WOODLAND SUCCESSION: STRUCTURE, COMPOSITION, AND THRESHOLDS

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SUMMARY

The effects of developing woodlands on community structure and composition were evaluated across several community types. Differences in stand structure of closed woodlands were also evaluated for these community types. Community types ranged from low sagebrush communities occupying shallow, heavy-clay soils to clay loam mountain big sagebrush communities to deep loamy soil occupied by aspen. Juniper woodlands at stand closure ranged from 21- to 90-percent cover and from 64 to 1731 full size trees/ha across these community types. Sagebrush declined across all mountain big sagebrush community types as juniper increased. Herbaceous cover and diversity significantly declined on Thurber needlegrass community types occupying southerly aspects. However, herbaceous cover and diversity did not appear to decline in Idaho fescue communities occupying northerly aspects.

INTRODUCTION

The conversion of shrub steppe communities in the Intermountain West to *Juniperus* woodlands has been an active and accelerating process during the past 120 years (Tausch et al. 1981, West 1984, Miller and Wigand 1994). Over 90 percent of the 3.2 million ha of the western juniper (*Juniperus occidentalis* Hook.) woodlands are less than 100 years old (USDI-BLM 1990) even though the life span of western juniper exceeds 1,000 years (Miller unpublished data). In spite of the large land area influenced by western juniper, there has not been a concerted effort to evaluate the stages of woodland development. There is also limited research on the relationship between juniper-stand density or cover and associated understory species across different community types. In addition, wildlife habitat suitability, which is often determined by stand structure and composition, is highly variable across site and stage of stand development.

This study was designed to provide a context for comparing sites and successional stages associated with western juniper. The objective of the study was to evaluate overstory/understory relations over a range of western juniper dominance and across community types. Several of our specific hypotheses were: 1) understory/overstory relations differ among community types; 2) at full woodland development, tree density, and cover is different across community types; and 3) within a community type there are predictable thresholds of juniper dominance, beyond which understory species are negatively impacted.

STUDY AREA

The study areas were located in the High Desert and Klamath Ecological Provinces in southeastern Oregon and northeastern California. A combination of basin and range, and weathered mountains of volcanic origin characterize the topography. Elevation ranges between 1200 and 3000 m. Climate is cool and semi-arid, characteristic of the northern Intermountain region. Precipitation in the juniper zone across the two provinces typically ranges between 300 to 400 mm (Taylor 1993). The two shrub types studied were low sagebrush (*Artemisia arbuscula*) and mountain big sagebrush (*A. tridentata* spp. *vaseyana*). In addition, we also evaluated aspen stands below 2100 m, associated with shrub steppe community types in the Steens Mountain and south Warner Mountains study areas. Evaluating juniper woodlands across the two shrub steppe and aspen types provided us with a broad range of soils, landforms, and topographic positions. Elevation of study plots ranged between 1450 to 2100 m.

METHODS

Plot Selection

We selected stands that represented a large proportion of the ecological provinces where western juniper is actively expanding into associated communities. We also attempted to ensure that stands could be grouped by similar soils and plant-community type, with the primary variable of interest being degree of western juniper dominance. To reduce variability we avoided stands where disturbances may have influenced community dynamics. Woodland development phases were categorized into one of four successional phases, early, mid, late, and closed, based on tree growth and stand-structural characteristics (Table 1). We defined stand closure as full occupation by western juniper. Tree growth characteristics used to determine woodland developmental stage were lateral- and terminal-leader growth on sapling and full size trees. Stand structure characteristics were tree density, cover, and height, and proportion of live and dead-shrub canopy. The early phase of stand development contained < 5 percent juniper cover and young sapling trees with > 6 cm of lateral and terminal leader growth. Early-development juniper stands also contained an intact shrub layer. The key characteristic for stand closure was the near lack of sapling leader growth, generally < 1 cm, and lateral-leader growth on dominant trees < 2 cm. However, terminal-leader growth still may exceed 6 cm on canopy-dominant trees. We attempted to locate plots within each community type in the four different phases of woodland development.

Plot Measurements

Plant composition and soil characteristics were measured in 108, 60 x 46 m macroplots across the five-study areas. Within each macroplot plant canopy cover was measured for all species in addition to density for juniper and aspen trees. Cover of bareground, rock, and litter were also measured. Soils were described and samples collected within each horizon for textural analysis. Aspect, slope, and elevation were also measured.

