

## NEGLECTIBLE INFLUENCE OF SPATIAL AUTOCORRELATION IN THE ASSESSMENT OF FIRE EFFECTS IN A MIXED CONIFER FOREST

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### ABSTRACT

Hktg"ku"cp"ko rqtvcpv"hgcvwtg"qh" o cp{ "hqtguv"gequ{uvgo u."cnvjqw i j"vjg"swcpvkŁecvkqp"qh"kvu"ghhgevu"ku"eqo rto kugf"d{"vjg"nctig"uecng"cv"y jkej"Łtg"qeewtu"cpf"kvu"kpjgtgpv"wp rtgfkev-ability. A recurring problem is the use of subsamples collected within individual burns, potentially resulting in spatially autocorrelated data. Using subsamples from six different Łtgu"\*cpf"vj tgg"wpdwtpgf"eqpvtqn"ctgcu+"yg"ujqy"nkvnng"gxkfgpeg"hqt"uvtqpi"urcvkcnc"cwvqeqt-tgncvkqp"gvjgt"dg hqtg"qt"chvgt"dwtpkpi"hqt"gkijv"ogcuwtgu"qh"hqtguv"eqpfkvkqpu"\*dqvj"hwgnu"cpf"xgigvevkqp+0""Cf fkvkqpcnm{"kpenwfkpi"cvgt o"hqt"urcvkcnc{"cwvqeqttnvcvf"gttqtu"rtqxf-ed little improvement for simple linear models contrasting the effects of early versus late season burning. While the effects of spatial autocorrelation should always be examined, it oc{"pqv"cnyc{"u"itgcvn{"kplwgpeg"cuuguuogpvu"qh"Łtg"ghhgevu0""Kh"jki j"rcvej"uecng"xctkcdknk-ty is common in Sierra Nevada mixed conifer forests, even following more than a century qh"Łtg"gzewukqp."vtgcvogpvu"fgukipgf"vq"gpewtcig"hwvtvjt"jvgvtqigpgkv{"kp"hqtguv"eqpfk-vkqpu"rtkqt"vq"vjg"tgkpvttqfwvkvqp"qh"Łtg"yknn"nkmgnc{"dg"pwpgeguuct{0

**Keywords:** hqtguv"tguvqtcvkqp."rtguetkdgf"Łtg."rugwfqtgrnkecvkqp."Ukgttc"Pgxcfc."uvcvkuvkeu

**Citation:**""xcp"Ocpvigo."ROL."cpf"FOY0"Uej ykno""422;0""Pginkikdng"kpłwgpeg"qh"urcvkcnc"cwvqeqttn-cvkqp"kp"vjg"cuuguuogpvu"qh"Łtg"ghhgevu"kp"c"okzgf"eqpkhgt"hqtguv0""Hktg"Geqniq{"7\*4+<"338/3470

### INTRODUCTION

Fire is fundamental in shaping most terres-  
vtkcnc"gequ{uvgo u."\*Dqpf"cpf" Mgng{" 4227+0"  
Jqyngxgt."wpfgtuvcpfkpi"Łtg"ghhgevu"tgo ckpu"  
gnwukxg"kp"rctv"dgecwug"Łtgu"ctg"v{rkecnc{"wp-

planned, not normally under experimental con-  
trol, and occur at spatial scales of hundreds to  
thousands of hectares; these features are at  
odds with classical experimental design and  
analysis. Experimental burning in forests,  
where it has been attempted, is constrained by

