between the area on private lands and representation on conservation easements ($rho = 0.09$, $p = 0.53$) (Fig. S7).

Conservation easements on average scored slightly lower on the regional priority index ($\bar{x} = 0.28$, $sd = 0.11$) versus the national priority index ($\bar{x} = 0.34$, $sd = 0.19$) ($p < 0.001$, $t = -19.822$). However, while easements with higher national priority index tended to have higher regional priority index scores, the converse was not always true (Fig. 4). Conservation easements and public land differed only slightly in terms of the mean regional priority index ($\bar{x} = 0.28$ and $\bar{x} = 0.29$, respectively; $p = 0.001$, $t = -3.32$) and national priority

Table 3

Total cumulative current flow, mean area-weighted current flow (flow/km^2), and average current flow (mean of pixels within each easement/public land unit) across conservation easements, public land areas, and the null model of private land conservation (i.e., randomly distributed areas) in the High Divide.

	Total area (km^2)	Total cumulative current flow across all area	Area-weighted current flow (flow/km^2)	Average current flow
Conservation easements	4855	101,702.7	25.0 (range: 4.2–216.7, sd = 5.2)	15.6 (range: 8.5–54.6, sd = 20.4)
Public land	80,000	1,812,759.1	41.5 (range: 5.6–2495, sd = 123.2)	19.4 (range: 7.9–59.58, sd = 7.1)
Null model of private land conservation[a]	4855	Mean: 89,338 (range: 80,545–101,282)	23.8 (range: 3.3–245.1, sd = 18.1)	15.3 (range: 7.7–72.4, sd = 4.9)

[a] Mean and range reported from 100 iterations of the null model of private land conservation.

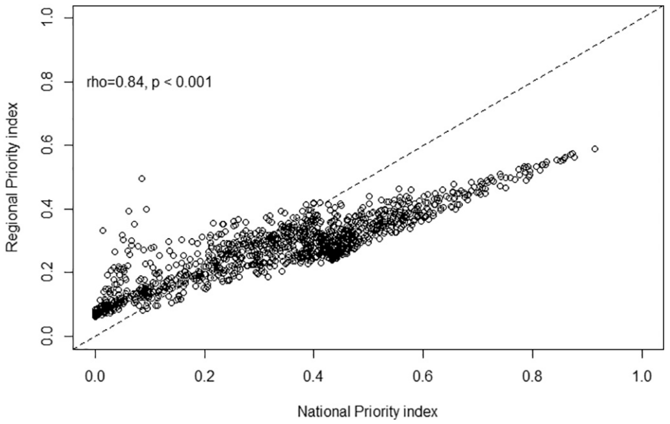

Fig. 4. Regional priority index scores plotted against national priority index scores for 1223 conservation easements in the High Divide region.

index scores ($\bar{x}$ = 0.34; $\bar{x}$ = 0.36, respectively; $p = 0.01$, $t = -2.68$). However, the distribution of mean regional priority index scores for both conservation easements and public lands were markedly different from and tended toward higher scores than areas chosen at random from private lands (Fig. 5a). To a lesser extent, both conservation easements and public lands tended toward higher mean national priority index scores than areas chosen at random from private lands (Fig. 5b).

3.3. Contribution of CE to conservation of landscape connectivity

Patterns of current flow varied across the High Divide, with high current density (i.e., area-weighted current flow) attributed to both conservation easements and public lands across the region (Fig. S8). Public lands had higher cumulative current flow and mean current density versus conservation easements ($p < 0.001$, $t = -3.54$; Table 3). However, conservation easements tended to contain similar cumulative current flow and current density (total flow per km^2) compared to randomly chosen areas on private land (Table 3, Fig. 5c).