Twinspan was used to verify and report initial classification of community types made in the field. Twinspan is a computer program for grouping similar stands based on relative plant species abundance using cover data. Assimilation tables were developed to describe plant assemblages and physical characteristics for each community type. Regression analyses was used to evaluate the relationship of tree-canopy cover with shrub and herbaceous-canopy cover. Student's t-test was used to compare herbaceous and bareground cover between early- and closed-juniper stands within community types. We did not compare community types where the number of early or closed macroplots was less than three. Hill's diversity indices [species number (N0), Shannon's index (N1), Simpson's index (N2), and an evenness index N2/N1 (E21)] were developed for the herbaceous understory for both early and closed stands using cover data. Mean diversity indices for macroplots in open and closed stands within community types are reported. Analysis of Variance and Duncan's New Multiple Range Test were used to compare juniper canopy cover and density at stand closure between community types.

RESULTS

Community Types

Twinspan separated out several major community types (Table 2). Within the ARTRV/FEID community type several subgroups were further separated out by study location.

Juniper stand structure across community types

Both cover and density of mature juniper trees (>3m) at stand closure were significantly different ($p \leq 0.0001$) across community types (Table 3). Woodland-canopy cover of closed stands ranged from 19 percent in the ARAR/POSA community type to a high of 90 percent in the POTR type. Across community types, tree density at stand closure ranged from 64 and 1731 trees/ha. As woodland development approached stand closure, maximum density of young trees (< 3 m in height) declined (Fig. 1).

Shrub and aspen canopy

The relationship between canopy cover of low sagebrush and juniper was not significant. Low sagebrush appeared little affected in the juniper interspace, but was noticeably absent beneath juniper canopies. However, there was a strong relationship between canopy cover among juniper and mountain big sagebrush (Fig. 2). As juniper-canopy cover increased mountain big sagebrush cover declined. Mountain big sagebrush canopy cover declined to about 10 percent as juniper canopy cover approached 9, 13, and 24 percent in the ARTRV/STTH, ARTRV/FEID, and ARTRV-STOR/STCO community types, respectively. Limited cover values and high variability for other shrub species made it difficult to evaluate their relationship with juniper cover. However, increasing juniper cover appeared to have little affect on *Symphoricarpos oreophilus* and *Ribes cereum* in ARTRV-SYOR/ FEID or POTR community types. Results were inconsistent for *Purshia tridentata.* Several closed-juniper stands contained 80 percent dead *Purshia,* while other closed stands showed little *Purshia* mortality. Active *Purshia* recruitment and mixed-age classes between 1 and 120 years were also present in the latter closed stands. We measured only two *Cercocarpus ledifolius* stands that contained a closed-juniper canopy. In both stands > 90% of the *Cercocarpus ledifolius* canopy was dead.

There was a very strong inverse relationship between juniper-overstory cover and aspen overstory cover ($p < 0.0001$) and density ($p < 0.003$)(Fig. 3). As juniper-overstory canopy increased, aspen saplings did not replace dying aspen overstory trees.

Table 1. Characteristics of transitional stages during succession from shrub steppe communities to fully developed juniper woodlands.

Characteristics (Post Settlement Stands)	Early	Mid	Late	Closed
Tree Canopy	Open, actively expanding, cover ≤ 5%	Actively expanding, cover 6 to 20%	Canopy expansion greatly reduced, cover 21-35%	Canopy expansion stabilized, over > 35%
Leader Growth (Dominant Trees)	Good terminal & lateral leader growth	Good terminal & lateral growth	Good terminal growth, reduced lateral growth	Good to reduced terminal growth, lateral growth absent
Crown Lift (Dominant Trees)	Absent	Absent	Lower limbs beginning to die where tree canopy > 35%	Present where tree canopy > 35%
Potential Berry production	Low	Moderate to High	Low to Moderate	Rare to Low
Tree Recruitment	Active	Active	Reduced, limited primarily to beneath trees	Absent
Leader Growth (Understory Trees)	Good terminal & lateral leader growth	Good terminal & lateral growth	Greatly reduced terminal & lateral growth; reduced ring growth	Absent, some mortality
Shrub Layer	Intact	Nearly intact to showing mortality around dominant trees	≥ 40% dead	≥ 85% dead

Table 2: Plant community types sampled where n>3. Groupings were done by Twinspan (total n=108).

