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RESEARCH PAPER

Influence of directional side of sagebrush canopies and interspaces on microhabitats ☆,☆☆

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ABSTRACT

Shrubs can contribute to spatial heterogeneity in plant communities by creating distinct microsites under their canopies compared to between their canopies (interspaces). This results in distinct microhabitats that differ in understory vegetation characteristics and ground cover. However, microhabitats may also differ under the north and south side of canopies because of differences in shading and other microsite characteristics. We investigated if microhabitats varied among north and south sides of sagebrush canopies, and interspaces in 16 plant communities. Several understory vegetation characteristics and most ground cover variables varied among north sides, south sides, and interspaces. Moss and litter cover were greatest and bare ground was lowest in north sides. Moss and litter cover decreased and bare ground increased from north to south sides and from south sides to interspaces. Exotic annual grass cover and abundance was less in north side microsites compared to south side and interspace microsites, implying that sagebrush creates heterogeneity in resistance to invasion. This may be critical in allowing native herbaceous vegetation to persist under annual grass invasion pressure. Our results provide evidence that sagebrush creates distinct microhabitats. This highlights the pivotal role of shrubs in creating heterogeneity in shrub steppe communities and indicates that preventing the loss of shrubs in these communities should be a management priority. This also suggests that it is critical to restore sagebrush, and potentially other shrubs in similar ecosystems, after they are lost to maintain differences in microhabitats that promote diversity and coexistence.

Introduction

Spatial heterogeneity is important in plant communities because it promotes coexistence and diversity by providing a variety of niches for different species (Silvertown, 2004; Do Carmo et al., 2016; Feeser et al., 2018). In dryland plant communities, woody vegetation often contributes to spatial heterogeneity. Woody plants can create soil fertile islands (a.k.a., resource islands) under their canopies where soil nutrients are concentrated (Jackson & Caldwell, 1993a, b; Schlesinger et al. 1996). Heterogeneity in soil resources associated with fertile islands may affect the spatial distribution of plants (Brooks 1999; Esque et al. 2010). Woody vegetation can also influence herbaceous vegetation and ground cover by modifying the solar radiation, soil temperature, and soil moisture beneath their canopies (Pierson & Wright 1991; Forseth et al. 2001; Thompson et al. 2005; Davies et al. 2007). Thus, there are two distinct and widely recognized understory vegetation and ground cover microhabitats in shrublands, under shrub canopies (canopy) and between shrub canopies (interspace).

Shrub canopy effects, however, may differ depending on directional side (e.g., north vs. south) of the shrub. Soil temperatures can be cooler on the north compared to the south side of woody vegetation in the northern hemisphere (Tiedemann & Klemmendson 1977). Soil characteristics can also differ between sides of the shrub (Brooks 1999; Walker et al. 2001; Schafer et al. 2012). Thus, shrub-induced vegetation and ground cover microhabitats may also differ depending on directional side of the shrub, not just between canopy and interspace microsites. For example, annual plant abundances were higher on the north side of shrubs in the southwest deserts of the US (Schafer et al. 2012) and

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survival of two planted pine (*Pinus* L.) species was greater on the north compared to the south side of shrubs in southeast Spain (Castro et al., 2004). Thus, shrubs may create three distinct vegetation and ground cover microhabitats in shrublands: (1) interspaces, (2) north side under canopies, and (3) south side under canopies.

We investigated if shrubs create three distinct vegetation and ground cover microhabitats by comparing microsites in Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) steppe communities. Wyoming big sagebrush is a shrub native to western North America that occupies the warmer and drier, and thus often less resilient and resistant parts of the sagebrush steppe (Chambers et al. 2014). In sagebrush steppe, vegetation and ground cover differences between interspace and canopy microsites are associated with shrub-induced heterogeneity in soil resources (Doescher et al. 1984; Davies et al. 2007, 2009a, 2022b) and microenvironments (Chambers 2001; Davies et al. 2007). Some plant species occur preferentially in canopy microsites or interspaces (Davies et al. 2007). Similarly, plant functional group abundance may also differ between microsites (Eckert et al. 1986; Davies et al. 2007, 2022b). It is unknown if understory vegetation and ground cover differ between directional sides of sagebrush canopies.

