

Effects of Succession on Species Richness of the Western Juniper Woodland/Sagebrush Steppe Mosaic

Stephen C. Bunting
James L. Kingery
Eva Strand

Abstract—The development of mature juniper woodlands has often been associated with decreases in the herbaceous and shrub components of the community. This study focused on changes in species richness and diversity along a successional gradient at both the community and watershed scale in the Owyhee Mountains in southwestern Idaho. Community species richness was relatively constant across the sere. Community species diversity changed as species became less equitably distributed when juniper dominated the site in the later stages of succession. Landscape-scale species richness is predicted to be greatest when all successional stages are represented in the watershed.

Western juniper (*Juniperus occidentalis* subsp. *occidentalis*) dominates approximately 17 million ha in the northwestern portion of the Great Basin and southern Columbia Basin (West 1988). During the Pre-Euro-American period western juniper is thought to have primarily occurred as dense stands on the more dissected topography or to have occurred as open savanna-like woodlands on canyon slopes and more regular topography (Burkhardt and Tisdale 1969, 1976, Miller and Rose 1994, Miller and Wigand 1994). Western juniper has primarily encroached into many adjacent vegetation types but the expansion of dominance has been most dramatic on the deeper soils (Young and Evans 1981, Eddleman 1987, Miller and Rose 1994, Miller and Wigand 1994, Miller and others 1995). These types include those dominated by mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*) steppe, aspen woodlands and Idaho fescue (*Festuca idahoensis*)/ bluebunch wheatgrass (*Agropyron spicatum*) grassland. Encroachment has also occurred into low sagebrush (*Artemisia arbuscula*) dominated vegetation but the rate has been much lower due to the less productive site conditions.

The causes of encroachment have been attributed to effects of overgrazing on plant competition by domestic livestock, climatic change and reduction wildfire occurrence by active suppression and livestock grazing (Blackburn and Tueller 1970, Burkhardt and Tisdale 1976, Young and

Evans 1981, Gruell 1986, Miller and Wigand 1994). Research has shown that change in plant competition is probably not a factor in western juniper encroachment since plant composition did not affect the rate of establishment (Burkhardt and Tisdale 1976, Eddleman 1987, Miller and Rose 1994). However, heavy utilization of rangelands by livestock in the 19th and early 20th centuries would have facilitated juniper establishment through secondary effects. The resulting low fine fuel loads due to high forage utilization would have decreased fire occurrence (Miller and others 1995) and increased sagebrush seedling establishment (Ellison 1960, Tisdale 1969). Increased sagebrush density provides greater availability of safesites for juniper since the majority of seedlings are found under sagebrush or other shrub canopies (Burkhardt and Tisdale 1976, Eddleman 1987, Miller and Rose 1994, Miller and others 1995).

Fire history studies in western juniper have indicated that pristine fire-free intervals (FFI) varied from 25-30 years (Burkhardt and Tisdale 1969, 1976) but may have been shorter than 25 years in associated mountain big sagebrush steppe (Bunting and others 1987, Miller and others 1995). Young and Evans (1981) estimated, based on the growth rate of young western juniper seedlings, that a fire every 50 years would control the encroachment process in northern California. The encroachment of juniper usually reduces the herbaceous production on the site (Tausch and Tueller 1990) and thereby greatly reduces fire potential (Bunting and others 1987, Everett 1987). In dense stands of mature juniper fires may burn only under the most severe weather conditions.

The effects of encroachment are well documented for many juniper woodlands and are remarkably similar across the different juniper species and vegetation types. In general, there is a reduction in the herbaceous and shrub biomass production (Everett and Koniak 1981, Tress and Klopatek 1987, Wilson and Schmidt 1990, Vaitkus and Eddleman 1991). Other ecological changes which have been attributed to juniper encroachment include: increased soil erosion (Carrara and Carroll 1979), increased water use (Miller and Schultz 1987, Angel and Miller 1994, Miller and Wigand 1994), altered nutrient cycles (Klopatek 1987, Doescher and others 1987, Tiedemann and Klemmedson 1995), reduced seed reserves (Koniak and Everett 1982) and reduced fire potential (Bunting and others 1987, Everett 1987).

Often associated with this reduction of herbaceous and shrub species is a reduction in plant and animal species diversity (Blackburn and Tueller 1970, West and others 1979, Balda and Masters 1980, Koniak and Everett 1982,

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Stephen C. Bunting is Professor and James L. Kingery is Assistant Professor, Department of Range Resources and Eva Strand is GIS Analyst, Landscape Dynamics Lab, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, ID 83844-1135.