Community Type	Sample size	Elevation (m) Range (mean)	General Aspect	% Slope	Soils A & B Horizons
Artemisia arbuscula / Poa sandbergii	12	1482-1824 (1626)		<2	A: Shallow clay loam to clay B: clay
Artemisia tridentata spp. *vaseyana/*					
Stipa thurberiana	15	1575-1990 (1737)	Southerly	8-22	A: Sandy clay loam to clay loam B: Sandy clay loam to silty clay loam
Agropyron spicatum	5	1545-1890 (1715)	South to West	8-26	A: Sandy to clay loam B: Clay loam to clays
Festuca idahoensis	49	1525-2006 (1723)	Northwest to Southeast	0-45	A: Loam to clay loam B: Clay loam to clay
-*Symphoricarpos oreophilus / Stipa columbiana*	12	1560-2100 (1846)	Northwest to Northeast	10-25	A&B: Loam
Populus tremuloides	15	1780-2045 (1906)	North to East	8-35	A&B: Loam

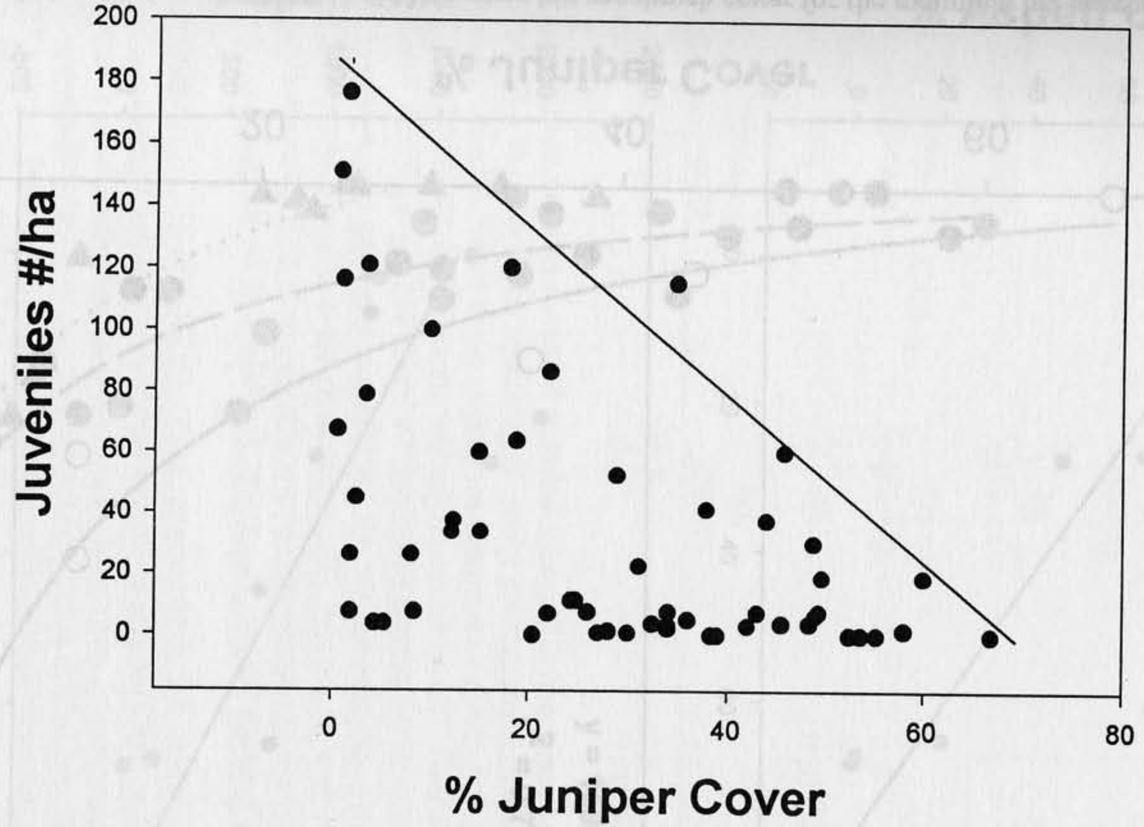

Figure 1. Relationship between juvenile juniper tree density (trees < 3m tall) and mature overstory tree canopy cover for mountain big sagebrush community types. The line represents a boundary layer of maximum juvenile juniper trees occurring with varying juniper overstory canopy cover.