Heterogeneity in herbaceous vegetation is important to maintaining ecosystem goods and services (e.g., diversity, soil heterogeneity, habitat, co-existence, etc.) in shrub steppe communities (Silvertown 2004; Doherty et al. 2010; Davies et al. 2022b). Therefore, it is important to know if shrubs create distinct microhabitats within canopies because vegetation establishment and growth may vary among directional sides of the canopy. This could be especially important if different functional groups are favored by one side or the other as recruitment of many native species is infrequent and often a restoration challenge in drylands (Svejcar et al. 2017). To better understand the influence of shrubs in shrublands and to inform management and restoration decisions, information detailing vegetation and ground cover characteristics under north and south side of shrub canopies and interspaces is needed.

The purpose of this study was to investigate if vegetation and ground cover characteristics differed among north and south side canopy microsites and interspaces. We speculated that Wyoming big sagebrush creates three different vegetation and ground cover microhabitats within plant communities. Specifically, we hypothesized that canopy microsites compared to interspace microsites, and north compared to south side canopy microsites would have (1) greater cover and density of herbaceous vegetation and (2) greater moss, lichen biological soil crust, and litter cover and less bare ground. We also expected that species richness, diversity and evenness would vary among north side, south side, and interspace microsites.

Materials and methods

Study area

This study was conducted on the >6000 ha Northern Great Basin Experimental Range (NGBER) approximately 56 km west of Burns, Oregon, USA (lat 43°29′N, long 119°43′W). Wyoming big sagebrush was the dominant woody plant at all study sites. Sagebrush densities were 0.3 to 0.5 individuals•m^{-2} across the study sites. Dominant bunchgrass was bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth) or Idaho fescue (*Festuca idahoensis* Elmer) depending on study site. Other common bunchgrass species at the study sites were bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), Sandberg bluegrass (*Poa secunda* J. Presl), and prairie Junegrass (*Koeleria macrantha* (Ledeb.) J.A. Schultes). Needle-and-thread (*Hesperostipa comata* (Trin. and Rupr.) Barkworth) and Indian ricegrass (Achnatherum hymenoides (Roem. and Schult.) Barkworth) were also common on some of the study sites. Most precipitation occurs during the winter-spring period and summers are hot and dry. Long-term (1991–2020) annual precipitation at the study area was 252 mm (PRISM, 2021). Crop year precipitation (Oct. 1, 2020-Sept. 30, 2021) was 175 mm (PRISM, 2021). Study sites range in elevation from 1390 to 1489 m above sea level. Slopes range from 0 to 15° and aspects from north to south at study sites. Soils are Aridisols and Andisols with shallow to moderately deep soil profiles before reaching a restrictive layer (Lentz & Simonson 1986). Historic fire return intervals are estimated to be 50–100+ years for these types of sagebrush steppe communities (Wright & Bailey 1982; Mensing et al. 2006).

Experimental design and measurements

We used a complete block design with 16 blocks to investigate the effects of microsites on vegetation and ground cover. Blocks were located by randomly selecting a point within 16 Wyoming big sagebrush-dominated pastures on the NGBER. Each block consisted of three microsites: (1) interspace between sagebrush canopies (interspace), (2) under the sagebrush canopy on northeast side of the stem (north side), and (3) under the sagebrush canopy on the southwest side of the stem (south side). In each block, 50 interspace, north side, and south side microsites were randomly selected for measuring herbaceous cover and density and ground cover. Only mature sagebrush plants that were large enough for sampling quadrats (0.2 m^2) to fit entirely under the canopy were used for this study. Most mature sagebrush plants in these plant communities fit this criteria (Davies et al., 2007). Sagebrush was considered mature if it had reproductive stems. Sagebrush largely grew as individuals with interspaces on all sides, thus, selected sagebrush plants had interspaces on the north and south sides of the shrub.

