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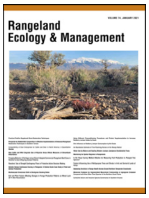

Evaluation of the Gap Intercept Method to Measure Rangeland Connectivity

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ABSTRACT

Characterizing the connectivity of materials, organisms, and energy on rangelands is critical to understanding and managing ecosystem response to disturbances. For over twenty years, scientists and rangeland managers have used the gap intercept method to monitor connectivity. However, using gap intercept measurements to infer ecosystem processes or inform management actions and conservation practices on rangelands has been limited because there are few tools and syntheses to help managers pragmatically interpret gap measurements. In this synthesis, we review the different ways the gap intercept method is conducted and highlight considerations when collecting and using gap intercept data. We discuss what is known about how gap intercept data can be used to assess wind and water erosion, biocrust abundance and composition, soil fertility, plant community dynamics, wildlife habitat characteristics, and fuel connectivity and fire behavior. Finally, we identify emerging opportunities regarding the collection and use of gap intercept data to assess rangeland connectivity, ecosystem function, and ecological processes. Through this synthesis we demonstrate the value of the gap intercept method, particularly "all-plant" (i.e., whole-community) canopy gap, in supporting assessments of rangeland condition and vulnerability, and in planning future management actions.

Introduction

Connectivity of materials, organisms, and energy have a fundamental influence on rangeland ecosystem dynamics (Okin et al., 2015). Connectivity can be structural or functional. Structural connectivity describes the spatial and temporal continuity of resources and organisms across longitudinal, lateral, and vertical dimensions (Keesstra et al., 2018; Iwaniec et al., 2021). Functional connectivity, or flows of energy (e.g., wind, water, fire), mass (e.g., nutrients, soil), and organisms, has mutual, multi-dimensional interactions with structural connectivity. Natural and anthropogenic factors such as geomorphology, climate, grazing and agriculture,

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and development affect both structural and functional connectivity (Keesstra et al., 2018; Ziegler et al., 2023). Moreover, the ecosystem impacts of these factors can be modulated by the strength of structural and functional connections. Ecological state changes are often associated with changes in connectivity, where a shift in structure results in a change in ecosystem function and ecological processes (Allen, 2007). For example, invasion of annual grasses can decrease the amount and connectivity of open spaces between perennial bunchgrasses and shrubs (D'Antonio and Vitousek, 1992), but also change fuel loads (Brooks et al., 2004; Abella, 2020; Smith et al., 2023), shift soil erosion risk (Wilcox et al., 2012; Li et al., 2022), alter soil chemistry (Mahood et al., 2022), and reduce wildlife habitat availability (Germano et al., 2012; Fulbright et al., 2013). Both structural and functional connectivity are reliant on ecosystem potential and spatial scale, where connectivity at one site or scale may produce a different functional response at another site or scale. For example, site susceptibility to wind erosion is influenced by inherent site characteristics, with fine sandy soils typically being more susceptible (Duniway et al. 2019), but also is accelerated following disturbances such as wildfire and management treatments (Whicker et al., 2008). Consequently, understanding where, when, and how shifts in connectivity are occurring is critical information for rangeland managers.

Assessing changes in connectivity requires indicators and monitoring methods that capture the spatial distribution and patterning of resources (e.g., vegetation, soils, animals, microbes; Tongway and Ludwig 1990). One of the most important and basic structural components of vegetation communities is the "gap" – the unvegetated space – between individual plants. The number, size, and configuration of gaps in an area can be determined effectively and with meaningful inference, especially if consistent and appropriate sampling methods and designs are employed. A standardized gap intercept method for measuring lateral (horizontal) connectivity at the site scale was put forward as a core rangeland and open woodland monitoring method in the *Monitoring Manual for Grassland, Shrubland, and Savannah Ecosystems* (Herrick et al., 2005, 2018). The gap intercept method quantifies the size of the gaps between vegetation and therefore provides a measure of spatial connectivity of "openness", or its inverse, the continuity of specific resources, such as vegetation canopies or basal areas. Gap intercept complements other transect-based core methods, such as the line-point intercept method (Herrick et al. 2018) which provides additional information about vegetation composition abundance and other ground-cover components but does not describe the distribution or connectivity of vegetation and soil. The gap intercept method has been applied by land management agencies and researchers worldwide at over 85,000 locations (Oliva et al., 2020; McCord et al., 2023) to understand the sensitivity of systems to temporal variation in temperature and precipitation (Ziegler et al., 2023), effects of livestock grazing (Condon and Pyke, 2018), wind and water erosion responses to disturbances (Webb et al., 2014; Williams et al., 2014), and vegetation and post-fire restoration treatment success (Germino et al., 2019; Traynor et al., 2020). Different responses in gap distributions observed across different management strategies or after disturbances could help managers decide on appropriate strategies in the future (Rango et al., 2005; Traynor et al., 2020), improve restoration effectiveness (Kimiti et al. 2020; Williams et al. 2020), and assess rangeland health (*sensu* Pellant et al., 2020). Shifts in gap distributions also provide early warning indicators of potential shifts in ecological dynamics (Webb et al., 2020).

Gap information has been used to describe forest structural connectivity and ecosystem dynamics for over 40 yr (Muscolo et al., 2014; Schliemann and Bockheim, 2011). However, using gap intercept measurements to infer ecosystem processes or inform management actions and conservation practices on rangelands has been limited because there are few tools and syntheses to help managers pragmatically interpret gap measurements. Structural connectivity information is typically limited or absent altogether from ecological site descriptions (ESDs), which are used to inform rangeland management in the United States and elsewhere (Caudle et al., 2013). Vegetation composition and structure information in ESDs are often developed based solely on plant production and plant cover data. Gap measurements are an optional way of measuring some indicators for Interpreting Indicators of Rangeland Health assessments (Pellant et al., 2020), but quantitative gap benchmarks, which are critical for interpreting quantitative information in assessments, are not readily available for many ecological processes and indicators (Turnbull et al., 2012; Webb et al., 2020; Lupardus et al., 2023b). Furthermore, there are unanswered questions regarding the use of gap indicators to improve our understanding of ecological dynamics. For example, although there may be logical insights into ecological patterns and dynamics regarding biological diversity, other relationships such as epidemiology, predator-prey relationships, resistance and resilience, shifts in biocrust composition, fuel continuity and wildfire spread and ecosystem structuring and stability have not yet been formally connected to gap indicators (Lau et al., 2017). Linking gap measurements to ecosystem processes and management decision making could enhance our ability to maintain and improve ecosystem function and structure.

We convened a group of rangeland scientists and managers at the 2023 annual meeting of the Society for Range Management to help clarify how the gap intercept method could be better used to quantify rangeland connectivity and to provide examples of how the method can help inform management with respect to a range of ecological processes. Here, we: 1) review the different ways the gap intercept method is conducted; 3) discuss what is known about how gap intercept data can be used to assess wind and water erosion, biological soil crust (biocrust hereafter) abundance and composition, soil fertility, plant community dynamics, wildlife habitat characteristics, and fuel connectivity and fire behavior; 3) highlight considerations when collecting and using gap intercept data; and 4) identify emerging questions regarding using gap intercept data to assess rangeland connectivity, ecosystem function, and ecological processes.

The Gap Intercept Method

The gap intercept method is a transect-based method in which observers record the beginning and ending of gaps between plants (Fig. 1). Following Herrick et al. (2018), the distance along the transect where plant gaps begin and end are recorded, with plants qualifying as bounding a gap if they are within a two-dimensional vertical plane along one edge of the transect tape. Measuring all-plant (i.e., annual and perennial) canopy gap, perennial plant canopy gap, and perennial basal gap are standard variations of the method (Table 1, Herrick et al. 2018). Starting at the beginning of the transect, the observer evaluates if the transect edge is considered a gap or vegetation. The plant parts considered depend on the gap type of interest. For canopy gaps, all above-ground plant parts are considered (i.e., leaves, flowers, fruits, stems, above-ground roots), while for basal gap, only plant bases are considered (Fig. 1). For canopy gap (Fig. 1A), a gap starts when vegetation canopy covers less than fifty percent of the 3-cm moving window along the transect and ends at the beginning of where the plant canopy cover becomes fifty percent or greater of three centimeters. Basal gaps begin and end with any amount of basal cover (Fig. 1B). In most implementations, a gap must be larger than the minimum size (e.g., 20 cm) to be recorded. The gap intercept method may be further refined to measure distances between plant species, plant functional groups (e.g., woody species, shrubs, bunchgrasses;

Table 1
The gap intercept method provides valuable indicators of ecosystem processes and threats to ecosystem processes.