4. Discussion

Our analysis reveals that conservation easements, though only a small part of the regional land base, contribute substantially to landscape-scale representation of ecosystems and provide complementary conservation value to public land at the regional scale, even where public lands dominate the landscape. Specifically, we found that easements contribute additional protections to 10% of the ecosystems in the region while only occupying 3.5% of the landscape. While the dominance of public land (i.e., 60% of the study area) might suggest that “the bases are covered” and additional land conservation would be redundant, we found that conservation easements provide an important complement to existing public land and enhance ecological representation across the protected areas network. Given the potential conservation gains in this public-land dominated system, our results suggest that small protected areas such as conservation easements may lead to even greater gains in landscapes with little public land. Indeed, complementarity between private conservation areas (e.g., easements) and public lands is not unique to our study; in South Africa, where public land comprises only 24% of the landscape, private conservation areas were found to be complementary to public lands, and were especially important for endangered habitat types (Gallo et al., 2009).

To be effective, regional networks of protected areas must be representative of the biodiversity and ecosystem processes present in the region (Gaston et al., 2008). Consistent with national and global trends in protected areas (Joppa and Pfaff, 2009), public lands within the study region are biased toward higher elevations and less productive soils and thus, insufficient to be representative of the region.

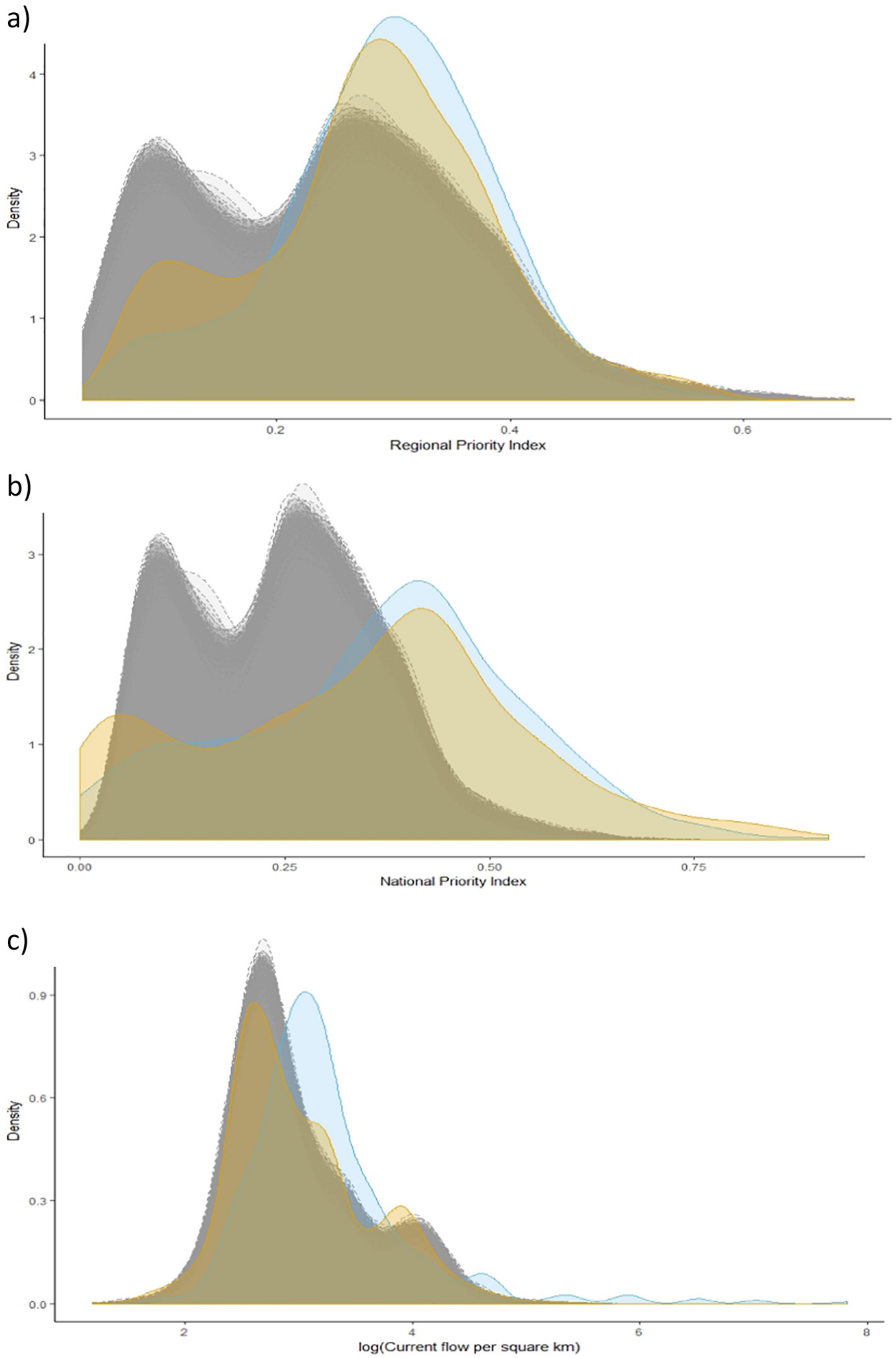

Fig. 5. Density plots showing the distribution of regional priority scores (a), national priority scores (b), and area-weighted current flow (c) for conservation easements (orange), public lands (blue), and null models of conservation (gray). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Conservation easements, which are currently distributed across mid to lower elevations and provide some protection on more productive soils in the region, have continued potential to play an important role in protecting areas with lower elevations and more productive soils. However, comparisons of soil productivity and elevation on conservation easements and non-conserved private lands indicate that conservation practitioners should continue to target conservation easements on the most productive soils in the region to fully represent these areas in the conservation portfolio. In the High Divide, conservation easements account for only 3.5% of the land area; however, they contribute to protecting approximately 10% of the agricultural (cropland and pasture) land in the region suggesting that conservation easements may be particularly important in protecting agricultural landscapes and related cultural ecosystem services, e.g., agricultural heritage and landscape aesthetics.