Herbaceous canopy cover and density and ground cover in each north side, south side, and interspace microsite were measured in June of 2021 using one 0.2 m^2 (40 × 50 cm) quadrat. For north and south sides, quadrats were placed against the stem on the appropriate side of the canopy. To sample interspace microsites, quadrats were placed in the center of the interspaces. Herbaceous vegetation, bare ground, ground litter, moss (*Tortula ruralis* (Hedw.) G. Gaertn., B. Mey. & Scherb.), and lichen biological soil crust (lichen biocrust) cover were visually estimated in the 0.2 m^2 quadrats to the nearest 1%. Cover estimates were aided by markings on the quadrats that divided them into 5%, 10%, 25%, and 50% segments. Density was measured by counting all individuals rooted inside the 0.2 m^2 quadrats. Species richness, diversity (Shannon-Wiener Diversity Index), and evenness (Shannon Evenness Index) were calculated from density measurements (Krebs, 1998).

Statistical analyses

We used analysis of variance (ANOVA) using a mixed model approach in SAS v. 9.4 (PROC MIXED SAS Institute Inc., Cary, NC) to evaluate the effects of microsites on herbaceous vegetation and ground cover characteristics. Fixed variables were microsite and random variables were blocks and the interaction between blocks and microsites. Means were separated with the LS function in SAS v. 9.4. Data that violated assumptions of ANOVAs were log or square root transformed. Data in the text and figures are presented in their original (non-transformed) dimensions. For analyses, vegetation was grouped into five categories: Sandberg bluegrass, large perennial bunchgrass (excluding Sandberg bluegrass), perennial forb, exotic annual grass, and annual forb. Sandberg bluegrass was analyzed individually from other native bunchgrasses because it develops earlier, is smaller in size, and responds differently to management and disturbances (McLean & Tisdale 1972; Yensen et al. 1992; Davies et al. 2021a). The perennial grass and forb groups were comprised solely of native species. The exotic annual grass group was primarily comprised of cheatgrass (*Bromus tectorum* L.). The annual forb group was comprised of native and non-native species. Significance was set at $P \leq 0.05$ and means were reported with standard errors (mean + S.E.).

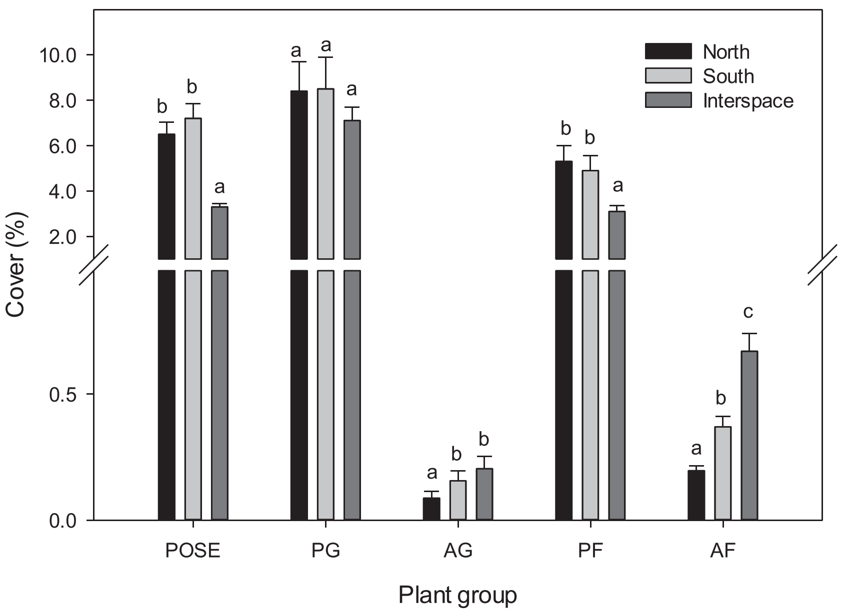

Fig. 1. Plant group cover (mean + S.E.) in north side, south side and interspace microsites in Wyoming big sagebrush communities. Different lower-case letters indicate differences between microsites ($P < 0.05$). POSE = Sandberg bluegrass, PG = large perennial grass, AG = exotic annual gras, PF = perennial forb, and AF = annual forb.