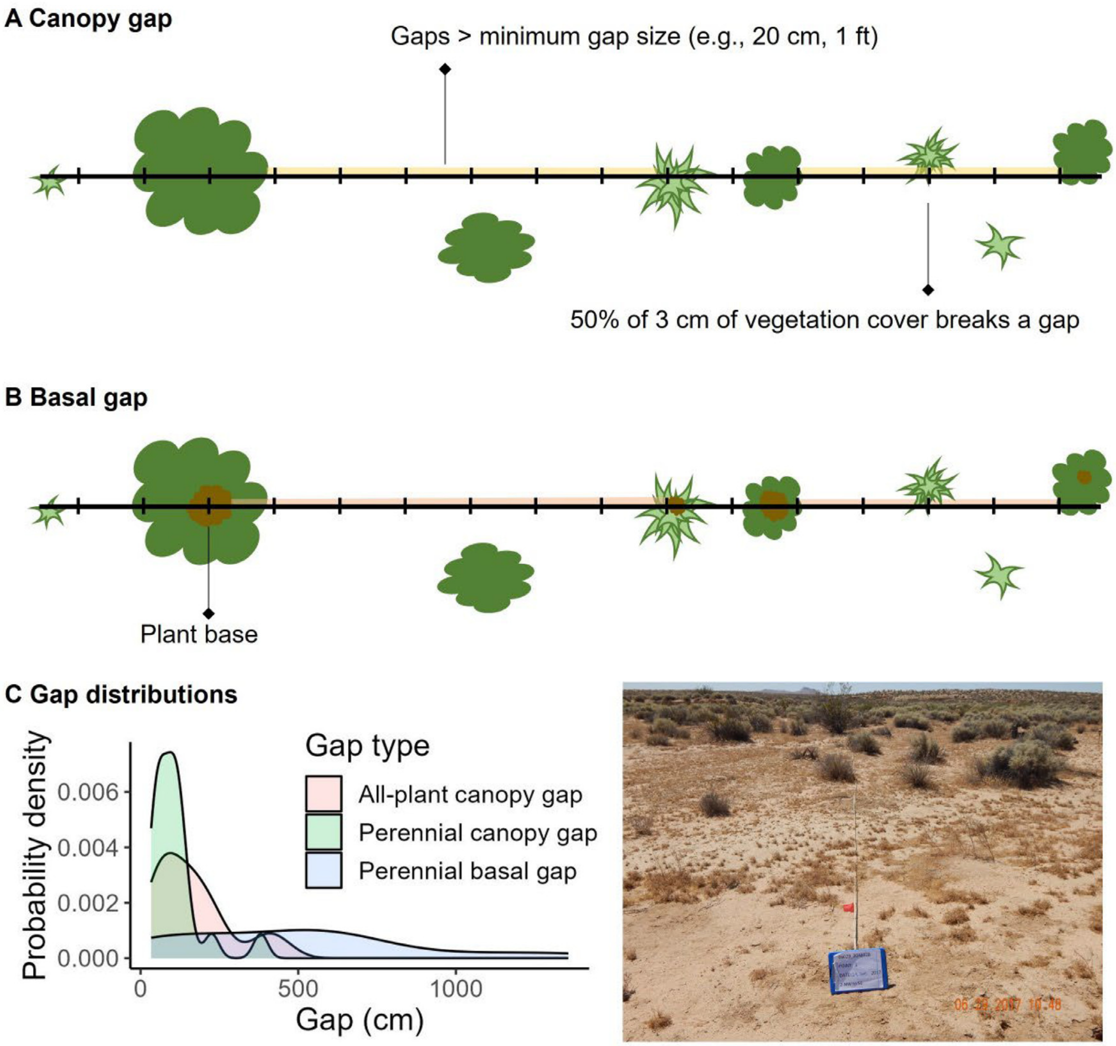
Ecosystem process	Implementations of gap intercept method				
	All-plant canopy gap	Perennial canopy gap	All plant basal gap	Perennial basal gap	Other gap methods
Wind erosion (aerodynamic roughness and sheltering)	Strong relationship (Aubault 2014, Cheng et al. 2023, Webb et al. 2014, Ziegler et al. 2023, Shumack et al. 2022, Merino-Martin et al. 2014). Required for wind erosion models AERO (Edwards et al. 2022), WEMO (Okin, 2008); >20% of plot gaps 1 > m likely to indicate increased risk of wind erosion (Webb et al. 2014).	Weak relationship, especially in mixed annual and perennial systems (Flagg et al. 2014). Some studies use perennial canopy gap as a proxy for drought conditions (Bowker et al. 2012, Munson et al. 2011).	No empirically demonstrated relationship exists (Flagg et al. 2014).	Hypothesis: weak to no relationship.	Hypothesis: erodible gap, which involves removing rocks, biocrusts, litter from gap.
Water erosion (overland flow)	Limited relationship to measured and modeled water erosion (Hernandez et al. 2013, Pierson et al. 2010).	Hypothesis: No relationship.	Variable across sites and studies. Some studies show weaker relationships (Pierson et al. 2010, Williams et al. 2019), while others found strong relationships (Johnson et al. 2021, Polyokov 2020, Hernandez et al. 2013, Fick et al. 2020). Basal gaps > 1 m indicate where concentrated flow processes might be more active (e.g., Williams et al. 2014).	Variable across sites.	Hypothesis: “Ecohydrologic gap” that looks at erodible soil only (Wilcox et al. 2023).
Biocrust development and community composition	Different canopy gap size distributions related to different biocrust communities (Fig. 4).	Standard deviation perennial gap sizes strongly correlated with biocrust composition (Condon and Pyke 2018).	Unknown relationship	Biocrust cover increased in gap interspaces after rainfall events, particularly when grazing was removed (Jimenez Aguilar et al. 2009). Perennial basal gaps composed of biocrusts have a protective effect against water erosion (Fick et al. 2020) and exotic annual grasses (Reisner et al. 2013).	Unknown relationship
Soil Fertility (Nutrient availability (N-Nitrogen) and soil organic carbon (SOC) content)	Hypothesis: Relationship similar to perennial canopy gap. Relationship likely diminishes with smaller all-plant canopy gap size (Chen et al., 2007).	More nutrients and SOC beneath perennial plant canopy than within canopy gap (Johansen et al., 2001; Kushwaha et al., 2021; Schlesinger and Pilmanis, 1998).	Hypothesis: Relationship similar to perennial basal gap. Relationship likely diminishes with smaller basal gap sizes.	Decreases in N and SOC as distance increases from plant stem to drip line (Throop and Archer, 2008; Throop and Lajtha, 2018).	Reduced nutrient and SOC levels in inter-canopy gaps when there is a gap in biocrust (Belnap, 2003b; Young et al., 2022).

(*continued on next page*)

Table 1 (*continued*)

Ecosystem process	Implementations of gap intercept method				
	All-plant canopy gap	Perennial canopy gap	All plant basal gap	Perennial basal gap	Other gap methods
Plant community composition (realized and potential niche space)	Hypothesis: Relationship when interpreted with plant composition data (e.g., cover).	Standard deviation of perennial gap sizes was strongly correlated with cover of annual brome (Condon and Pyke 2018).	Hypothesis: Relationship when interpreted with plant composition data (e.g., cover).	Strong positive effect on the magnitude of invasion; large basal gaps characterized by bare soil have strong positive association with *Bromus tectorum* cover (Reisner et al. 2013, Germino et al. 2019). Perennial basal gap > 200 cm >50%–at risk or transitioned to invaded state (Reisner et al. 2013); Perennial basal gap > 200 cm > 25% –strong threshold of invasion post-fire (Germino et al. unpublished).	Unknown relationship.
Wildlife habitat characteristics (habitat structure for nesting, foraging, sheltering, and moving; “Fearscapes”)	Relationship to songbird diversity (Williams et al. 2011a, 2011b, Salas and Desmond), Greater Sage-Grouse nesting habitat (Zabihi et al. 2017, 2019), pollinator habitat (Begosh et al. 2022). Proposed as an indicator of desert tortoise habitat (Farwell and Wallace 2021).	Unknown relationship	Indicator of songbird habitat (Salas and Desmond, Williams et al. 2011a, 2011b), Lepidoptera caterpillars were negatively associated with basal gaps (Ersch 2009). Sage sparrows (*Artemisiospiza nevadensis*) were strongly associated with Wyoming big sagebrush and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) communities with basal gaps > 200 cm (Williams et al. 2011).	Unknown relationship	Gaps between shrubs/woody species an important indicator of songbird diversity (Williams et al. 2011a), prairie dog habitat (Connell et al. 2018); sage-grouse nesting sites (Sink 2023).
Fuels and fire behavior (fuel connectivity; wind momentum and forward rate of spread)	Hypothesis: Increased canopy continuity facilitates fire spread,. Gaps create heterogeneity in fire behavior and effects.	Hypothesis: Weak relationship when annuals are prominent; perennial dominated systems similar to all-plant canopy gap.	Hypothesis: Increased basal continuity facilitates fire spread. Gaps create heterogeneity in fire behavior and effects.	Hypothesis: Weak relationship when annuals are prominent; perennial dominated systems similar to all plant basal gap.	Unknown relationship

The degree of understanding regarding the relationship between ecosystem processes and different implementations of the gap intercept method varies by process and method. In some cases where we did not find a published relationship, we pose a potential hypothesis based on ecological processes.



D Gap indicators

	Mean gap (cm)	Gap st. dev (cm)	Gap > 25-50 cm (%)	Gap > 50-100 cm (%)	Gap > 100-200 cm (%)	Gap > 200 cm (%)
All-plant canopy gap	109.0	78.5	1.9	5.9	9.5	6.6
Perennial canopy gap	473.4	371.9	4.7	13.5	26.9	115.6
Perennial basal gap	164.9	118.8	2.3	5.0	16.0	30.8

Figure 1. The most common variations of the gap intercept method characterize gaps between plant canopy (A) or plant bases (B). Gaps (highlighted) are recorded along the transects (tic marks represent 5 cm) where there are breaks between focal vegetation (e.g., canopy or basal plants) and are typically only recorded if greater than a minimum threshold (e.g., 20 cm). The distribution of gaps measured at a plot may differ by gap type (C). Gap distributions may be summarized as mean or standard deviation of gaps, or as the percent of the plot covered by gaps of different sizes (D).

Miller et al., 2007; Williams et al., 2011; Schantz et al., 2017), or other plant features (e.g., litter, woody debris; Ross et al., 2012). It is crucial to know what type of gap was measured in a study, as changes in one gap type may not always be reflected in another, and those changes may influence ecosystem processes differently.

Indicators derived from gap measurements are produced by estimating one or more aspects of the distribution of gap sizes (Figs. 1C and D). In addition to the frequency distribution of gap sizes, these indicators may include mean gap size, standard deviation of gap sizes, gap classes with a set of break points (e.g., 25–50 cm, 51–100 cm, 101–200 cm, > 200 cm width), or percent of a plot with gaps greater than certain size classes (e.g., > 50 cm, > 100 cm). Benchmarks for gap intercept data used by land managers are typically focused on gaps of a certain size. For example, Brewer's sparrows (*Spizella breweri*) generally favor habitats with basal gaps > 100 cm (Williams et al., 2011) and perennial basal gaps > 60 cm have been associated with increased risk of invasion by exotic annual grasses (EAGs) in sagebrush steppe (Reisner et al., 2013; Rau et al., 2014; Germino et al., 2019). Other gap intercept benchmarks may be further refined by describing the proportion of a plot with gaps of a certain size before a functional ecosystem response occurs (Webb et al., 2024), such as when 20% or more of a plot has all-plant canopy gaps > 100 cm, this could indicate increased risk of wind erosion in grassland and shrub-invaded grasslands of the Chihuahuan Desert (Webb et al., 2014).