Conservation easements provided increased protection for multiple mesic and riparian ecosystems (Table S1, Wallace et al., 2008). In the arid and semi-arid Western U.S., mesic and riparian resources provide crucial habitat for an estimated 60–80% of wildlife species (Belsky et al., 1999; Peck and Lovvorn, 2001; Thomas et al., 1979) including for high-profile species such as the Greater sage-grouse (*Centrocercus urophasianus*, Donnelly et al., 2016) and anadromous fish (Lohse et al., 2008). Given the increased urbanization and development pressure in the "New" West (Hansen et al., 2002), limited riparian and mesic areas may be at increased risk which highlights the role of conservation easements as a tool for protecting these resources.

Regional and national assessments are commonly used to develop conservation prioritization plans with the intention of representing all of the biodiversity and ecosystem types to ensure their persistence (Fisher and Dills, 2012). Because ecological patterns and processes operate at multiple, hierarchical scales (Poiani et al., 2000), conservation plans created based on information at one scale may not identify areas that are important for conservation of biodiversity and ecosystem processes at other scales (Huber et al., 2010). Our ecosystem priority maps highlighted different areas depending on whether prioritization was focused on regional or national scales (Fig. 3).

These results highlight the conclusion that planning at the national scale can overlook important regional conservation needs, and vice versa. With regard to conservation easement placement, our study found that easements with high national priority scores (i.e., those that protected areas of national priority) tended to also protect the areas important for regional ecosystem diversity whereas easements with high regional priority scores (i.e., protected those areas most important regionally) often had lower national priority scores. Our results suggest that conservation easements, which represent actions at local and regional scales, do not necessarily amalgamate to protect areas important at national scales. These finding are consistent with previous research showing that local planning efforts do not provide adequate substitutes for regional and national planning (Groves, 2003; Huber et al., 2010).