Severson 1986, Miller and others 1995). The effects of encroachment of western juniper woodlands into adjacent sagebrush steppe results in a decrease of herbaceous and shrub biomass production (Vaitkus and Eddleman 1991, Miller and Wigand 1994, Miller and others 1995). A reduction of plant species richness and species diversity has been documented for western juniper and other Great Basin woodlands (Blackburn and Tueller 1970, West and others 1979, Koniak and Everett 1982, Miller and others 1994). Studies indicate that breeding bird density and species richness increases as western juniper stands become more mature and structurally diverse (Maser and Gashwiler 1978, Sedgwick and Ryder 1987). Sedgwick and Ryder (1987) found that while bird densities decreased with juniper control, small mammals increased in response to greater herbaceous production. It seems most probable that in the process of conversion between juniper woodland and sagebrush steppe, some species will be affected positively and others negatively (Belsky 1996). The primary focus of this study is the landscape-scale influence of encroachment on vascular plant species diversity and richness.

Methods

Two watersheds, Red Canyon Creek and Smith Creek, were selected for analysis (fig. 1). They are tributaries of the South Fork of the Owyhee River in southwestern Idaho and contain a variety of successional stages. The areas of Red Canyon Creek and Smith Creek watersheds are 63.7 and 140.2 km², respectively. Elevation varies from 1,500 to 2,000 m. Domestic livestock have grazed the watersheds for over 100 years and currently cattle grazing occurs under a rest-rotation system. Less than 10 percent of each watershed has been treated with prescribed fire during the past 20 years.

Forty macroplots of approximately 0.25 ha within the western juniper-mountain big sagebrush mosaic were selected for sampling. These occurred over the successional gradient from herbaceous dominated (recently burned) to those dominated by stands of old juniper (greater than 500 years in age). Sampling was limited to sites which currently or potentially may support sagebrush steppe vegetation in the successional sequence. This restriction was based on soil type and the presence of sagebrush plants or dead material. Macroplot vegetation was classified into one of 9 structural stages based on composition and structure which were developed by the Interior Columbia Basin Ecosystem Management Project (ICBEMP) (Quigley and others 1996) (table 1). Macroplots were sampled for composition based on canopy coverage. The line intercept method was used to estimate shrub and tree coverage (Canfield 1941, Hanley 1978). A modification of Daubenmire's (1959) cover class method was used to estimate coverage of the herbaceous species. A total macroplot inventory was done to determine the total number of species present on the site at the time of sampling. Species not included in the microplot or line intercept data were ranked from 0 to 5 based on foliar coverage and distribution. Sampling occurred near peak biomass production for the sites (late June-early July). Species richness was determined from a single inventory and was based on those species which occurred in the

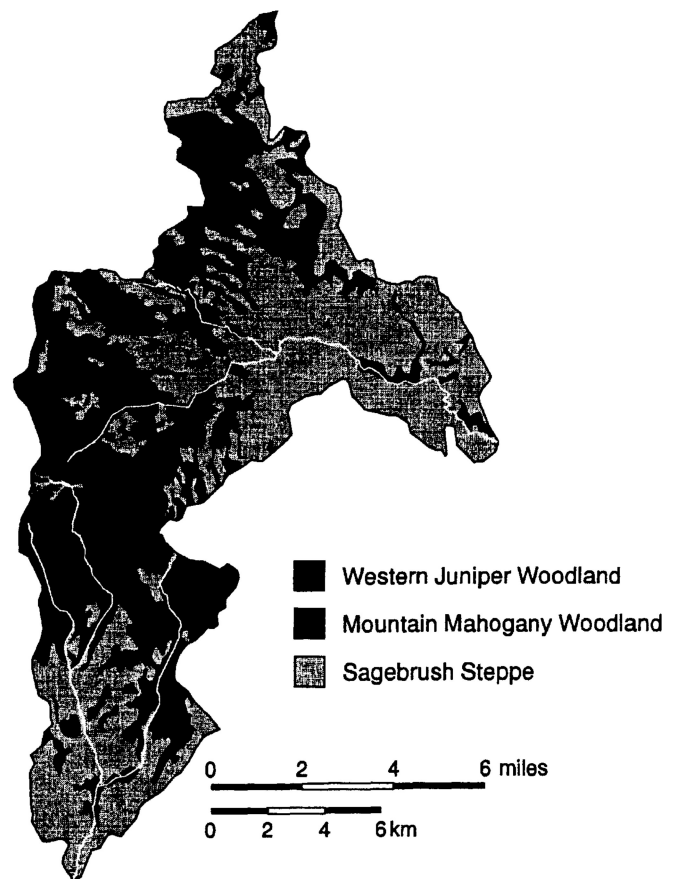


Figure 1—Potential vegetation of Red Canyon Creek (lower) and Smith Creek (upper) watersheds which are tributaries of the South Fork of the Owyhee River in southwestern Idaho. Without disturbance, most of the upper portions of the watersheds will become dominated by western juniper vegetation. (Source: ICBEMP data)