Gap Intercept Describes Important Ecological Processes and Ecosystem Services

The gap intercept method provides information about structural connectivity that is related to functional responses in important rangeland ecological processes and ecosystem services (Table 1), including wind erosion, water erosion, biological soil crust community dynamics, nutrient availability, plant community dynamics, wildlife habitat characteristics, and fuel connectivity and fire behavior.

Wind erosion

Wind erosion processes both respond to changes in soil surface and plant connectivity and promote connectivity change through positive feedback mechanisms (Okin et al., 2006). The influence of connectivity on wind erosion manifests through the effects of vegetation and other non-erodible roughness (e.g., rocks, embedded litter, biocrusts) that: 1) physically cover the soil surface, thereby reducing the area of exposed soil that could be entrained by the wind; 2) aerodynamically shelter the soil surface by creating drag and reducing the wind shear stress (erosivity) over the land and at the soil surface (i.e., drag partitioning); and 3) intercept and trap sediment that has been entrained by the wind (Wolfe and Nickling, 1993; Webb et al., 2021). Together, vegetation and other non-erodible roughness elements reduce wind erosion risk and the mass flux of sediment moving across a landscape (Raupach et al., 1993). The height of vegetation and connectivity of bare ground between plants have been shown to have an order-of-magnitude effect on aeolian sediment mass fluxes (Webb et al., 2014). Smaller vegetation height and greater bare ground connectivity enable more rapid recovery of wind erosivity behind plants, larger wind erosivity at the soil surface that can entrain soil particles, and larger fluxes of sediment across the landscape (Bradley and Mulhearn, 1983). When aeolian sediment transport occurs, it selectively removes and redistributes nutrients and carbon – potentially reducing site productivity (Webb et al., 2013; Chappell et al., 2019), abrading biocrusts, and scouring soil surfaces. These initial impacts reduce surface resistance to erosion, creating conditions that are not conducive to seed germination and establishment (Belnap, 2003a). Furthermore, saltating soil grains abrade plant stems and leaves and soil loss exposes roots – increasing plant mortality (Niu et al., 2023). Quantifying connectivity is, therefore, important for monitoring wind erosion risk and identifying functional thresholds for wind erosion that managers may seek to avoid.

Various indicators of vegetation structure and surface aerodynamic roughness have been used to model wind erosion, including lateral cover, aerodynamic roughness length, fractional vegetation cover, and bare soil cover (Raupach, 1992; Raupach et al., 1993; Marticorena and Bergametti, 1995). However, because of the sensitivity of wind erosion to bare ground connectivity, integration of canopy gap intercept data with vegetation height in a “scaled gap” indicator representing canopy gap sizes divided by the height of vegetation breaking canopy gaps, or by the average canopy height, has transformed the accuracy of wind erosion models (Okin, 2008; Li et al., 2013; Edwards et al., 2022). Figure 2 shows the relationship among vegetation height, canopy gap size, surface wind shear velocity (u_{s*}, m s^{-1}) and the horizontal aeolian sediment mass flux (Q, kg m^{-1} s^{-1}) as described by the Okin (2008) drag partitioning scheme. The interactive effects of vegetation height and canopy gap size mean that, for a given spacing between plants (gap size), taller vegetation will create more drag and more effectively reduce the wind shear velocity and sediment mass flux than shorter vegetation. Wind shear velocity is lowest in the immediate lee of vegetation but increases exponentially further downwind until fully recovering at a distance around 10 to 20 times the height of the vegetation. Understanding the gap size distribution of plant canopies is needed to assess wind erosion because drag and shear stress partitioning interactions occur between the wind, plant canopies and the soil surface. Similarly, describing gaps between both annual and perennial vegetation is critical because all types of vegetation attenuate wind erosion. As the measurements represent a single point in time, it critical to accurately represent vegetation structure and bare ground connectivity accurately at that time.

The availability of all-plant canopy gap intercept and vegetation height data has enabled new applications of wind erosion models to standardized monitoring datasets (Munson et al., 2011; Webb et al., 2014a; Edwards et al., 2022). Such applications have supported assessment of wind erosion risk alongside other indicators of ecosystem structure and function, as well as incorporation of wind erosion assessment into land health assessments and use planning (Kachergis et al., 2020). However, there remain opportunities to further develop the utility of canopy gap intercept data for wind erosion monitoring, modeling, and assessment. For example, observed increases in wind erosivity around plant canopies are yet to be represented in wind erosion models and, for the Okin (2008) drag partition scheme, will depend on connectivity and could utilize canopy gap intercept data. Representing this effect should improve wind erosion model performance where wind speeds are close to the sediment entrainment threshold and can produce dust haze that degrades air quality. Regional wind erosion assessments and forecasting could benefit from spatial predictions of canopy gap sizes using satellite remote sensing, like those produced by Zhang et al. (2019) and Zhou et al. (2020). Further research could improve the accuracy and gap size class resolution of these products to benefit regional models.

Water erosion

Water erosion and hillslope hydrologic vulnerability in rangelands and woodlands are largely controlled by the magnitude and duration of water input, the amount and connectivity of vegetation and ground cover, surface conditions, soil properties, and topography (Pierson et al., 2011; Williams et al., 2014). Water input greater than soil infiltrability accumulates in sparsely vegetated and bare patches and provides a source for downslope runoff. On sloping terrain, runoff sources throughout well-connected sparsely vegetated and bare patches accumulate into high-velocity concentrated overland flow. These flowpaths are the primary mechanism for downslope movement of rainsplash- and flow-detached sediment (Pierson et al., 2009; Wainwright et al., 2011; Williams et al., 2014; Nouwakpo et al., 2016). On some sites, prolonged soil loss associated with combined rainsplash, sheetflow, and concentrated overland flow processes through well-connected sparsely-vegetated and bare patches results in an ecological state transition or irreversible ecological trajectory (Chartier and Rostagno, 2006; Turnbull et al., 2012; Williams et al., 2014). Vegetated- and litter- covered patches on well-vegetated hillslopes dissipate erosive energy of rainfall and overland flow, effectively capture water by interception, and facilitate infiltration by enhancing soil structure and macropores. Overall, the likelihood of event runoff concentration along hillslopes is a function of the runoff amount, the amount of bare soil, and slope steepness (Al-Hamdan et al., 2013). Collectively, these components represent the ecohydrologic connectivity of runoff and sediment sources (Williams et al., 2016; Keesstra et al., 2018; Wilcox et al., 2022), which is dynamic with the rate and magnitude of precipitation and water input (Wilcox, 1994; Williams et al., 2014). These fundamental relationships have been used to characterize rangeland and woodland ecohydrologic responses to disturbances such as drought, excessive grazing, woody plant encroachment, and wildfire.

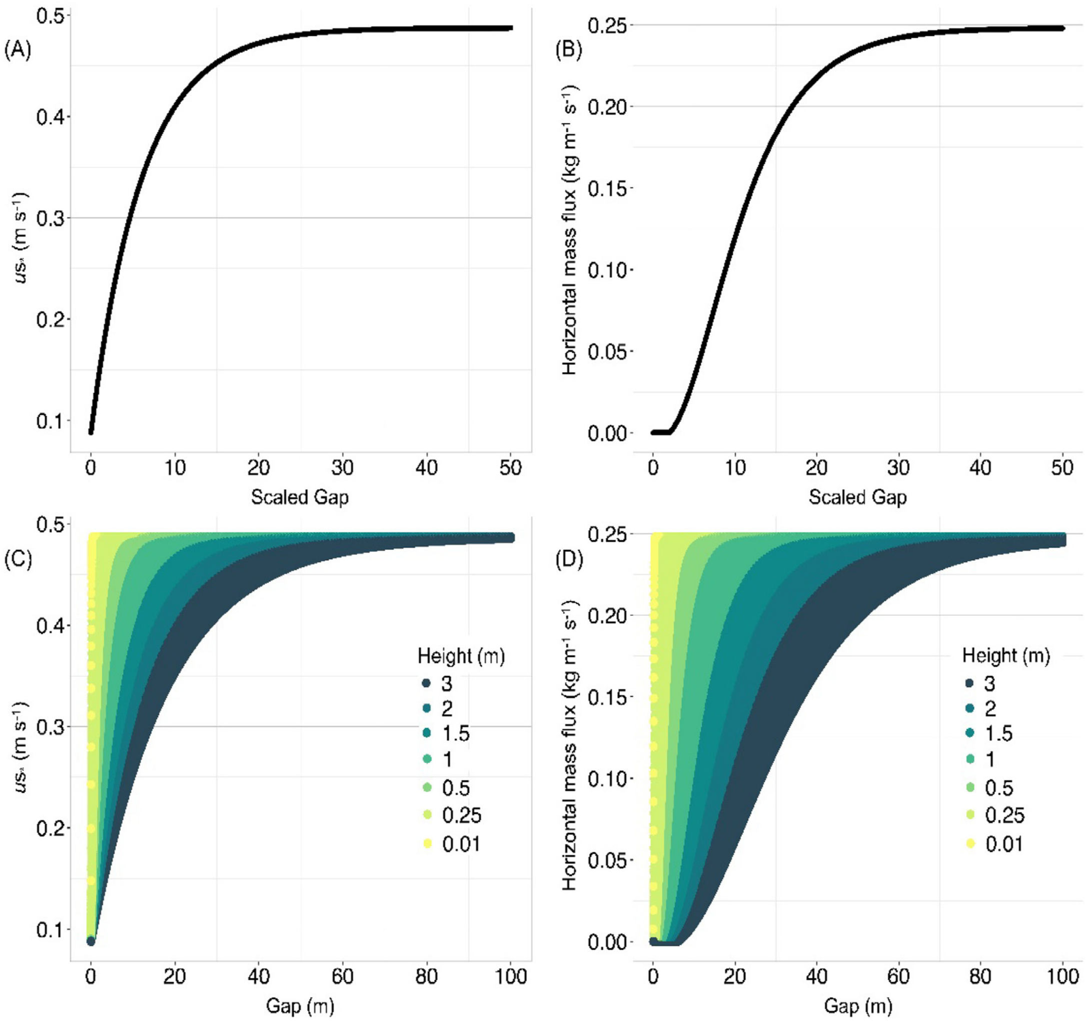


Figure 2. The simulated relationship between scaled gap (gap/height) and wind shear velocity (A) or horizontal mass flux (B), and gap and wind shear velocity (C) or horizontal mass flux (D). Responses in (C) and (D) are dependent on height (m; indicated by color). All estimates are calculated following Edwards et al. (2022) using Q2 parameter values. Shear velocity was calculated for 11 ms^{-1} wind speeds at 2.5 m height, with a set shear stress ratio of 0.18. Horizontal mass flux was estimated for points using 50% bare soil cover, representing the cover of loose erodible sediment.