Results

Cover

Sandberg bluegrass cover was greater in north and south side microsites than in interspaces (Fig. 1; $F = 47.05$, $P < 0.001$), but we did not detect a difference between north and south side microsites ($t = -1.37$, $P = 0.181$). We did not detect a difference in large perennial bunchgrass cover among microsites (Fig. 1; $F = 0.64$, $P = 0.530$). Annual grass cover varied among microsites (Fig. 1; $F = 4.75$, $P = 0.013$) and was less in north sides compared to south sides and interspaces ($t = -2.27$ and -3.02, $P = 0.028$ and 0.004, respectively). We did not detect a difference in annual grass cover between interspaces and south sides ($t = 0.41$; $P = 0.681$). Perennial and annual forb cover varied among microsites (Fig. 1; $F = 14.84$ and 34.41, $P < 0.001$ and < 0.001, respectively). Perennial forb cover was less in interspaces than in north and south sides (Fig. 1; $t = -4.92$ and -4.02, $P < 0.001$ and < 0.001, respectively), but we did not detect a difference between canopy microsites ($t = 0.87$, $P = 0.390$). Annual forb cover was greater in interspaces than north and south side microsites ($t = 8.06$ and 4.50, $P < 0.001$ and $<$ 0.001, respectively) and was less in the north compared to south sides ($t = -3.14$, $P = 0.003$).

Bare ground and litter varied among microsites (Fig. 2; $F = 171.69$ and 181.54, $P < 0.001$ and < 0.001, respectively). Bare ground was greater in interspaces compared to north and south sides ($t = 17.36$ and 13.18, $P < 0.001$ and < 0.001, respectively). Bare ground was less in north compared to south sides ($t = -4.23$, $P < 0.001$). Litter cover was the inverse of bare ground with it being greater in north sides compared to south sides and interspaces ($t = 3.38$ and 17.57, $P < 0.001$ and 0.003, respectively) and greater in south sides than interspaces ($t = 14.47$, $P < 0.001$). Moss cover varied among microsites (Fig. 2; $F = 53.57$, $P < 0.001$). Moss cover was 2.5- and 4.3-fold greater in north sides compared to south sides and interspaces, respectively ($t = 7.57$ and 10.06, $P < 0.001$ and < 0.001, respectively). Moss was also greater in south side microsites compared to interspaces ($t = 2.19$, $P = 0.043$). Lichen biocrust cover did not appear to differ among microsites (Fig. 2; $F = 2.39$, $P = 0.102$).

Density and diversity

Sandberg bluegrass density varied among microsites (Fig. 3; $F = 20.43$, $P < 0.001$). Sandberg bluegrass density was less in interspaces than north or south side microsites ($t = -5.50$ and -5.03, $P < 0.001$ and < 0.001, respectively), but we did not detect a difference between north and south sides ($t = 0.48$, $P = 0.635$). Large perennial bunchgrass and exotic annual grass density varied among microsites (Fig. 3; $F = 4.46$ and 4.33, $P = 0.018$ and 0.019, respectively). Large perennial bunchgrass density was less in interspaces compared to north sides ($t = -3.02$, $P = 0.006$), but we did not detect a difference between north and south sides ($t = 1.22$, $P = 0.233$) and between interspaces and south sides ($t = -1.64$, $P = 0.114$). Exotic annual grass density was less in north sides compared to south sides and interspaces ($t = -2.50$ and -2.72, $P = 0.016$ and 0.009, respectively), but we did not detect a difference between interspaces and south sides ($t = -0.15$, $P = 0.879$). Perennial forb density varied among microsites (Fig. 3; $F = 8.09$, $P = 0.003$) and was less in interspaces compared to north and south sides ($t = -3.87$ and -2.72; $P < 0.001$ and 0.013, respectively), but we did not detect a difference between canopy microsites ($t = 1.19$, $P = 0.245$). Annual forb density varied among microsites (Fig. 3; $F = 28.57$, $P < 0.001$) and was greater in interspaces compared to north and south sides ($t = 7.43$ and 3.74, $P < 0.001$ and < 0.001, respectively) and less in north sides compared to south sides ($t = -3.24$, $P = 0.002$). We did not detect a difference in species richness among microsites (Fig. 4; $F = 2.42$; $P = 0.100$). Diversity and evenness varied among microsites (Fig. 4; $F = 5.71$ and 8.53, $P = 0.011$ and $= 0.002$, respectively). Diversity and evenness were greater in interspaces compared to north sides ($t = 3.14$ and 3.77, $P = 0.006$ and 0.001, respectively) and south sides ($t = 2.34$ and 3.01, $P = 0.031$ and 0.007, respectively), but potentially similar between canopy microsites ($t = -0.71$ and -0.69, $P = 0.485$ and 0.498, respectively).