microplots and on the total macroplot search. The Shannon-Weiner (Magurran 1988) and Simpson's diversity indices (Simpson 1949, Magurran 1988) were used to quantify differences in species diversity.

Results

Consistent with previous research (Vaitkus and Eddleman 1991, Miller and Wigand 1994, Miller and others 1995) development of western juniper woodland vegetation resulted in the reduction of shrub and herbaceous plant coverage (fig. 2). A reduction of plant species richness has been documented for sites dominated by western juniper and for other Great Basin juniper woodlands (Blackburn and Tueller 1970, West and others 1979, Koniak and Everett 1982, Miller and others 1995), however, this did not occur in the watersheds studied in the Owyhee Mountains in Idaho. While there is a major change in plant community species composition with increased juniper dominance, species richness on a macroplot basis did not change across the successional gradient (fig. 3). This was true for species richness based on species sampled with microplots and for species

Table 1—Description of structural stages used to classify vegetation within the mountain big sagebrush steppe-western juniper woodland mosaic of the Owyhee Mountains, Idaho. Structural stages used are modifications of those developed by ICBEMP.

Structural stage	Description
Herbland	Herbaceous cover <67 percent, shrub cover <5 percent
Open shrubland	Low and medium shrub cover <10 percent, tree cover <5 percent
Moderate cover shrubland	Low and medium shrub cover 10-67 percent, tree cover <5 percent
Stand initiation woodland	Tree cover (all size classes) <5 percent, seedling-sapling cover >5 percent
Stem exclusion woodland	Large tree cover < 5 percent, small and medium tree cover >5 percent, seedling-sapling cover <5 percent
Understory re-initiation woodland	Large tree cover <5 percent, seedling-sapling cover >5 percent
Young multi-story woodland	Large tree cover 0-5 percent, small and medium tree cover 5-14 percent, seedling-sapling cover 5-14 percent
Old multi-story woodland	Large tree cover 5-14 percent, other size classes 5-14 percent
Old single strata woodland	Large tree cover >5 percent, other size classes <5 percent