Although numerous studies suggest that bare ground cover greater than 50-60% increases hillslope runoff and water-driven erosion (Figure 3; Gifford, 1985; Johansen et al., 2001; Pierson et al., 2008, 2009, 2010, 2013; Williams et al., 2014; Vega et al., 2020), few studies to date have examined the effectiveness of canopy and basal gap connectivity indicators as predictors of runoff and erosion potential. Hernandez et al. (2013) found larger basal gaps and greater predicted water erosion rates using the Rangeland Hydrology Erosion Model (Hernandez et al., 2017) in shrub and annual grass/forb communities relative to bunchgrass communities in southeastern Arizona, but the differences were significant at $P < 0.05$ for only a subset of ecological sites in their study area. Other studies have also found a correlation between bare ground and/or basal and canopy gaps with runoff and erosion rates (Pierson et al., 2010, 2013, 2015; Williams et al., 2014; Williams et al., 2020, 2022; Johnson et al., 2021). However, bare soil and rock cover alone was the strongest predictor of runoff and sediment yield responses to applied rainfall events in most of these studies (Pierson et al., 2010, 2013, 2015; Williams et al., 2020, 2022; Williams et al., 2014).

The weak observed relationship between canopy and basal gap indicators and measured runoff and erosion rates may be attributable to differences in methodologies (Pierson et al., 2010). Gap data are frequently collected without regard to surface attributes within the gaps. For example, a litter-covered soil surface within canopy and basal gaps is well protected from rainsplash effects and buffers runoff generation and soil detachment by overland flow (Pierson et al., 2010, 2014). In contrast, exposed bare and highly erodible soil within canopy and basal gaps is prone to runoff and soil erosion by rainsplash, sheetflow, and overland flow processes (Blackburn, 1975; Reid et al., 1999; Wainwright et al., 2000; Turnbull et al., 2010; Williams et al., 2014). Rock cover is also an important predictor of water erosion, but the effect varies by ecosystem. In general, rocks lying on the surface facilitate infiltration and dissipate erosive energy of rainfall and overland flow whereas rocks embedded in the soil surface can promote runoff generation and facilitate erosion (Poesen et al., 1990). However, desert pavements, such as those commonly found on southwestern US rangelands, can dissipate the erosive energy of overland flow and limit further soil erosion (Abrahams and Parsons, 1991; Hernandez et al., 2013). Therefore, neither basal nor canopy gaps may effectively represent hydrologic and erosion conditions across rangeland ecosystems. For example, dense forb cover, common in the first-year post-fire may result in limited canopy gaps, but the soil surface underneath the dense canopy may remain largely bare and susceptible to runoff and soil detachment until both litter depth and spatial continuity re-establish over time

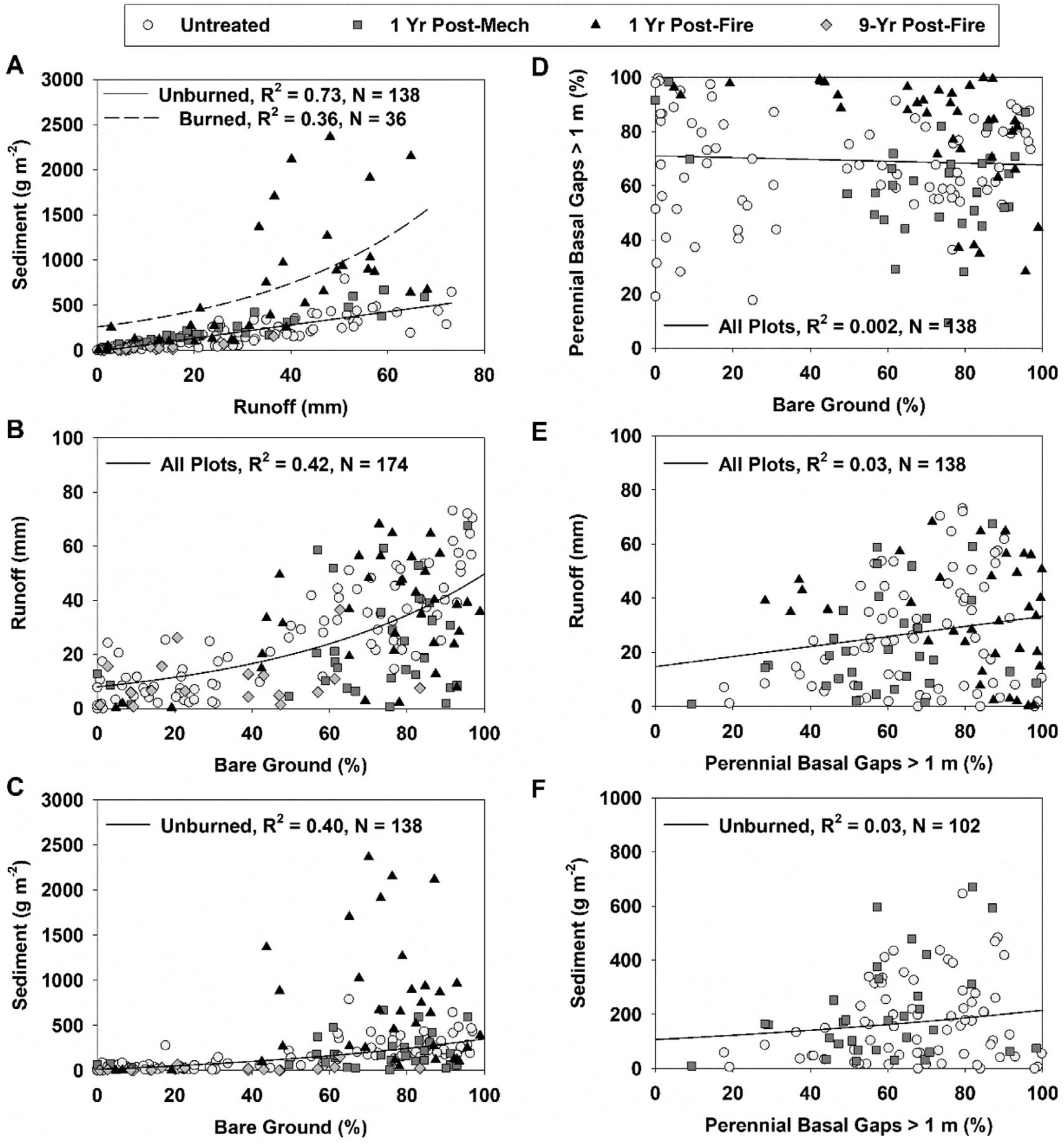


Figure 3. Cumulative sediment vs. cumulative runoff (A), cumulative runoff vs. bare ground (bare soil and rock cover) (B), cumulative sediment vs. bare ground (C), percent of plot with perennial basal gaps $>$ 1 m vs. percent bare ground (D), cumulative runoff vs. percent of plot with perennial basal gaps $>$ 1 m (E), and cumulative sediment vs. percent of plot with perennial basal gaps $>$ 1 m (F) for rainfall simulation (102 mm h^{-1}, 45 min duration) experimental plots (12 to 13 m^2) at multiple pinyon (*Pinus* spp.) and juniper (*Juniperus* spp.) encroached sagebrush (*Artemisia* spp.) sites in the Great Basin, USA. Untreated refers to all plots not receiving tree removal treatments. 1 Yr Post-Mech and 1 Yr Post-Fire respectively refer to plots in which trees were removed by cutting/shredding or by burning 1 year prior to sampling. 9 Yr Post-Fire refers to plots in which trees were removed by burning 9 years prior to sampling. Regression line notations for Unburned refers to all plots except those burned 1 year prior to sampling and for Burned refers to plots burned 1 year prior to sampling. Data from Pierson et al. (2010, 2013, 2015), Nouwakpo et al. (2020), and Williams et al. (2014a, 2019, and 2020b).

(Pierson and Williams 2016). Under such conditions, basal gaps may better reflect ground cover conditions (surrogate for basal cover), but likely do not adequately characterize persistent bare soil availability and erosion potential (that can persist more than three years post-fire; Pierson et al., 2008).

Establishing new indicators to quantify canopy and basal gaps that also incorporate surface conditions may more effectively quantify hydrologic and soil erosion risks on rangeland and woodlands (Pierson et al., 2010). We could explore new indicators that relate canopy and basal gaps to bare ground or conditions highly susceptible to runoff and soil cover and other ground attributes collected from the line-point intercept method. This could be an important advancement for quantifying hydrologic vulnerability and erosion potential on degraded hillslopes (Williams et al. 2022) with implications for rangeland health protocols (Pellant et al., 2020), ecological site descriptions (Williams et al., 2016), and the Rangeland Hydrology and Erosion Model (Hernandez et al., 2017).

Biological soil crust dynamics

Soil surfaces in rangelands and open woodlands are often colonized by microbial communities forming biological soil crusts (biocrusts; Jimenez Aguilar et al., 2009). Biocrusts are living soil surface aggregates harboring diverse communities of microorganisms, lichens, and bryophytes that can cover up to 85% of the ground surface (Pietrasiak et al., 2013; Weber et al., 2016; Hansen et al., 2023). Biocrust formation, structure, community composition, and activity are sensitive to changes in climate, soils, and land use and therefore can be influenced by alteration of ecosystem properties such as structural and functional connectivity (Bowker et al., 2016; Stovall et al., 2022). For example, an increase in gap sizes between perennial plants could open colonization space for photosynthetic biocrust organisms that cannot compete well with vascular plants for light. However, plant canopies can also function as biocrust refuges, such as in actively grazed land where interspace crusts are exposed to mechanical disturbance impacts such as livestock trampling (Jimenez Aguilar et al., 2009; Reisner et al., 2013; Garcia et al., 2015; Condon and Pyke, 2018, 2018b). In hyper-arid systems, mosses, green algae, and chlorolichens may be less likely to be found in plant canopy gaps than underneath plant canopies where microclimate and nutrient concentrations are more favorable for the development of these organismal groups. In contrast, dense canopy structures with high litter loads can limit light availability and soil exposure underneath the canopy and restrict biocrust establishment and growth (Ding and Eldridge, 2020, 2021).