Discussion

Our results provide evidence that shrubs create distinct vegetation and ground cover microhabitats in shrub steppe communities. The differences were not as straightforward as we hypothesized, with some vegetation characteristics being potentially similar between north and south side microsites and some potentially similar among canopy and interspace microsites. However, several vegetation and most ground cover characteristics differed between north and south sides of sagebrush canopies. This supports findings from other ecosystems that suggested trees and shrubs may create distinct microhabitats under canopies on the north and south side as well as in interspaces (e.g., Tiedemann and Klemmedson 1977, Rousset and Lepart 2000, Schafer et al. 2012).

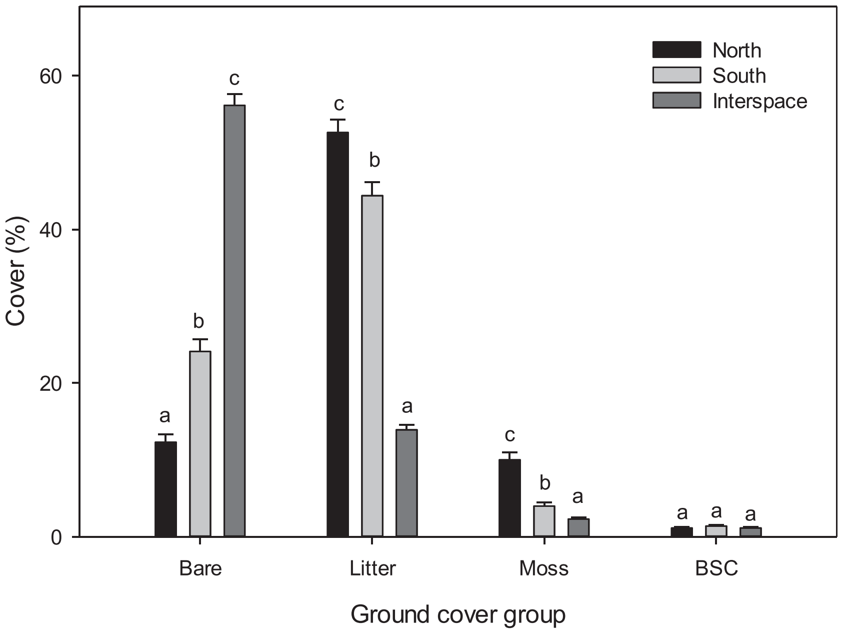

Fig. 2. Bare ground (Bare), litter, moss, and lichen biological soil crust (BSC) cover (mean + S.E.) in north side, south side and interspace microsites in Wyoming big sagebrush communities. Different lower-case letters indicate differences between microsites ($P < 0.05$).

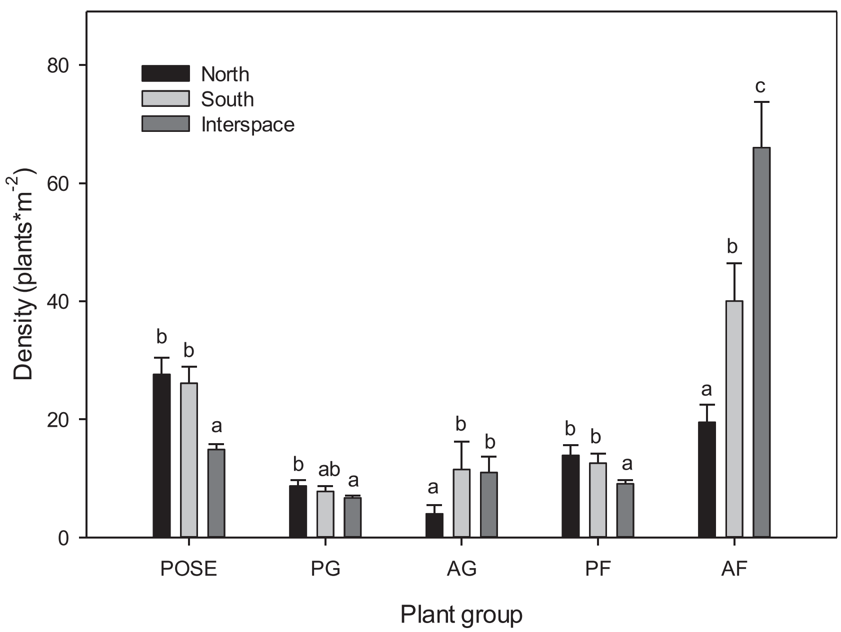

Fig. 3. Plant group density (mean + S.E.) in north side, south side and interspace microsites in Wyoming big sagebrush communities. Different lower-case letters indicate differences between microsites ($P < 0.05$). POSE = Sandberg bluegrass, PG = large perennial grass, AG = exotic annual gras, PF = perennial forb, and AF = annual forb.