v j g " n q i k u v k e c n " c p f " L p c p e k c n " t g u q w t e g u " p g g f g f " v q " e q p f w e v " v j g " L t g u . " n k o k v k p i " v j g " u k | g . " k p v g p u k v { " and number of replicated burning treatments \*Hwn<sup>2</sup>" *et al.* 2004, Stephens and Moghaddas 4227." Hwn<sup>2</sup>" *et al.* 2006, North *et al.* 2007, Schwilk *et al.* 422; +0" Q r r q t v w p k u v k e " u v w f k g u " q h " L t g " g h h g e v u " h t g s w g p v n { " t g n { " q p " f c v c " e q m n g e v g f " from subsamples within a single burned area. These subsamples may be correlated both spatially and temporally, and when subjected to standard statistical testing provide reduced es- v k o c v g u " q h " x c t k c v k q p " \* g t t q t + . " k p e t g c u k p i " v j g " n k m g - n k j q q f " q h " e q o o k v k p i " c " V { r g " K " g t t q t " \* v j g " e j c p e g " q h " f g v g e v k p i " c " u k i p k L e c p v " g h h g e v " q h " L t g " y j g p " p q " o g c p k p i h w n " g h h g e v " j c u " q e e w t t g f + 0 " " V j c v " k u . " v j g " subsampled data underlying these tests are r u g w f q t g r n k e c v g f " \* J w t n d g t v " 3 ; : 6 + 0

K p v g t r t g v k p i " r u g w f q t g r n k e c v g f " L t g " g h h g e v u " f c v c " y k n n " c n y c { u " r t g u g p v " e j c m g p i g u " \* x c p " O c p - t g e m *et al.* 4223 + . " d w v " u q o g " q h " v j g u g " f k h L e w n v k g u " could be mitigated by estimating spatial auto- e q t t g n c v k q p " \* v j g " e q t t g u r q p f g p e g " q h " p g c t d { " u c o - r n k p i " w p k v u + " c p f " v g o r q t c n " c w v q e q t t g n c v k q p " \* v j g " similarity of samples measured repeatedly over v k o g + . " c p f " e q p v t q n k p i " h q t " v j g u g " t g n c v k q p u j k r u " k p " c p c n { u g u " q h " L t g " g h h g e v u " \* N g i g p f t g " 3 ; : 5 . " N g i - e n d r e and Legendre 1998, Fortin and Dale 2005, Bataineh *et al.* 4228 + 0 " " K v " k u " w p e n g c t = " j q y - e v e r , to what degree the consideration of auto- correlation, particularly spatial autocorrelation, y q w n f " k o r t q x g " q w t " w p f g t u v c p f k p i " q h " L t g " g h - h g e v u 0 " " U o c n n " u e c n g " j g v g t q i g p g k v { " k p " L t g " g h h g e v u " may be common as daily and seasonal differ- g p e g u " k p " L t g " y g c v j g t " c p f " h w g n " o q k u v w t g " k p v g t c e v " with variability in topography, fuel loading, c p f " x g i g v c v k q p " f w t k p i " d w t p k p i " \* M k n i q t g " 3 ; 9 5 . " M p c r r " c p f " M g g n g { " 4 2 2 8 + 0

The degree of spatial heterogeneity also has implications for an ongoing debate concerning the need for mechanical thinning prior v q " v j g " t g k p v t q f w e v k q p " q h " r t g u e t k d g f " L t g " k p " U k g t - r a n mixed conifer forests. Arguments in favor q h " r t g / L t g " v j k p p k p i " c t g " d c u g f " q p " v j g " p q v k q p " v j c v " c " e g p v w t { " q h " L t g " g z e n w u k q p " j c u " n g f " v q " v j g " j q - o q i g p k | c v k q p " q h " r t g x k q w u n { " j g v g t q i g p g q w u "

u v c p f u . " c p f " v j g " c r r n k e c v k q p " q h " L t g " y k v j q w v " r t g - c e d i n g silvicultural treatments will perpetuate v j g u g " e j c p i g u " k p " h q t g u v " u w t w e v w t g " \* D q p p k e m u g p " c p f " U v q p g " 3 ; : 3 . " 3 ; : 4 = " D q p p k e m u g p " 3 ; : ; + 0 " Here we show that there is only weak evidence for pervasive spatial autocorrelation both before and after prescription burning for mea- u w t g u " q h " L t g " g h h g e v u " t g n g x c p v " v q " o c p c i g t u . " c p f " that spatial autocorrelation had trivial effects when comparing the outcomes of early versus late season burning in a Sierra Nevada mixed conifer forest.