At regional scales, current patterns of conservation easements performed only slightly better than areas chosen at random with respect to providing for landscape connectivity. This suggests that the current pattern of conservation easements, which tend to be closer to existing public lands than other non-conserved private lands, either (a) has been intentionally or haphazardly placed in important areas of maintaining landscape permeability or (b) has, by conserving land, limited human modification (e.g., road and housing development) and maintained lower landscape resistance within easements. Previous research suggests that, while some easements may be intentionally placed in areas with high conservation value, more frequently easements are not placed in accordance with regional scale conservation plans (Carter et al., 2014; Fisher and Dills, 2012; Knight et al., 2008). Similarly, evidence is limited as to whether conservation easements limit local and surrounding human modification. Easements have contributed to limiting vegetation conversion (Byrd et al., 2009), but the impacts of conservation easements are mediated by the landscape context with human modification differences between easement and non-easements being greater in high development as opposed to rural areas (Pocewicz et al., 2011). Conclusions as to which mechanism drives the current conservation easement pattern with respect to landscape permeability are beyond the scope of our study; however, the question deserves further research.

Conservation currently emphasizes landscape approaches which focus on developing networks of protected areas spanning gradients of human land use and ecological conditions (Lindenmayer et al., 2008), enhance overall landscape and regional sustainability (McKinney et al., 2010), and rely on both "coarse-filter" and "fine-filter" strategies to address the challenges facing biodiversity and ecosystem function (Hobbs et al., 2014; Hunter, 2005). Prioritizing conservation easement placement within the context of existing public lands and protected areas follows landscape ecological theories related to the conservation of biodiversity (Meyer et al., 2015). Since public lands tend to be of high connectivity value regionally and nationally, it follows that proximity measures, such as "distance to protected area", may be an effective strategy for easement placement in terms of achieving connectivity benefits. Continued investigation into the best and most parsimonious strategies for easement placements could provide useful recommendations and increase the efficacy of land trusts.

Rissman et al. (2007) found that nearly half of conservation easements held by The Nature Conservancy were so-called "working lands" easements, which allowed for multiple uses (e.g., farming, ranching, forestry). In our dataset, over half of the easements were classified as having multiple use management. Our analysis, which relies on remotely-sensed and GIS datasets, may over or underestimate the potential conservation contribution of a single easement. Individual easements likely vary based on land use and land management (e.g., grazing, fire suppression, invasive species removal). However, our study endeavored to describe the relative trends in conservation easements rather than the effects attributed to parcel-level management and we believe our methods and findings may be readily generalizable to other regions.

We analyzed the current pattern of conservation easements and do not address the specific mechanisms driving the extant spatial pattern (Baldwin and Leonard, 2015; Davies et al., 2010). Conservation easement placement depends on the presence of a willing landowner as well as the institutional capacity in the area (Brenner et al., 2013; Farmer et al., 2011; Williamson et al., 2018). Conservation easement placement may be particularly motivated by local factors, including social and political dynamics (Gerber and Rissman, 2012; Rissman and Sayre, 2011) and grassroots conservation concern (Merenlender et al., 2004). Understanding the mechanisms behind spatial distribution of conservation easements could help conservation planners to better identify future conservation opportunities and develop strategies to target areas underrepresented by current conservation easement distribution.

Our study adds to a growing body of work critically evaluating the efforts to conserve private land and the corresponding public benefits (Baldwin and Fouch, 2018; Bernstein and Mitchell, 2005; Merenlender et al., 2004; Wallace et al., 2008). Overall, conservation easements contribute to biodiversity conservation at multiple scales and targeted conservation easements could better achieve large landscape conservation goals. For example, by identifying which ecosystems are predominantly present on private lands and are also high priority both regionally and nationally, conservation organizations could better maximize the potential benefit from conservation easements. Assessments such as ours, which allows conservation organizations to identify how the existing pattern of private lands conservation provides benefits – either by serendipity or design – can help to better plan and execute landscape-scale conservation.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.01.024.

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