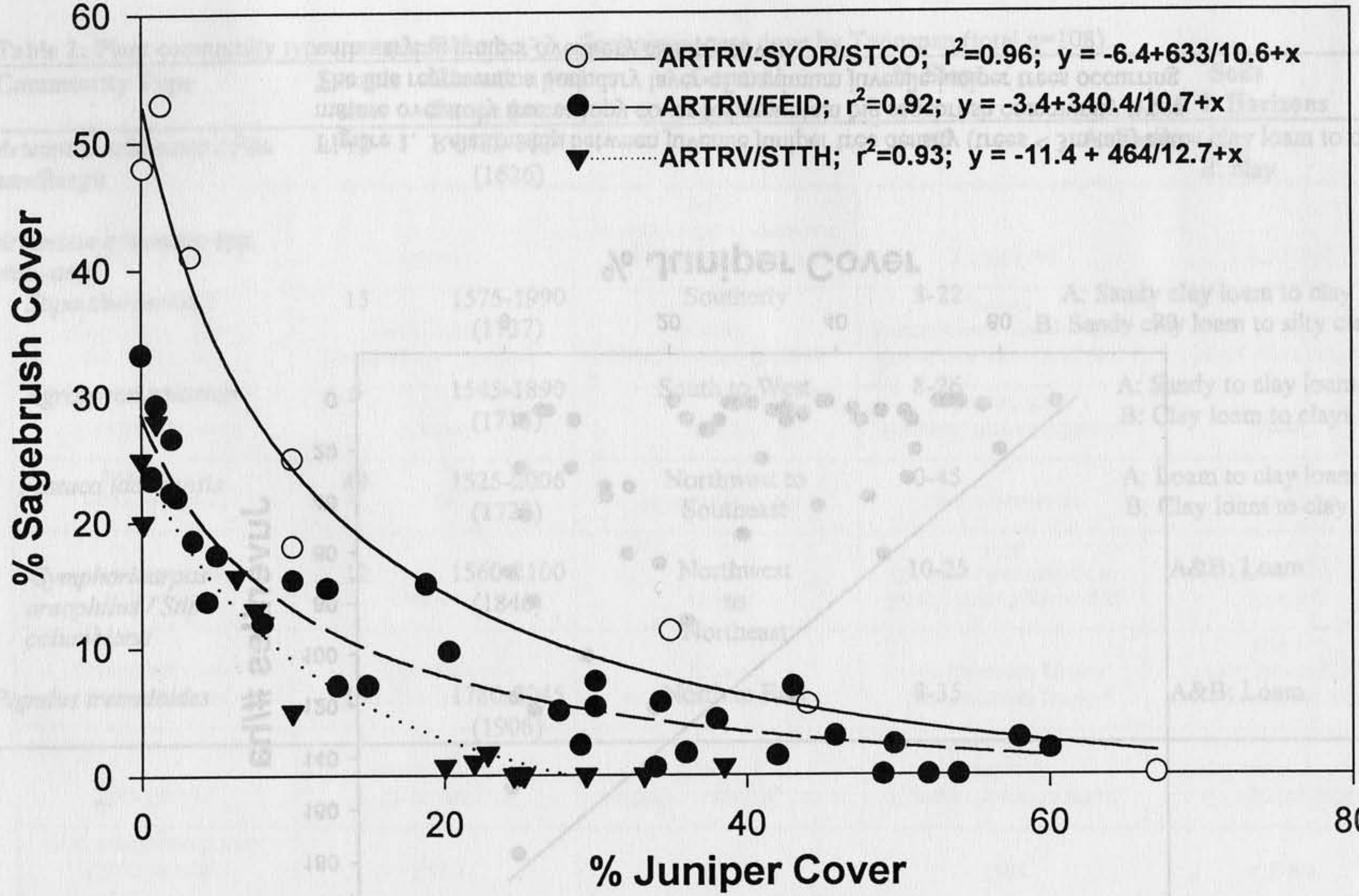

Figure 2. The relationship between juniper and mountain big sagebrush cover for the mountain big sagebrush / Thurber needlegrass, mountain big sagebrush / Idaho fescue, and mountain big sagebrush - snowberry / Columbia needlegrass community types.