South side microsites appear to be an intermediate, for at least some characteristics, between north side and interspace microsites. Moss and litter cover increased, and bare ground decreased from interspace to south side microsites and from south side to north side microsites. Further implying that the south side is an intermediary between north sides and interspaces, large bunchgrass density was greater in north side compared to interspace microsites, but we found no evidence that the south sides differed from the north sides or interspaces. Somewhat similar to our findings, basal area of perennial grasses was greater under the north compared to the south side of mesquite trees; however, canopy microsites were not compared with interspaces (Schott & Pieper, 1985). In our study, annual forb cover and density increased from north side to south side microsites and from south side to interspace microsites. In agreement with our findings, vegetation characteristics on south sides of a Mediterranean shrub were an intermediate between north side and interspace microhabitats (López-Pintor et al., 2006). These results imply that north sides may have a greater effect on the microenvironment than south sides.

The effects of directional side of shrub on ground cover characteristics may vary in different ecosystems. Similar to the greater cover of moss on north sides of sagebrush in our current study, mosses were overrepresented on north sides of shrubs in the Colorado Plateau (Bowker et al. 2005). However, Bowker et al. (2005) also found that biological soil crusts were greater on the north side, whereas we did not find it varied among microsites. This may be because biological soil crusts are more abundant in hotter and drier environments, in contrast with the cooler and less moisture limited sagebrush steppe of the northern Great Basin. Dissimilar to our findings of greater litter on the north side of sagebrush, litter accumulations under one-seed juniper (*Juniperous monosperma* [Engelm.] Sarg.) in New Mexico were greater on the south side (Schott & Pieper 1985). This was likely caused by the south side of junipers having a more closed canopy (Schott & Pieper 1985), which

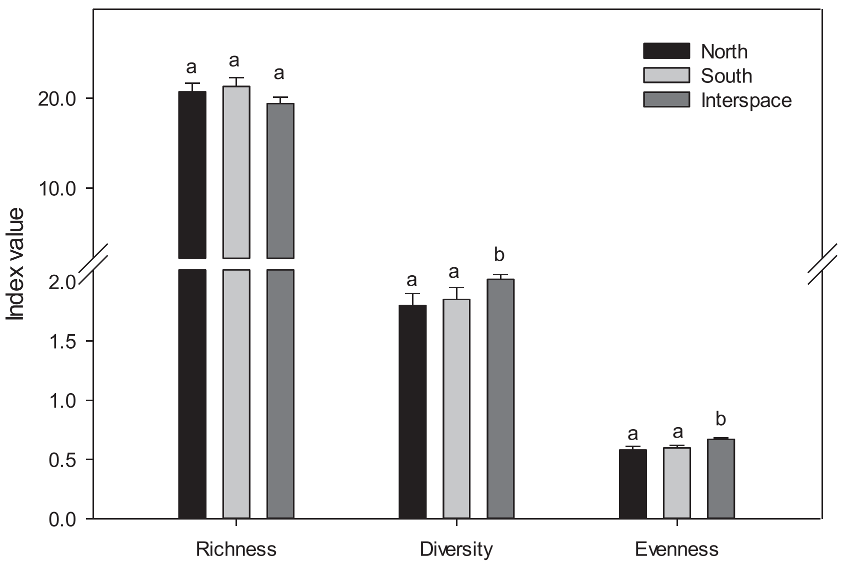

Fig. 4. Species richness, diversity (Shannon-Wiener Diversity Index), and evenness (Shannon Evenness Index (mean + S.E.) in north side, south side and interspace microsites in Wyoming big sagebrush communities. Different lower-case letters indicate differences between microsites ($P < 0.05$).

would probably increase the contribution of juniper needles to the litter fraction. In contrast with Schott and Pieper (1985) and in agreement with our results, litter under mesquite trees was greater on the north compared to the south side of canopies (Tiedemann & Klemmedson 1977). Clearly ground cover response to directional side of shrubs can vary by ecosystem.