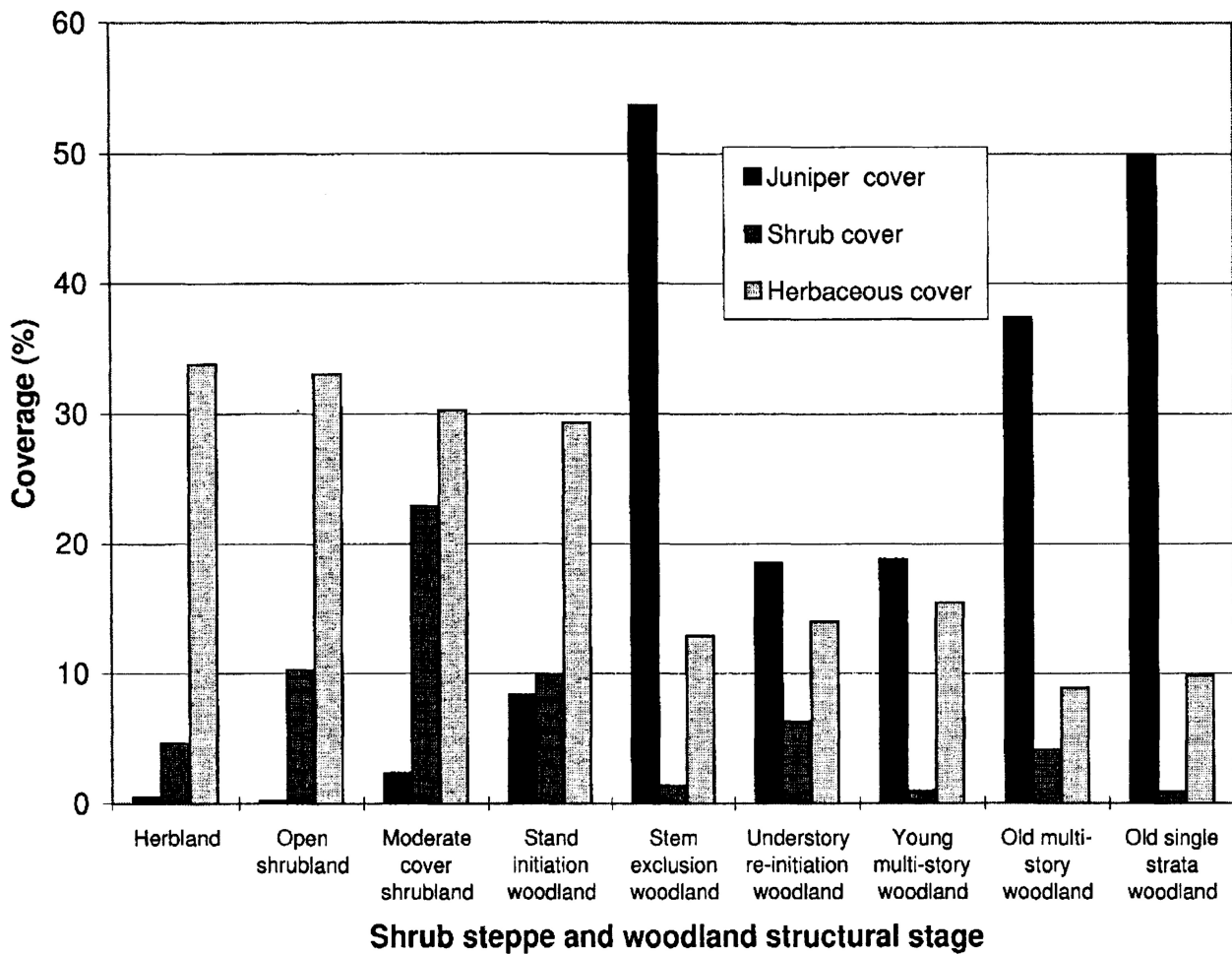


Figure 2—Data indicates that a reduction in the coverage of shrub and herbaceous species is associated with the development of western juniper woodlands. This is consistent with results from other juniper woodland studies from throughout the Great Basin and Southwest.