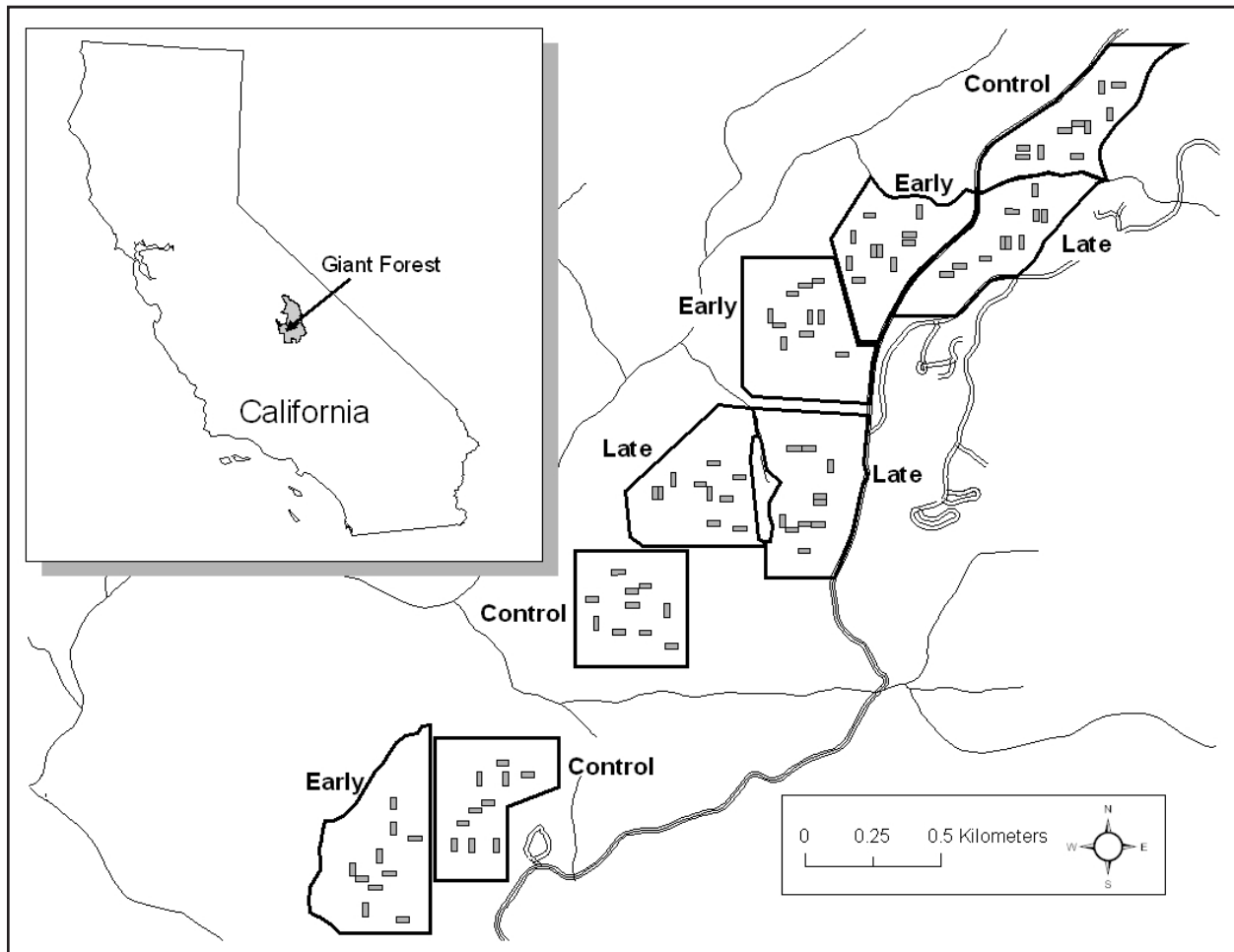
## METHODS

### Study Site

We conducted the study in an old growth mixed conifer forest within the Giant Forest region of Sequoia National Park, California, USA. The sites have never been logged. Fre- s w g p v " L t g u " e j c t c e v g t k | g f " v j g " h q t g u v u " r t k q t " v q " Euro-American settlement, but the area con- t a i n i n g the study plots has not burned since the n e v g " 3 : 2 2 u " \* U y g v p c o " *et al.* 3 ; : 4 + 0 " " V j g " e n k o c v g " is Mediterranean, with hot, dry summers and cool, wet winters, with about half of annual r t g e k r k v c v k q p " h c n n k p i " c u " u p q y " \* U v g r j g p u q p " 3 ; : : + 0 " " U q k n u " c t g " t g n c v k x g n { " { q w p i " \* o q u v n { " k p - e g r v k u q n u + " c p f " f g t k x g f " h t q o " i t c p k v k e " r c t g p v " o c - t e r i a l .

### Burning Treatments

We compared the effects of early season burning, late season burning and no burning across nine experimental units using data from the southern Sierra Nevada node of the Fire c p f " H k t g " U w t t q i c v g " p g v y q t m " \* U e j y k n m " *et al.* 422; + " \* H k i w t g " 3 + 0 " " V j g " g z r g t k o g p v c n " w p k v u " y g t g " g c e j " 3 7 " j c " v q " 4 2 " j c " k p " u k | g " c p f " y g t g " n q e c v g f " within larger burn areas on west to northwest facing aspects of variable slope at elevations ranging from 1900 m to 2150 m. Burning treatments were applied using a completely



**Figure 1.** Shows the plot layout for the Sequoia National Park site of the National Fire and Fire Surrogate study. Plot layout includes Control, Early, and Late treatments across multiple experimental units. The inset map shows the location of the study site within California's Giant Forest.

Experimental units were established in 2003 and were subjected to different fire treatments.