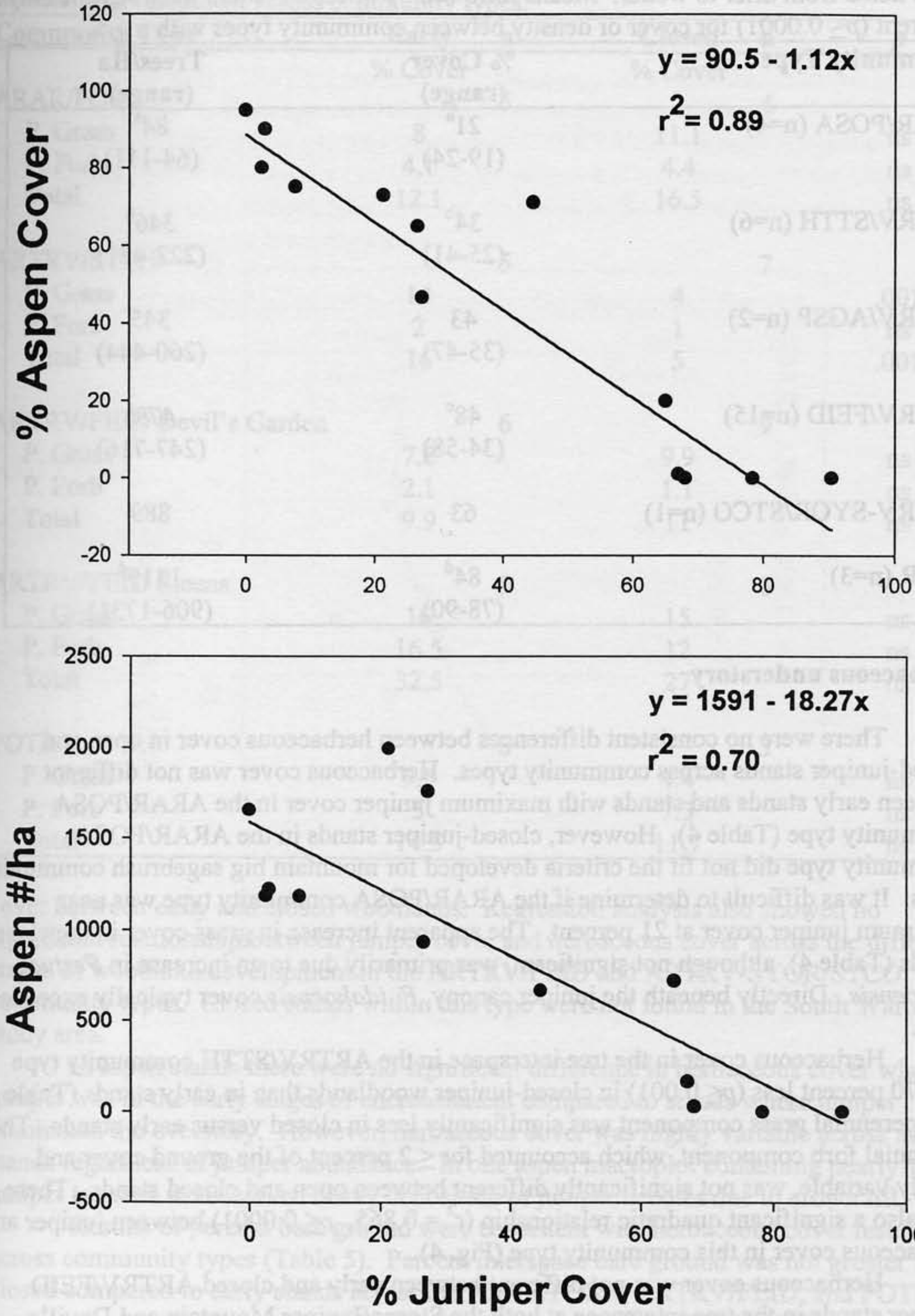

Figure 3. Relationship between juniper canopy cover and aspen cover ($p \leq 0.0001$) and density ($p \leq 0.003$).

Table 3. Mean and range of juniper cover and density in closed stands for six community types listed from drier to wetter. Means followed by different letters were significantly different ($p \leq 0.0001$) for cover or density between community types with $n \geq 3$.

Community Type	% Cover (range)	Trees/Ha (range)
ARAR/POSA (n=4)	21^a (19-24)	84^a (64-111)
ARTRV/STTH (n=6)	34^b (25-41)	346^b (222-481)
ARTRV/AGSP (n=2)	43 (35-47)	345 (260-444)
ARTRV/FEID (n=15)	48^c (34-58)	479^c (247-716)
ARTRV-SYOR/STCO (n=1)	63	889
POTR (n=3)	84^d (78-90)	1319^d (906-1731)

Herbaceous understory

There were no consistent differences between herbaceous cover in open and closed-juniper stands across community types. Herbaceous cover was not different between early stands and stands with maximum juniper cover in the ARAR/POSA community type (Table 4). However, closed-juniper stands in the ARAR/POSA community type did not fit the criteria developed for mountain big sagebrush community types. It was difficult to determine if the ARAR/POSA community type was near maximum juniper cover at 21 percent. The apparent increase in grass cover in the closed stands (Table 4), although not significant, was primarily due to an increase in *Festuca idahoensis*. Directly beneath the juniper canopy, *F. idahoensis* cover typically exceeded 65%.