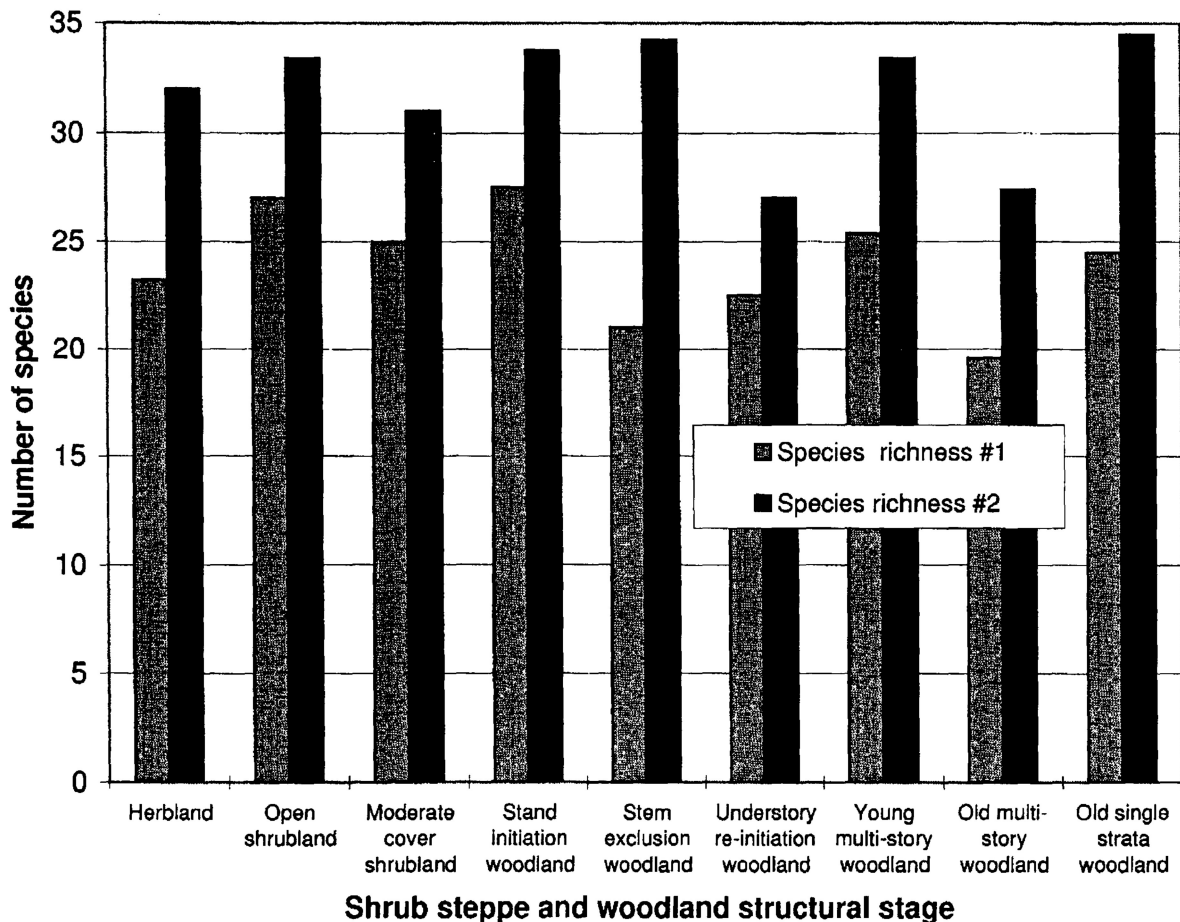


Figure 3—Species richness did not change as a result of the development of juniper woodland development. Species richness 1 is based on those species encountered when sampling the stand. Species richness 2 is based on those species resulting from a one-time macroplot inventory.

richness based on a complete macroplot inventory. Average species richness varied between 27-34 species for structural stages sampled across the successional gradient. The lowest average species richness occurred when young juniper began to dominate the site. At this stage many species found within sagebrush steppe were absent but those species associated with mature juniper woodlands had not become established.

Results indicated that many perennial herbaceous species are associated primarily with the early to mid seral communities and not found in the late seral communities (table 2). However, fewer instances of the reverse were evident. While late seral community species richness was as high as that of early and mid seral communities, the composition was comprised primarily of species that were also associated with other successional stages. In addition, due to the low perennial herbaceous plant cover, mature juniper communities contained high numbers of annual plants in the juniper interspaces. These included: cheatgrass (*Bromus tectorum*), Douglas knotweed (*Polygonum douglasii*), blue-eyed Mary (*Collinsia parviflora*), narrow-leafed collomia (*Collomia linearis*), Fremont's goosefoot (*Chenopodium fremontii*) and cryptantha (*Cryptantha* spp.). These annual species were also common in the early successional post-burn communities.

Table 2—Forb species associated with early to mid and late seral conditions within the mountain big sagebrush steppe-western juniper woodland mosaic in the Owyhee Mountains, Idaho.

Species associated primarily with grassland and sagebrush steppe communities:	Species associated primarily with old mature juniper woodland communities:
<i>Astragalus lentiginosus</i>	<i>Agastache urticifolia</i>
<i>Calochortus nuttallii</i>	<i>Aster chilensis</i>
<i>Castilleja applegatei</i>	<i>Habenaria unalascensis</i>
<i>Castilleja viscidula</i>	<i>Hackelia cusickii</i>
<i>Eriogonum caespitosum</i>	
<i>Eriogonum heracleoides</i>	
<i>Eriogonum ovalifolium</i>	
<i>Eriogonum sphaerocephalum</i>	
<i>Eriogonum umbellatum</i>	
<i>Geranium viscosissimum</i>	
<i>Geum triflorum</i>	
<i>Fritillaria pudica</i>	
<i>Linum perenne</i> var. <i>lewisii</i>	
<i>Linum micranthum</i>	
<i>Mertensia longiflora</i>	
<i>Paeonia brownii</i>	
<i>Penstemon perpulcher</i>	
<i>Penstemon procerus</i>	

Structural stages were grouped into 4 physiognomic types, grassland, sagebrush steppe, young juniper woodland and mature juniper woodland. Total species richness, those species found in at least 1 macroplot, for all physiognomic types was also similar across the successional gradient. Combined species richness for grassland, sagebrush steppe, young juniper woodland and mature juniper woodland macroplots was 65, 65, 60 and 70 species, respectively. These data indicate that highest landscape species richness (133 species) of the watersheds would occur when all structural stages were present on the landscape.