Early season burns were conducted on 20 and 27 June 2002. Late season burns were conducted on 28 September, and on 17 and 28 October 2003. Each experimental unit was designed to burn at low to moderate intensity, and resulted in a few cases of individual trees torching. Weather and fuel conditions at the time of the burns are provided in Knapp *et al.* (2007).

### Sampling

We took all pre- and post-treatment data in plots referenced to a 50 m grid in the interior of each experimental unit. A 50 m to 100 m buffer that was also treated. We averaged data from two transects at each of 36 grid points per experimental unit. We measured basal area, biomass, and other variables at each experimental unit. We took composite samples of soil and vegetation at each experimental unit.

ppkf"eqxgt."uj twd"eqxgt+"cv"vjg"uc o g"vgp"203"j c" subplots at each experimental unit, while understory species richness data were averaged from nine 1 m<sup>2</sup> quadrats at each 0.1 ha subplot. We measured fuels before and one year following burning. We measured trees, shrubs, and herbaceous vegetation before and three years following burning.

### Statistical Tests

We used the Mantel test to measure spatial fgrgpfpgpeg" c o qpi" uc o rngu" \*Ngi gpf t g" 3 ; ; 5." Legendre and Legendre 1998, Fortin and Dale 4227+0" "Vjg" Ocpvgn"vguv"eq o rctgu"vyq"qt" o qtg" fkuvcpeg" o cvtkegu."qpg" o cvtkz" \*A<sub>ij</sub> + being differ- gpegu"kp"vjg"xctkcdng"qh"kpvtgguv"\*g0i0."hwgn"nqcf- kpi."uvcpf" fgpukv{."gve0+." ykvj"vjg"qvjgt" o cvtkz" \*B<sub>ij</sub> + dgkpi"vjg" fkuvcpeg" dgvyggp"vjg"uc o rnkpi" units. The Mantel test computes the correlation between the two distance matrices, with the formula:

$$z = \frac{n}{i+1} \frac{n}{j+1} A_j B_j$$

The z"uvckuvke"ku"wuwcnn {"pqt o cnk | gf" \*r+<

$$r = \frac{1}{n} \frac{\sum_{i,j} A_{ij} \bar{A}_i \bar{B}_j}{s_A s_B}$$

where *n* is the number of elements in the distance matrix and *s<sub>A</sub>* and *s<sub>B</sub>* are standard deviations of the elements of the *A<sub>ij</sub>* and *B<sub>ij</sub>* matrices. Vjg"pqt o cnk | gf"uvckuvke"dgjcxgu"uk o knct"vq"vjg" Rgctuqp" eqttgncvkqp" eqghLekgpv." xct{kpi" dg- vyggp"ó3"cpf" -3."uq"vjcv"eqghLekgpvu"ecp"dg" compared to other variables at the same site or to similar variables at other sites. We deter- okpgf"vjg"qxgtcm"uk ipkLecpeg"qh"urcvkn"tgnc- vkqpujkrud{" rgt o wvcvkqp"vguvkpi" \*uvcpfctf"vguvu" are unreliable because the distances in the mat- vtkegu"ctg"pqv"kpfgpgfpgpv" ] I qungg"cpf" Wtdcp" 4229\_+0

We assessed spatial correlations among subplots within each experimental unit before cpf" chvgt" dwtpkpi" hqt" o gcuwtgu"qh" Ltg" ghggev" that are relevant for resource managers, includ- ing total surface fuels, large fuels, stand densi- ty, stand basal area, herbaceous vegetation cover, graminoid vegetation cover, shrub cov- er, and understory species richness. We sub- jected each of these measures within each ex- perimental unit to a Mantel test using Euclide- an distances, with 10000 permutations used to guvcndkuj"uk ipkLecpeg" \* " ?"2027+0" "Cnvjqwi j"vjg" large number of tests we performed would ar- gue for an adjustment of the critical value, we wanted these tests to be as liberal as possible vq"ugcte j" hqt" gxkfgpeg"qh"uk ipkLecpv"urcvkn"cw- vqeqtgncvkqp" \*g0i0." kh" yg" wugf" c" Dqphgttqpk" correction for our 144 tests, we would have a etkvecn"xcnwg"qh" " ?"2027"ü"366" ?"20222"57." \*c" xcnwg"pqv"uwtrcuugf" d {" cp {" qh" qwt"vguvu+0" "Hqt" dqvj"vjg"rtg/Ltg"cpf" rquv/Ltg"kpvtxcnu" yg"ecn- ewncvfg" vjg" tcvkq" qh" uk ipkLecpv" Ocpvgn"vguvu" versus the total number of tests conducted, and etgcvgf" ; 7" " eqpLfgpeg"kpvtxcnu" hqt"vjku"tcvkq" from 10000 bootstrapped samples.

To determine the effects of spatial autocor- tncvkqp" qp" cp" cuuguu o gpv" qh" Ltg" ghggev." yg" contrasted the results of tests that compared early versus late season burning using ordinary ngcuu/uswctgu" tgi tguukqp" \*QNU" cpf" c" urcvkn" igpgtck | gf" ngcuu" uswctgu" tgi tguukqp" \* I NU+0" Vjg"QNU" o qfgn"cuuwo gu"pq"urcvkn"cwvqeqtg- lation among samples, potentially leading to excessive reductions in standard errors of the rctc o gvt" guvk o cvgu" \*cpf" vjgtgd {" kp lcvkpi"vjg" rtdcdknkv {" qh" V { rg" K" gttqtu+." y jkng"vjg" I NU" model included spatial structure into the error vgt o" qh" vjg" tgi tguukqp" \*Rkpjgktq" cpf" Dcvgu" 4222+0" "Hqt"vjg" I NU" o qfgn." yg" wugf" c" urjgtk- cal spatial error structure, with the inclusion of c" pwi igv" ghggev" y jgtg" pggfgf" \*Etguugk" 3 ; ; 5+0" Qwt" tguqpug" xctkcdngu" ygtg"vjg" ejcpig" kp" c" hqtguv"cwtkdwvg" \*g0i0." rctgf" fkhgtgpegu"qh"uvgo" density<sub>rtg/Ltg</sub> - stem density<sub>rquv/Ltg</sub> + cu" rtgfkevgf" by season of burning. Season of burning con-



**Table 1b.** Mantel test results for relationships between spatial autocorrelation of stand characteristics and fire effects. The table shows the correlation coefficient (r) between the spatial autocorrelation of stand characteristics (Stand density, Basal area, Forb cover, Graminoid cover, Shrub cover, and Species richness) and the spatial autocorrelation of fire effects (Pre-fire and Post-fire). The correlation coefficients are shown in boldface. The significance level is indicated by asterisks (\*, \*\*, \*\*\*).