Similar to ground cover, understory vegetation characteristics also suggest directional side of shrub effects can differ among ecosystems. We found more annual grasses and forbs on south sides compared to north sides. In contrast, annual plant abundance was higher on the north side compared to the south side of creosote bush (*Larea tridentata* [DC.] Cov.) in the Mojave and Sonora Deserts (Schafer et al. 2012). These dissimilarities in the effects of directional side of shrubs are likely because of macro-environmental differences between the sagebrush steppe and hot deserts of the southwest United States. Shading differences, based on side of shrub, likely produce cooler and warmer micro-environment on the north and south side of shrubs, respectively (Valiente-Banuet & Ezcurra, 1991). In the sagebrush steppe, warmer sites compared to cooler sites generally favor exotic annual grasses (Leffler et al., 2013; Roundy et al., 2018), therefore, likely explaining the greater annual grass abundance on south sides compared to north sides. This is in contrast to hot deserts where more shade and cooler temperatures under the north side of shrubs may be critical for annual plant survival (Valiente-Banuet & Ezcurra, 1991). Our results viewed in context with other studies, suggest that the effects of canopy side on vegetation and ground cover variables are influenced by the macro-environment, and likely woody species.

Dissimilar to our expectations, we did not detect an influence of side of the shrub on species richness, diversity, or evenness. However, diversity and richness were greater in interspaces compared to canopies. In central Spain, interspaces between shrubs, with higher solar radiation, lower soil nutrient availability, and greater temperature extremes, had greater diversity and evenness compared to canopy microsites (López-Pintor et al., 2006). These stressful environments are less likely to be dominated by a highly competitive species, thereby allowing greater diversity and evenness (López-Pintor et al., 2006). Hence, even though canopy microsites may be favorable for plant establishment and growth, competitive relationships may explain why some species are not more abundant in these microsites.

Microhabitats appear to differ in their resistance to annual grass invasion. North sides had less exotic annual grass cover and density compared to the other microsites, implying that they may be more resistant to annual grass invasion. Though exotic annual grass abundance and cover were relatively low in our study sites, this suggests that sagebrush plants create heterogeneity in resistance. Therefore, their loss from the plant community may decrease the overall resistance of plant communities to annual grass invasion. This is important because exotic annual grasses are a major threat to the sagebrush ecosystem and species that depend on it (Knick et al., 2003; Davies et al., 2021b). Heterogeneity in resistance may also be critical for native plants to coexist with invasive plants (Melbourne et al., 2007). Thus, sagebrush may facilitate persistence of native plants under annual grass invasion pressure.

Conclusions

Our study provides information on the ecological role of Wyoming big sagebrush in rangelands that can be used to inform management and restoration decisions. The sagebrush-induced microhabitats are likely important for providing spatial heterogeneity for higher trophic levels. While under sagebrush canopies are known to be favorable for the establishment and growth of many plant species (Eckert et al., 1986; Pierson & Wight, 1991; Callaway et al., 1996; Chambers, 2001; Davies et al., 2007), our results highlight that these effects likely vary depending on side of canopy. Though it is clear that side of the woody vegetation is influential, its effects may be species and location specific. This suggests that the ability of species and functional groups to establish and persist under north and south sides of different woody species in diverse ecosystems should be investigated to identify favorable planting and seeding microsites. This information could then be used to improve restoration efficiency, which is particularly important with high value or propagule limited species that are difficult to establish (Davies et al., 2020, 2022a). Our results suggest that shrubs may be a pivotal contributor to spatial heterogeneity in shrub steppe plant communities. This strongly implies that maintaining shrubs in shrub ecosystems should be a management focus to promote heterogeneity of microhabitats. Consequentially, preventing frequent wildfires in sagebrush steppe communities with low resilience and resistance to annual grass invasion, which would likely lead to a permanent loss of sagebrush, should be a management priority. In shrub steppe communities where shrubs have been lost, restoration of shrubs will also be critical to recovering microhabitat heterogeneity.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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