Since species richness did not change across the successional gradient, the changes in species diversity resulted primarily from differences in relative species abundance within the community. As mature juniper woodland develops, greater amounts of the community's total plant coverage and biomass is concentrated into fewer species. The number of species represented by only a few individuals in the macroplot tended to increase and species abundance becomes less equitable. This resulted in an increase in Simpson's Index and a decrease in the Shannon-Weiner Index as mature juniper woodland developed (fig. 4).

Conclusions

Although major changes in species composition and total plant coverage occurred, community species richness remained relatively constant across the successional gradient within the western juniper woodland-mountain big sagebrush steppe mosaic in southwestern Idaho. Changes in species diversity resulted as species became less equitably distributed within the communities as succession occurred. Maximum landscape species richness and species diversity occurs when all structural stages are represented within the watershed emphasizing the need to include disturbance such a fire as a process in landscape dynamics.

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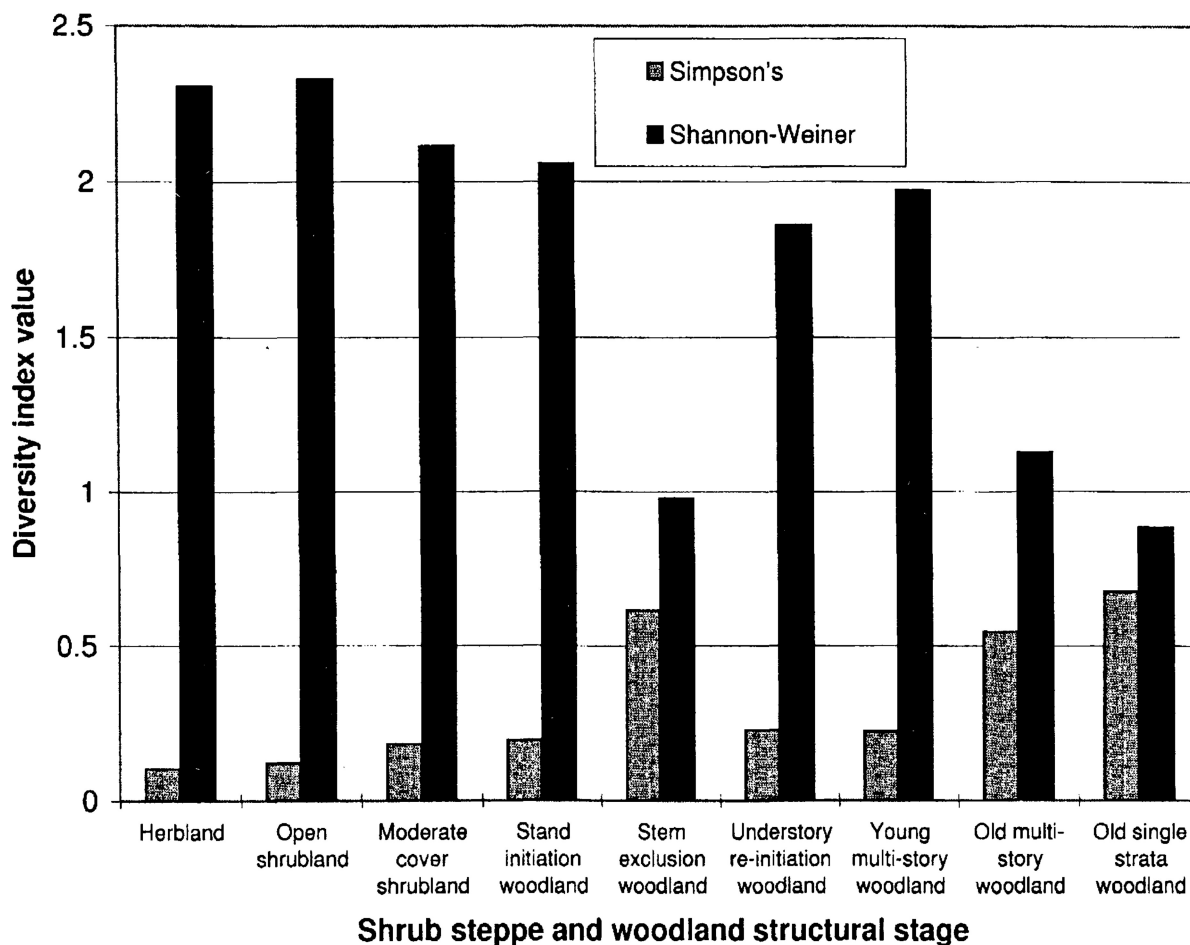


Figure 4—Changes in the Shannon-Weiner and Simpson's species diversity indices associated with western juniper woodland development in southwestern Idaho.

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