In turn, biocrusts themselves have impacts on structural and functional connectivity. The degree of structural connectivity of biocrust-filled gaps can influence functional connectivity processes, such as soil stability, water retention and runoff, carbon sequestration, and nutrient cycling (Eldridge et al., 2020; Fick et al., 2020). Biocrusts reduce wind and water erosive forces and protect the soil surface due to external features that generate microtopography (Williams et al., 2012) and internal features such as presence of filamentous microbes that bind soil particles, form bio-aggregates, improve tensile strengths and aggregate stability (Fick et al., 2020). In some instances, highly connected lichen-dominated biocrusts can increase water runoff, whereas highly connected cyanobacterial dominated biocrusts can increase filtration (Chamizo et al., 2016). Depending on biocrust external surface microtopography, they are also capable of trapping substantial amounts of dust (Williams et al., 2012). Dust inputs and biomass enhance soil resources in plant interspaces which has feedbacks to increased soil nutrient content, cycling, and water retention in a thin but fertile soil layer (Pietrasiak et al., 2013). Biocrusts therefore contribute to a variety of key ecosystem functions and represent essential ecosystem components, especially where plant cover is reduced (Fick et al., 2020).

Although direct and indirect relationships between biocrust and ecosystem connectivity are apparent, only a few studies have linked structural connectivity indicators such as gap intercept to biocrust characteristics and function in the Great Basin (Condon and Pyke, 2018; Reisner et al., 2013), Colorado Plateau (Fick et al., 2020), and Chihuahuan Desert (Schaefer unpublished data). Biocrust community composition has been found to be correlated to basal gap, perennial-gap, and all-plant canopy gap size, although this relationship varies by ecological site and state (Fig. 4; Reisner et al., 2013; Condon and Pyke, 2018; Fick et al., 2020). In general, more complex biocrust communities, such as dark cyanobacteria and lichens, most strongly correlated with relatively smaller gap size classes or less variability in gap size (Fig. 4, Condon and Pyke, 2018b). However, some ecological sites with large gaps can support well-developed complex biocrusts (Fig. 4B). This difference in composition throughout states may lead to a difference in ecosystem services provided by biocrust, such as water retention or nutrient cycling (Eldridge et al., 2020; Young et al., 2022). Also, locations with less variability in gap sizes and high biocrust cover may be more resilient to disturbances such as EAG invasion (Reisner et al., 2013; Condon and Pyke, 2018), whereas locations with extra-large gap sizes, or greater variability in gap sizes, will be more susceptible to biocrust loss due to disturbances such as livestock grazing and invasion (Reiner et al. 2013, Condon and Pyke 2018b, Duniway et al. 2018, Fick et al. 2020). However, the degree of vulnerability, resistance, and resilience of biocrust in large gaps can be influenced by climate, soil types, landscape position, as well as biocrust community composition and morphological complexity (Jimenez Aguilar et al. 2009, Stovall et al. 2022, Fig. 4). More work could help to understand how the variability in climate, parent material, soil types, and disturbances influences the relationship between plant canopy and biocrust structural and functional connectivity. Such work includes determining functional thresholds that induce biocrust community changes, which could enable predictions of biocrust-mediated ecosystem services across ecological sites and in response to ecological state change.

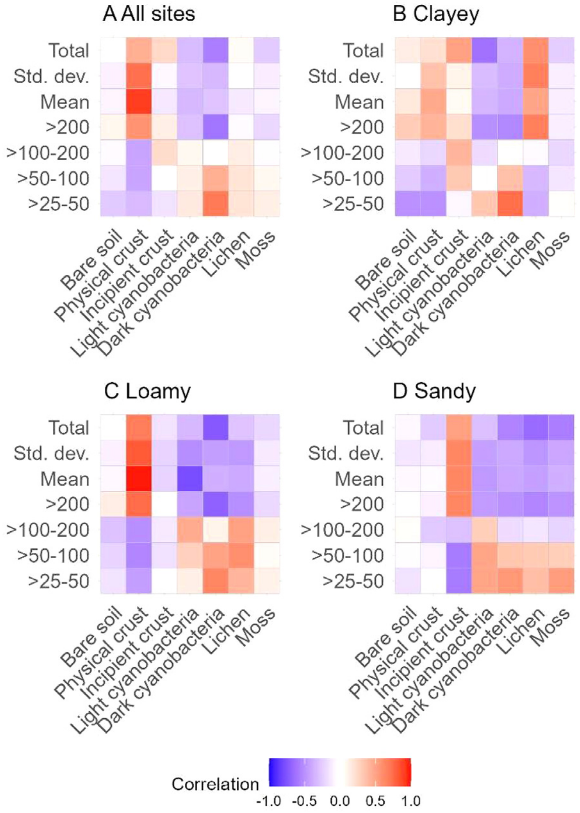


Figure 4. Biocrust and soil cover composition at 63 plots in the Chihuahuan Desert correlated to all-plant canopy gap indicators across all sites (A), and for Clayey (B), Loamy (C), and Sandy (D) ecological sites.

Soil fertility

Soil fertility is heterogeneous within and among rangeland types (e.g., grasslands, shrublands). Soil organic carbon (SOC) and nutrient values are often higher in soils beneath plant canopies than in soils within canopy gaps, a phenomenon known as the fertile island effect (Schlesinger and Pilmanis, 1998). Plant canopies typically create cooler, wetter, and less wind-exposed soil environments, while also passively collecting nutrients in dust and from surface water runoff (Schlesinger and Pilmanis, 1998; Gonzales et al., 2018). These conditions favor the accumulation of plant litter and microbial activity that contributes to the retention of SOC, nitrogen (N), and phosphorus (P) within soils beneath plant canopies. For example, a meta-analysis showed that soil organic matter, microbial biomass N, and N mineralization can be over 40% greater underneath plant canopies than in canopy gaps (de Graaff et al., 2014). Relatedly, canopy soils can have significantly higher microbial richness, more genetic and functional capacity for microbial N-mineralization, and larger amounts of litter accumulation (Throop and Archer, 2007; Kushwaha et al., 2021). Litter decomposition rates can be higher in canopy gaps than beneath plant canopies due to factors such as higher temperatures, greater UV exposure, and higher rates of soil-litter mixing (Throop and Archer, 2009; de Graaff et al., 2014). However, unlike in mesic systems, higher decomposition rates do not typically result in greater fertility in canopy gap soils due to limited downward movement into the soil (Throop and Belnap, 2019).

The degree of difference in soil fertility between plant canopies and canopy gaps is mainly determined by ecological site characteristics such as aridity, soil texture and pH, and the structure and composition of plant and soil microbial communities (Ochoa-Hueso et al., 2018). A global-study on fertile islands found greater differences in soil fertility between plant canopies and canopy gaps when soils were more alkaline, had more sand content, and when occurring in semiarid climates (Maestre et al., 2021; Ochoa-Hueso et al., 2018). Land uses, such as grazing can reduce soil fertility within the canopy gap and increase differences in soil fertility between the plant canopies and canopy gaps (Allington and Valone, 2012), however these differences collapse when sites are severely overgrazed and overall soil fertility decreases (Cai et al., 2020). As noted earlier, aeolian processes can be an important driver of litter, nutrient, and SOC redistribution from interspaces to beneath plant canopies (Okin et al., 2006). In some cases, the presence of biocrust in canopy gaps can increase soil fertility in the top few centimeters of soil, thereby reducing differences in topsoil ($<$ 5 cm) fertility between plant canopies and canopy gaps (Thompson et al., 2005; Young et al. 2022).

The fertile island effect has been observed across rangeland types; however, available data can lack the spatial and temporal resolution needed to elucidate relationships with indicators derived from the gap intercept method. Many studies, for example, measure total or extractable SOC and N beneath plant canopies and at random or composited locations within canopy gaps at single points in time. This approach hinders an understanding of the fine-scale distribution of SOC and nutrients across landscapes, particularly with regards to the influence of gap size and type (e.g., all-plant canopy, perennial canopy, all basal gaps, etc.) on nutrient and SOC distribution and how those change through time (but see Schlesinger et al., 1996). For example, plant canopy size largely determined the magnitude of the fertile island effect in Australian rangelands (Ding and Eldridge, 2021), an insight which would have been missed without detailed canopy/gap size measurements. In addition to understanding spatial variability at the soil surface, there has been limited exploration of SOC and soil nutrient variability with depth ($>$ 10 cm) beneath plant canopies and within canopy gaps (Rau et al., 2011). Notably, SOC at soil depths $>$ 60 cm was shown to decrease as perennial canopy gap size changed from patterns indicative of a sagebrush steppe to an annual grass system, underscoring the significance of sampling below the topsoil layer (Rau et al., 2011). An improved understanding of spatial and temporal differences in soil fertility between plant canopies and canopy gaps could help managers more accurately predict how land uses and land treatments that restructure vegetation communities may influence soil fertility and land management outcomes (Germino et al., 2018; Arkle et al., 2022).

Plant community dynamics

Vegetation connectivity is a key aspect of many plant-community types and is central to understanding the plant-environment feedbacks that underlie the diversity, resistance, and resilience of plant communities. Gaps among plants impart structural complexity to plant communities, including a greater variety of growth niches in space or time (Muscolo et al., 2014; Coverdale and Davies, 2023). The factors that create and maintain gaps and the effects of gaps on the biotic community tend to vary among plant community types according to their climate, productivity, and stand structure. For example, gaps are created by treefalls in temperate forests and they allow sunlight penetration into light-limited understories (Denslow, 1987). The abundance, size, and shapes of gaps often also change over disturbance-succession cycles, creating the different edaphic conditions described above along with variation in above-ground biophysical properties (Lowman and Wittman, 1996). Canopy gaps cause spatial variation in the penetration or attenuation of thermal radiation, convection, and precipitation through-fall or snow redistribution (and sublimation), in addition to their effects on sunlight penetration. Spatial variation in biotic factors, such as seed deposition and germination or mycorrhizae can also directly affect demographic rates of plant species or populations in relation to the distribution and size of canopy gaps. These factors collectively increase the diversity of niches and therefore plant communities (e.g., Terborgh, 1985), which, in turn, is predicted to generate greater ecosystem stability including resistance to invasion (Levine and D'Antonio, 1999; Loreau and de Mazancourt, 2013).