Herbaceous cover in the tree interspace in the ARTRV/STTH community type was 70 percent less ($p \leq 0.001$) in closed-juniper woodlands than in early stands (Table 4). The perennial grass component was significantly less in closed versus early stands. The perennial forb component, which accounted for ≤ 2 percent of the ground cover and highly variable, was not significantly different between open and closed stands. There was also a significant quadratic relationship ($r^2 = 0.865$, $p \leq 0.0001$) between juniper and herbaceous cover in this community type (Fig. 4).

Herbaceous cover was not different between early and closed ARTRV/FEID juniper stands in the tree interspace at both the Steens/Juniper Mountain and Devil's Garden study areas (Table 4). There was no difference between perennial grass or forb

Table 4. Perennial herbaceous cover and sample size for early and closed stages of woodland development across community types.

Community Type	Early % Cover	n	Closed % Cover	n	*p*
ARAR/POSA		5		4	
P. Grass	8		11.1		ns
P. Forb	4.1		4.4		ns
Total	12.1		16.5		ns
ARTRV/STTH		5		7	
P. Grass	14		4		.001
P. Forb	2		1		ns
Total	16		5		.001
ARTRV/FEID Devil's Garden		6		9	
P. Grass	7.8		9.9		ns
P. Forb	2.1		1.1		ns
Total	9.9		11		ns
ARTRV/FEID Steens		9		6	
P. Grass	16		15		ns
P. Forb	16.5		12		ns
Total	32.5		27		ns
POTR		8		3	
P. Grass	9.5		4.4		ns
P. Forb	5		7.3		ns
Total	14.5		11.7		ns

cover between early and closed woodlands. Regression analysis also showed no significant relationship between juniper cover and herbaceous cover across the different stages of woodland development in the ARTRV/FEID and ARTRV-SYOR/STCO community types. Closed stands within this type were not found in the South Warner study area.

In aspen stands there were no significant difference in herbaceous cover where juniper was in the early stages of encroachment compared to stands where juniper dominated the overstory. However, herbaceous cover was highly variable across aspen stands regardless of juniper abundance. In one aspen macroplot containing nearly 1000 juniper trees/ha we observed heavy deposition of juniper needles due to crown lift.

Results of percent bare ground were consistent with herbaceous cover results across community types (Table 5). Percent interspace bare ground was not greater for closed compared to early stands across the ARAR/POSA, ARTRV/FEID, and POTR community types. However, on the southerly aspects in the ARTRV/STTH types bare ground in the tree interspace was significantly greater in the closed stands compared to early woodlands.