While the importance of gaps for understanding plant community dynamics is well established in forest ecosystems (Schliemann and Bockheim, 2011; Muscolo et al., 2014), there are relatively few plant community dynamics studies that consider gaps in rangelands. In rangelands, gaps are created as plant communities assemble, sometimes resulting from the formation of surface physical or biological crusts that inhibit germination in gaps and may increase soil resource availability to the benefit of growth of neighboring perennials. An important function of plant communities is their ability to resist invasion or encroachment (hereafter referred to as invasion) and thereby maintain ecosystem stability. The gap intercept method provides both an early warning indicator and a descriptor of the loss of ecosystem services due to changing plant community composition and structure. In rangelands dominated by rhizomatous grasses, invasions by persistent, tall-stature species could lead to increasing of gaps, such as where woody species have invaded and increased bare-soil exposure (Bardgett et al., 2021).Where canopy and basal gaps are large and rock or biocrust cover is minimal, invasion by herbaceous species is more likely (Condon and Pyke, 2018, 2018b; Hoover and Germino, 2012; Reisner et al., 2013). One of the most problematic invasions of this sort are EAGs in the shrub-steppe rangelands of the USA, including cheatgrass (*Bromus tectorum*) in sagebrush steppe and red brome (*Bromus rubens*) in the blackbrush deserts (Brooks et al. 2016). After fire, EAGs readily establish where gaps or fertile islands created by perennial plants occurred before fire (Fig. 5; Germino et al. 2019). Progression of the invasion can lead to complete loss of any canopy-gap structure that existed before fire, and community transformation into temporally unstable but spatially homogenized annual grasslands that are exceedingly resistant to restoration of native perennials (Germino et al. 2016) and prone to reburning (Pilliod et al. 2017).

Measures of native plant connectivity are a dominant predictor of where and when invasion can occur, how invasion will affect ecosystems, and what management strategies can be used to address the invasion (Hoover and Germino, 2012; Reisner et al., 2013; Rau et al., 2014; Condon and Pyke, 2018, 2018b). Gap sizes can be indicative of resource “leakiness” in semiarid rangelands. When bare soil patches become too enlarged due to stresses on vegetation, native or resident perennials use fewer soil resources in the gaps and the gaps become more likely to be invaded by EAGs and woody species. When invasion occurs, the native plant community loses access to critical water and nutrient resources and becomes less resilient to other disturbances such as excess grazing pressure, drought, and wildfire, which in turn can further increase invasion rates. Other disturbances such as fire can also increase the likelihood of invasion by temporarily reducing perennial plants and thereby increasing the prevalence of large bare soil patches.

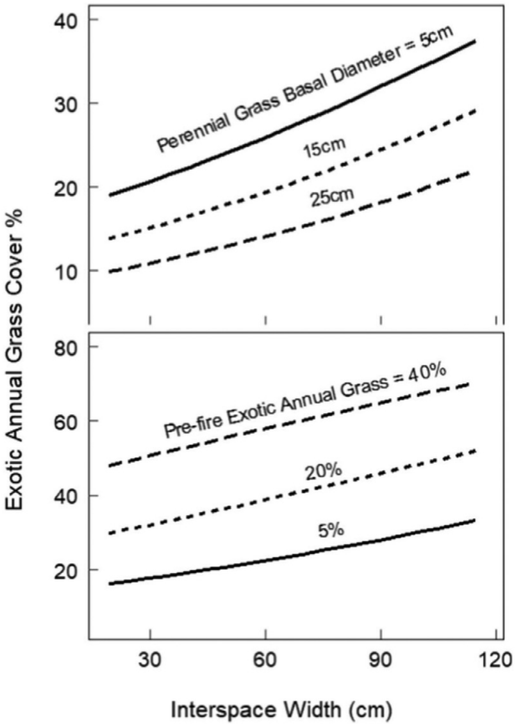


Figure 5. Relationship of exotic annual grass abundance to basal perennial gap sizes ("interspace width") as a function of the size of gap-bounding perennials (basal diameter, top) or pre-fire annual grass abundance (estimated from remotely sensed models) across ~400 plots in the first few years following the 2015 Soda Wildfire (Oregon and Idaho, USA). Annual grasses included *Taeniatherum caput-medusae* and *Bromus tectorum*, with trace amounts of *Ventenata dubia*. Reproduced with permission from Germino et al. 2019.

Further exploration of the relationship between gap intercept and rangeland plant community dynamics is needed, especially across the complex array of climate, weather, edaphic, plant-community state, and management conditions that occur within rangeland types. Models that help identify the extent to which the thresholds in gap-invasion relationships can be generalized or shift with different site or weather conditions will be particularly useful, because the thresholds likely vary and yet are needed by managers to guide management decisions. We still do not fully understand how the relationship of invasion-to-gap sizes varies among vegetation types. Below-ground structure and processes within gaps are not well studied, with few advances beyond the literature meta-analysis of Sankey et al. (2012). Information needs include the spatial pattern, demography and phenology of roots of gap-bounding plants in gap soils, to improve understanding of gap invasibility. While there are many studies examining the relationship of connectivity, gap intercept indicators, and EAG invasion, these studies include different variations of gap metrics, including perennial canopy gap (Condon and Pyke, 2018, 2018b), perennial basal gap (Reisner et al., 2013; Germino et al., 2019), and basal gap (Kachergis et al., 2011; Johnson et al., 2021). Consequently, while we can speak broadly to the relationship between invasion and connectivity, the lack of consistency (and sometimes clarity) in methods used by these studies can cause difficulty for land managers when establishing benchmarks for gap indicators to inform invasive species management. The plant-community canopy is related to many ecosystem processes, and so we encourage future plant community dynamics research studies to explore the use of the all-plant canopy gap method used by many monitoring programs along with cover and composition data from the line-point intercept method to describe invasion dynamics and the impact of invasion (e.g., Fig. 6, Supplement 1).

Wildlife habitat characteristics

Animals need specific resources in the environment to survive, develop, grow, and reproduce, and these resources are often spatially distributed such that individuals need to move periodically to obtain them (Buskirk and Millspaugh, 2006). Hence, animal movement and habitat connectivity are central tenets of wildlife ecology. The structure of vegetation and landforms, combined with distribution of specific soil types and water, largely determine the composition and structure of wildlife habitats and microhabitats and can explain animal use patterns and movements (George and Zack, 2001). Measuring the compositional and structural characteristics of the environment that are important to wildlife and their movements has been a focus of wildlife ecology and management for the last century. The space an animal occupies within a heterogenous matrix of vegetation may have trade-offs between concealment from predators and visibility (Olsoy et al., 2015; Stein et al., 2022). Larger gaps in vegetation may provide increased visibility and decreased concealment. All-plant canopy and basal gaps have been shown to be important habitat indicators for some wildlife species, such as sagebrush-obligate songbirds (Williams et al., 2011; Zabihi et al., 2019) and prairie dogs (Connell et al., 2018). Other studies have shown that canopy and basal gaps may also provide important thermal cover for insects (Ersch, 2009).

Although vegetation cover is often a major part of habitat guidelines for species management plans, widely available gap intercept data (e.g., those available from the BLM Assessment, Inventory, and Monitoring program; AIM) are rarely used when generating these plans or assessing habitat suitability (e.g., greater sage-grouse nesting, Zabihi et al., 2019; and brood-rearing, Ersch 2009). Some studies rely more on wildlife species-specific definitions of gaps, such as gaps between shrubs (Williams, 2010; Williams et al., 2011; Connell et al., 2018; Sink, 2023). However, these specific definitions are not generally interoperable with the way gaps are measured in standard monitoring programs (e.g., the BLM AIM program, the NRCS Natural Resources Inventory; NRI) and therefore may have limited utility for wildlife habitat management. Consideration of how canopy and basal gaps are measured in relation to indicators of wildlife habitat suitability and combining these data with vegetation height measurements may further increase their utility to both managers and researchers for wildlife habitat assessments (Pilliod et al. 2022).

Fuel connectivity and fire behavior

Wildfire behavior is a function of combustible fuels, weather, and topography. Fuel characteristics that influence fire behavior include fuel moisture, amount, size, depth, compactness, and spatial arrangement. The spatial arrangement or connectivity of fuel includes both vertical continuity – where fuels allow fire to spread from the surface to the canopy (ladder fuels), and horizontal continuity – the degree to which surface fuels are connected (Graham et al., 2004; Zouhar et al., 2008; Drury, 2019). Increases in horizontal continuity heighten the probability of ignition and increase rates of fire spread resulting in more homogenous patterns of combustion and larger, more frequent fires. Large, continuous fires, in turn, can be rapidly colonized by early successional invasive grasses, having lasting effects that change an ecosystem's fire regime (Brooks et al. 2004). While few field studies have experimentally manipulated fuel continuity, a modeling exercise suggests that increasing gap size will reduce fire spread; however, other factors, such as fuel patch size, fuel height, ember generation and spotting potential, wind gusts, and topography, will influence the effect of gap size on fire behavior (Finney et al., 2021).

Altered plant community structure is a primary reason for changes in fuel continuity. EAG invasions have contributed to dra-

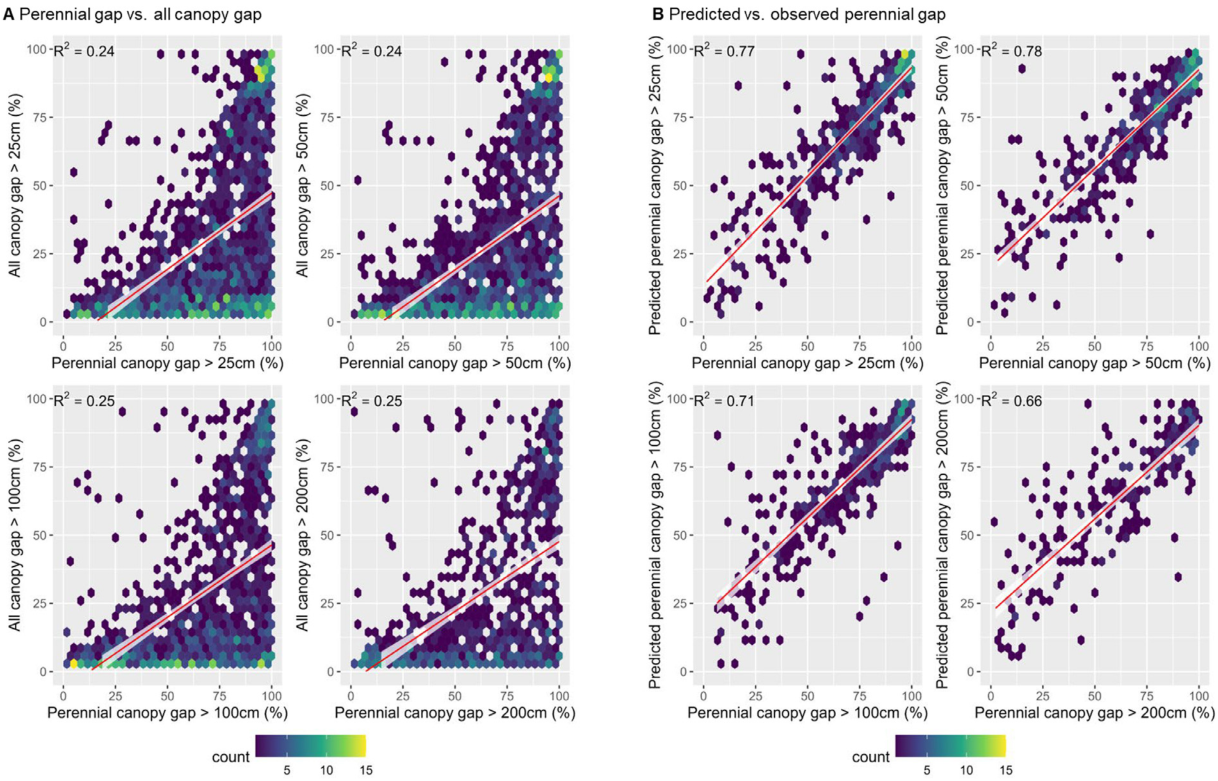


Figure 6. The relationship between all-plant canopy gap and perennial canopy gap using data collected across US rangelands by the BLM AIM and NRCS NRI programs (McCord et al. 2023). All-plant canopy gap and perennial canopy gap are correlated across gap classes (A). Linear models can be used to predict perennial canopy gap classes from all canopy gaps together with plant community data from the line-point intercept method when perennial canopy gap data are needed for analysis and assessment (B). For a description of the linear models developed from a sample, see Supplement 1.

matic increases in the horizontal continuity of fine fuels in the Great Basin and Mojave deserts (Brooks and Zouhar, 2008; Davies and Nafus, 2012). In contrast, woody plant invasion or encroachment may decrease surface fuel continuity by decreasing herbaceous fuels due to low light availability, as well as hydrologic and soil changes, while canopy fuels increase resulting in canopy closure (Zouhar et al., 2008; Archer et al., 2017; Morford et al., 2022). Therefore, although woody plant invasions may reduce surface fire risk by decreasing understory fuel and thus increasing fire return intervals, in turn, woody plant invasions can increase the chances of canopy fire with continuous tree cover (Williams et al., 2023).

There is currently no established method for measuring fuel continuity, but the gap intercept method may address this issue by measuring horizontal continuity. However, using basal and/or canopy gap intercept data in a fuels management context has not been rigorously tested. Although studies report changes in gap size after fuel treatments (Davies et al., 2015;Williams et al., 2019; Pyke et al., 2022), there has been no direct link to altered fire behavior. Additionally, changes in canopy or basal gaps will depend on the type of fuel treatment (herbicide, chaining, lop and scatter, grazing, etc.) (Ross et al., 2012; Gentilcore, 2015; Price et al., 2023).

There are several considerations for using gap intercept data in fuels management. First, many fuels monitoring datasets only include perennial gaps (e.g., SageSTEP; http://sagestep.org). While this may be appropriate for determining risk for annual plant invasion (Reisner et al., 2013; Rau et al., 2014), measurements of gaps between both annual and perennial plants would improve understanding of fuel arrangements at spatial scales that are relevant to wildfire spread. Second, both all-plant canopy and basal gaps should be included since each measurement may be informative about canopy and surface fire spread, respectively. Since fuel treatment types vary on how they remove and/or redistribute fuel (Williams et al. 2023), choosing whether to include annuals/perennials and canopy/basal gaps is a critical consideration. Furthermore, the effects of fuel treatments on gaps will likely vary by plant density and vegetation composition (e.g., shrubland vs. woodland, perennial bunch vs. sod-forming grasses). Effective gap size will be highly variable by fuel type, depending on height, packing ratio, density, fuel chemistry, and fuel moisture, as well as weather and topography.

Although several challenges exist to using gap intercept data in fuels management, there are opportunities to explore its applicability in several ways. First, conducting burn table and field experiments could help us better understand what an effective gap size is to reduce fire spread under various fuel, weather, and topographic conditions. Second, gaps may be a helpful indicator of post-fire burn severity and thus soil susceptibility to wind and water erosion. Finally, gap intercept data may also be used to monitor post-fire recovery of both soils and plants.

Considerations When Collecting and Using Gap Intercept Data

When seeking to apply the gap intercept method to understand rangeland ecosystem processes and services, it is important for project managers, data collectors, analysts, and decision makers to consider steps to both minimize observer error and use gap data appropriately to meet objectives.

Minimize observer errors

Observer error (i.e., uncertainty introduced by observers) can compromise the quality of gap intercept observations but there are strategies to minimize their introduction or impact

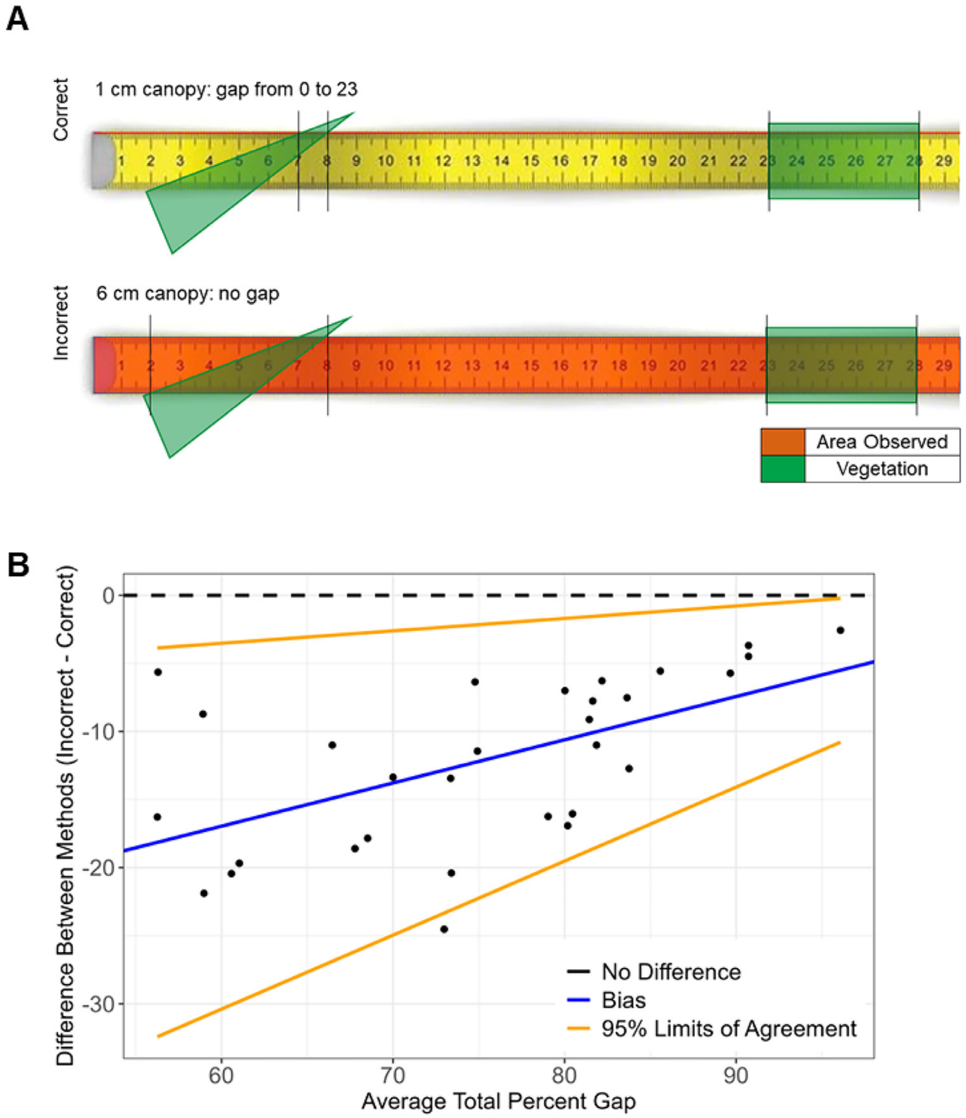


Figure 7. When observers record canopy gap start and stop based on the area under the 1.2 cm (0.5 inch) transect rather than the edge of the transect (A), gap estimates are biased to underestimate total canopy gap (B).

(McCord et al., 2021). Training prior to data collection should encourage observers to know and follow proper protocols; to be aware of common errors, such as parallax; and to take steps to catch and reduce errors through quality assurance and quality control (McCord et al., 2022). Misunderstanding of protocols or project-specific requirements (e.g., minimum gap size, vegetation types to consider) can lead to biased or systematic over- or underestimation of gaps and misrepresent the ecosystem. For example, from observations of 31 field-crew members performing canopy gap intercept in 2022, we found inconsistencies in how gap starts and stops were determined with crew members either correctly considering vegetation intercepting the two-dimensional vertical plane on the outer edge of the transect or incorrectly observing the entire area under the transect tape (a three-dimensional space). This method deviation led to more vegetation being encountered and a reduction in the number of gaps measured (Fig. 7). Emphasis of proper procedure and expert-guided calibration at training could help prevent this error and similar types of error.