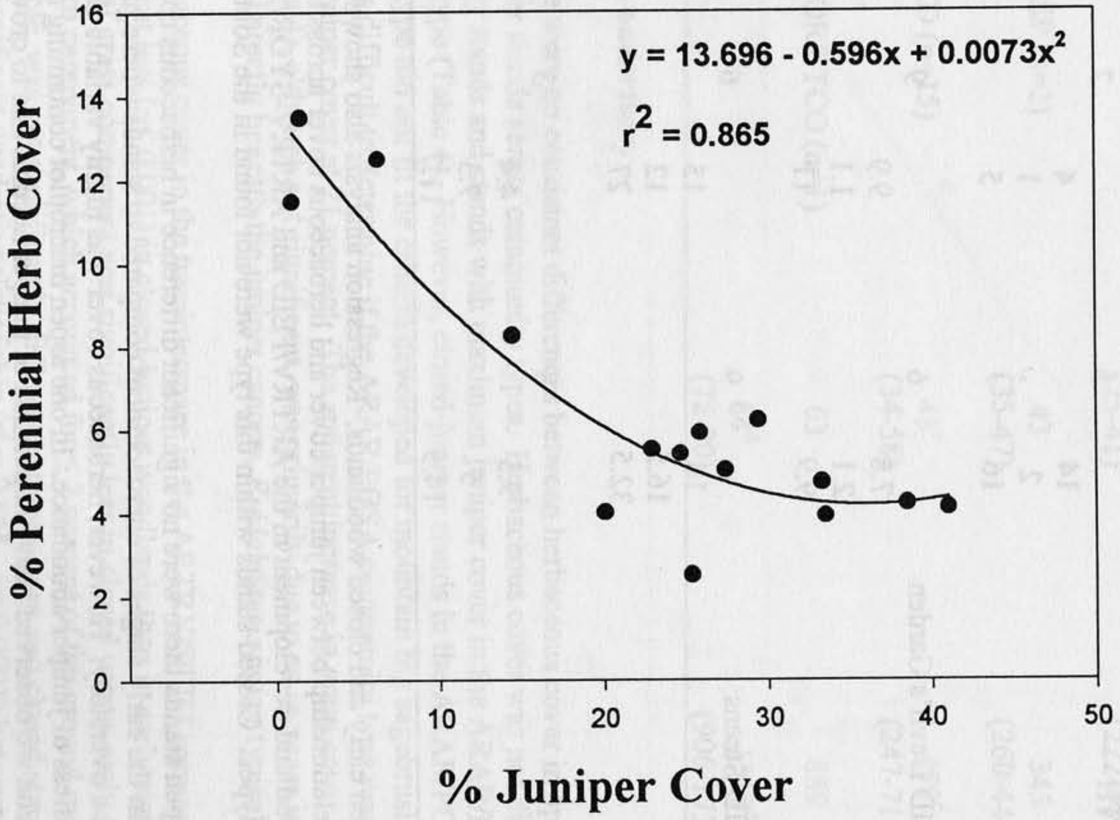

Figure 4. Relationship between perennial herb and juniper cover in the mountain big sagebrush Thurber needlegrass community type.

Diversity

The pattern of species diversity across community types was similar to cover response (Table 6). Species diversity indices were consistently lower in closed-juniper woodlands in the ARTRV/STTH community type compared to woodlands in the early development stage. Indices appeared similar between early and closed stands in the ARAR/POSA, and POTR community types, and ARTRV/FEID Oregon subgroup. However, ARTRV/FEID Devil's Garden subgroup was not consistent with the Oregon sites. Species diversity indices N1 and N2 were lower in the closed stages of woodland development compared to the early phase.

Table 5. Percent bareground in the tree interspace for five-community types.

Community Type	Open	n	Close	n	*p*
	% Cover		% Cover		
ARAR/POSA	56	5	54	4	ns
ARTRV/STTH	55	5	90	7	.001
ARTRV/FEID DG	34	6	32.4	9	ns
ARTRV/FEID Steens	16	9	18	6	ns
POTR	5	8	3.8	3	ns

CONCLUSIONS

Both mountain big sagebrush and aspen consistently declined during western juniper woodland development. However, herbaceous understory response was not consistent across community types as woodland dominance increased. The herbaceous cover and diversity declined with increasing woodland dominance on the dry sites, particularly in the mountain big sagebrush / Thurber needlegrass type occupying southerly aspects. However, in mountain big sagebrush community types occupying the wetter northerly aspects, western-juniper dominance appeared to have little impact on herbaceous cover. In the absence of fire, woodlands will continue to increase in mountain big sagebrush community types. Our bird surveys show composition of avian populations changes during woodland development. As trees gain dominance and shrubs decline, a threshold is crossed when understory fuels (primarily the shrubs) drop to a level where fire is unlikely to carry through the stand or generate enough heat to kill trees > 10 ft tall (Fig. 5).