Even with well-trained observers, there will still be variability introduced into gap intercept data by observers due to human limitations. Some variability can be reduced by having crew members come to consensus with calibration activities throughout the field season. Variability can also be minimized through smart project design since individuals have limited ability to stay engaged with the same task for extended periods of time (Hopstaken et al., 2015). For example, avoiding protocols with small minimum gap sizes, long transect lengths, or multiple variations of gap (e.g., all-plant canopy, perennial canopy, and basal) on the same transect can help observers stay engaged with the task. Project design should also consider tradeoffs between data availability and data quality, such as the observer's ability to accurately distinguish between different vegetation components (e.g., correctly identifying perennial canopy in a mixed annual-perennial ecosystem).

Use gap data appropriately

Although variations in gap intercept implementation may be related (Fig. 6), they should not be directly compared because variations in gap implementation are describing different ecosystem functions. When considering how the scientific literature describes the relationship between gap intercept and an ecosystem function, it is important to know what type of gap was measured in the research study as mismatched minimum gap length thresholds and whether or not annuals were considered to stop a gap can result in misleading conclusions because changes in one gap type may not always be reflected in another, and those changes may influence ecosystem processes differently.

A key step to avoid inappropriate comparisons is documenting the specific implementation of the gap intercept method used in a study. Simply citing a protocol (e.g., Herrick et al. 2005, 2018) is insufficient as these references generally provide options on how to implement the method. Moreover, the guidance in protocol references may change. The second edition of the *Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems* (Herrick et al., 2018) evolved from the first edition (Herrick et al. 2005) to include perennial canopy gap as an explicit method, so stating that the canopy gap method was used does not clarify if all vegetation or only perennial vegetation stopped a gap. Important metadata to capture alongside gap observations include: which vegetation components stop a gap (canopy vs. basal, all vegetation vs. a subset), number of transects, transect length, minimum gap size, the purpose of the study, and training, calibration, and QA and QC procedures (McCord et al., 2022).

It is important to adequately describe gap methods when reporting results limits the utility of studies to managers and other researchers. For example, Zabihi et al. (2019) demonstrated that the ratio of canopy gap variance to mean square error was an important indicator of sage grouse nest sites. However, the type of gap used was not clear in the methods therefore the extent to which this indicator could be applied to existing monitoring data is unclear and could lead to potentially inaccurate conclusions. Other studies do not clearly define gap methods (Rau et al., 2014; Fick et al., 2020; Heller et al., 2022), which in addition to constraining the contribution of these studies, may unintentionally propagate error to future studies.

Emerging Opportunities for Measuring and Interpreting Rangeland Connectivity

The applications of the gap intercept method discussed here represent a significant advance in understanding rangeland connectivity. There is an ongoing need to evaluate the relationships between gap intercept and ecological processes (Table 1). The rangeland community has several emerging opportunities to further improve our understanding of the causes and consequences of shifts in connectivity. Specifically, opportunities may include:

Reconsider use of the perennial gap intercept method

All-plant canopy gap has been used to represent wind erosion, water erosion, biocrust community composition, and wildlife habitat (e.g., (Okin, 2008; Pierson et al., 2010; Toledo et al., 2010; Williams et al., 2011; Begosh et al., 2020; Fick et al., 2020; Omari et al., 2022). All-plant canopy gap is also the default method for large monitoring programs such as the Bureau of Land Management's Assessment, Inventory, and Monitoring program (Toevs et al., 2011; Kachergis et al., 2022). Basal gap, particularly perennial basal gap, provides insights into plant community shifts due to invasive species, wildlife habitat, and water erosion (Hernandez et al., 2013; Reisner et al., 2013; Rau et al., 2014; Pyke et al., 2022). However, the perennial canopy gap method is used less frequently to understand fewer ecosystem processes. Both Munson et al. (2011) and Flagg et al. (2014) found a relationship between perennial canopy gap and wind erosion, arguing that perennial canopy gap represents resistance to erosion during drought conditions when annuals may not be present. In contrast, the application of perennial canopy gap for wind erosion is not recommended where the goal is to represent conditions at the site at the time of data collection. Furthermore, perennial plant responses to drought and even interannual phenology shifts can impact gap distributions and therefore wind erosion potential (Ziegler et al., 2023). Assuming that annual plants are not present in spring, but also that other types of cover (perennial grasses and shrubs) and their height would not change, would introduce potentially large errors and inconsistencies into erosion assessments. Interpreting all-plant canopy gap data together with species composition data from the line-point intercept method may provide the needed insights to ecosystem dynamics during drought that perennial canopy gap currently captures.

Although perennial canopy gap correlates to important ecosystem functions (e.g., resistance to invasion), we find all-plant canopy gap to be a broadly applicable measure of ecosystem conditions that is less susceptible to observer error. Examination of gap intercept data collected across all rangeland ecosystems in the US shows that a linear relationship can be established between all-canopy gap and perennial canopy gap in combination with vegetation composition data from the line-point intercept method (Fig. 6, Supplement 1). Collecting perennial canopy gap in lieu of all-plant canopy gap may also under-represent other ecosystem attributes including fuel connectivity (Table 1). To limit observer fatigue, we recommend against collecting multiple variations of the gap intercept method if possible. However, if required for management objectives, collecting both all-plant canopy gap and perennial basal gap may be the most efficient data collection strategy as those represent the most distinct types of information with respect to connectivity-driven processes. Rangeland scientists and managers could consider selecting standardized monitoring methods that address multiple ecosystem processes (Toevs et al., 2011) as well as new approaches to analyzing gap data that are ecologically relevant. In doing so, users can leverage the large all-plant canopy gap data that currently exist through the BLM AIM and NRCS NRI monitoring programs.

Consider new opportunities for collecting and interpreting connectivity indicators

This synthesis establishes the breadth of what is known about how to collect and interpret gap intercept data. However, there are opportunities to improve upon this understanding to better describe rangeland ecosystems by developing new techniques for collecting and calculating rangeland connectivity indicators. Remote sensing data collection technologies such as structure-from-motion and LiDAR could allow rangeland scientists to go beyond one-dimensional (1D) gaps on a transect into the area (2D) or volume (3D) of canopy gaps to produce a continuous structural map of the landscape. All-canopy gap is more easily distinguished using remote sensing imagery than perennial-canopy or basal gap. Prioritizing collection of all-canopy gap could accelerate the transition from field- to remote-sensing-based monitoring. These technologies offer the opportunity to characterize additional connectivity metrics such as structural diversity, landscape heterogeneity, patch structure, and arrangement of rangeland vegetation at resolutions fine enough to capture basal and canopy gaps across broad spatial areas (Armston et al., 2013; Olsoy et al., 2015, 2018; Zabihi et al., 2019; Ilangakoon et al., 2021; Zhang et al., 2021).

For both field and remotely-sensed gap observations, synthetic indicators, using data from multiple monitoring methods, may prove to be informative for many processes. Ground cover and vegetation composition data from the line-point intercept method can help to interpret gap results. Understanding if gaps are mainly composed of bare soil or other functional bare ground elements that protect from soil erosion (i.e., biocrust, rock, litter) can be helpful for interpreting the risk of ecosystem service loss due to bare ground connectivity. Vegetation cover and composition can describe the plant community breaking the gaps, which can be useful for understanding water erosion risk, invasion risk and stage, biocrust communities, and nutrient cycling. Emerging indicators of connectivity and structural diversity may also provide new insights (LaRue et al., 2019).

Although the gap intercept method has been widely adopted as a data collection method by researchers and land managers (McCord et al., 2023); managers do not readily use these data in decision making (Veblen et al., 2014). One barrier to the use of gap data to inform land management has been the lack of benchmarks for interpreting gap data for different ecosystem processes and management goals across diverse ecosystems. Quantitative benchmarks help managers identify where distribution changes might trigger a shift in ecosystem function and provide a decision point to adjust shift management or implement restoration action if needed (Webb et al., 2020, 2024). Researchers should clearly identify relevant gap benchmarks in published studies. For example, Webb et al. (2014) identified a benchmark for increased wind erosion (gaps $>$ 1 m) which has since been applied to assessments of wind erosion nationally (Reeves et al., 2023). Similarly, including gap indicators in ESDs and state-and-transition models, along with expanding and standardizing their use in rangeland health reference sheets (Pellant et al., 2020) could provide a useful resource for managers to access information about structure and connectivity in addition to existing vegetation composition indicators. Benchmarks can also be established using the large amounts of gap data already collected across a range of conditions and land ownerships, such as those available in the Landscape Data Commons (Lupardus et al., 2023a; McCord et al., 2023). As new indicators are developed, associated benchmarks will also be required to apply those indicators in decision making. The availability of benchmarks for gap data could help managers evaluate the success of treatments and understand the impacts of ecosystem threats and disturbances.

Conclusions

Rangeland researchers and managers have used the gap intercept method as a standardized method to understand rangeland connectivity for over twenty years. Gap data provide critical information about vegetation structure that can be used to understand ecosystem structure and function including soil erosion by wind and water, biocrust community shifts, changes in plant community dynamics, nutrient availability, fire risk due to fuel connectivity, and wildlife habitat. Understanding these ecosystem functions and threats can be used to guide future management decisions and to understand the success of management actions, including restoration treatments. While a substantive body of research has demonstrated the utility of the gap intercept method for characterizing rangeland connectivity, there are many opportunities to address how gap distributions, shifts in gap distributions, and novel gap-based indicators represent rangeland connectivity and respond to land management. There are opportunities to explore the utility of the gap intercept method to understand other ecosystem processes and services, such as carbon dynamics, and microclimate effects. Continued collection of standardized gap data has many benefits. We have highlighted the value of gap metrics here as well as new opportunities for understanding ecosystems through a lens of connectivity by applying gap indicators to other ecosystem processes and by developing new indicators of connectivity leveraging gap data.

Declaration of competing interest

We declare that we have no conflicts of interest regarding this manuscript.

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Supplementary materials

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