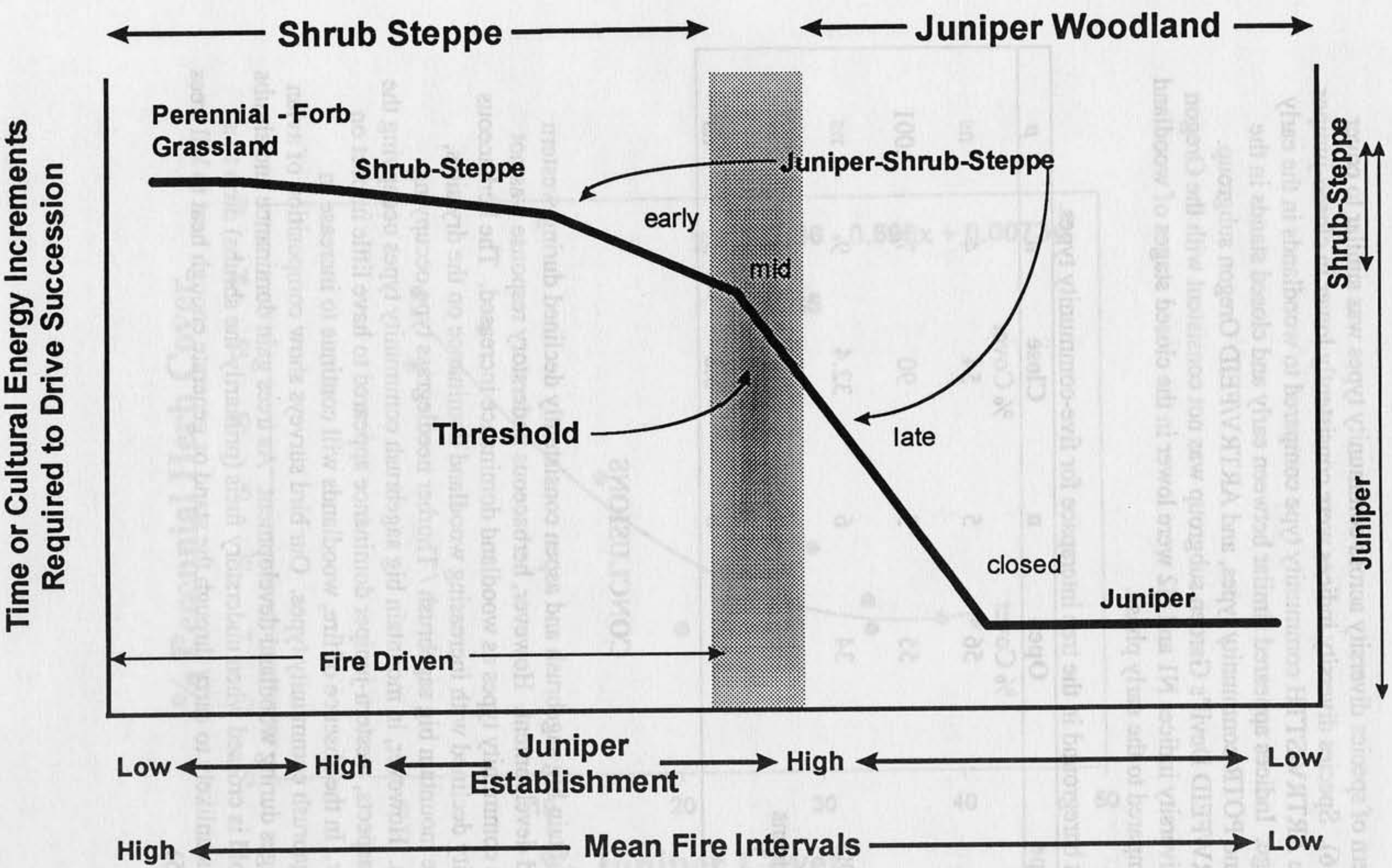

Figure 5. Conceptual diagram of changes in a shrub steppe community in the absence of fire (modeled after Archer 1989). In the absence of fire the abundance of shrubs decline as juniper trees gain dominance. The threshold has been crossed when understory fuels drop to a level where fire is unlikely to carry through the stand or generate enough heat to kill trees > 10 ft tall. The probability of the woodland crossing the threshold and reverting back to shrub steppe is very low in the absence of a major disturbance or very costly inputs. Changes in juniper establishment are due to changes in plant community structure (presence of shrubs) and competition from overstory trees.

Table 6. Mean plant diversity indices across macroplots within community types for early- and closed-juniper woodlands. Hills diversity numbers: N0 = species number; N1 = the number of abundant species based on Shannon's index; N2 = the number of very abundant species based on Simpson's index. Both mountain big sagebrush and juniper cover were not included in calculating diversity indices.

Community Type	N0	N1	N2
A. Arbuscula / Poa sandbergii			
Open (n=5)	35	8.4	5.9
Closed (n=4)	37	9.5	6.4
A. Tridentata spp. *vaseyana / Stipa thurberiana*			
Open (n=5)	45	10.6	7.2
Closed (n=6)	39	2.5	1.6
Festuca idahoensis (Devils Garden)			
Open (n=6)	33	9.2	6.3
Closed (n=9)	38	4.0	2.4
Festuca idahoensis (Steens Mt)			
Open (n=9)	43	10.7	6.2
Closed (n=6)	41	10.3	6.6
Populus tremuloides			
Open (n=9)	35	8.8	5.7
Closed (n=4)	35	8.9	5.7

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