Observation	Treatment	Mantel r					
		Stand density (stems ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Forb cover (%)	Graminoid cover (%)	Shrub cover (%)	Species richness (m <sup>2</sup> )
Pre-fire	early	-0.0214	0.0046	-0.0574	0.1624	-0.1282	-0.1241
	early	0.0664	0.0454	0.2591	-0.0434	<b>0.4878</b>	<b>0.4589</b>
	early	0.0459	0.0297	0.0781	0.0021	0.0961	0.1743
	late	0.1907	0.0830	-0.0162	-0.2049	-0.1395	-0.2009
	late	<b>0.3339</b>	-0.1076	-0.0544	<b>0.3857</b>	-0.0753	0.2311
	late	0.0156	0.1366	-0.0358	0.0495	0.2654	-0.1754
	unburned	0.1313	0.1064	<b>0.4808</b>	0.1083	0.2900	0.2333
	unburned	<b>0.4008</b>	0.3319	-0.1771	0.1789	-0.1207	-0.1056
	unburned	-0.0372	-0.1592	0.0045	0.1470	-0.0513	-0.0950
Post-fire	early	<b>0.4763</b>	-0.0393	0.0168	-0.0029	0.2973	-0.0155
	early	-0.2356	0.0397	0.1430	-0.0480	-0.0185	0.2230
	early	0.2779	-0.0373	0.0191	0.0564	-0.2011	0.0013
	late	-0.0844	-0.2104	-0.1105	-0.0790	-0.0584	-0.1062
	late	0.1009	0.0935	0.0673	-0.0742	-0.1050	-0.0010
	late	<b>0.4551</b>	0.2165	0.0049	-0.0055	0.1364	0.1905
	unburned	0.2032	0.1414	<b>0.5612</b>	<b>0.3111</b>	0.2978	0.1827
	unburned	<b>0.3826</b>	<b>0.3597</b>	-0.0660	0.1680	-0.0039	-0.1181
	unburned	-0.0320	-0.1168	0.1633	-0.0147	0.1916	-0.1625

**Table 2.** Comparison of OLS and GLS models for the relationship between stand characteristics and fire effects. The table shows the parameter estimates (̂), standard errors (SE), p-values (P), Akaike weights (AICc), and the difference in Akaike weights (ΔAICc<sub>GLS</sub>) between the OLS and GLS models. The significance level is indicated by asterisks (\*, \*\*, \*\*\*).

Post-fire change	OLS			GLS			ΔAICc <sub>GLS</sub>
	̂ ± SE	P	AICc	̂ ± SE	P	AICc	
Total fuels (Mg ha <sup>-1</sup> )	35.16 ± 10.43	0.001	2497.7	35.06 ± 10.98	0.002	2506.2	-8.4
Large fuels (Mg ha <sup>-1</sup> )	9.4 ± 7.61	0.218	2361.6	9.76 ± 7.92	0.219	2365.2	-3.6
Stand density (stems ha <sup>-1</sup> )	27.96 ± 32.42	0.392	761.3	17.96 ± 44.55	0.688	752.3	9.1
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	0.93 ± 3.59	0.796	497.3	-0.61 ± 4.22	0.885	496.1	1.1
Forb cover (%)	6.11 ± 3.16	0.058	482.1	6.18 ± 4.6	0.184	467.6	14.5
Graminoid cover (%)	-0.54 ± 0.26	0.040	181.1	-0.54 ± 0.26	0.041	186.1	-5.0
Shrub cover (%)	5.85 ± 2.05	0.006	429.7	5.62 ± 2.24	0.015	434.7	-5.0
Species richness (m <sup>2</sup> )	0.28 ± 0.27	0.309	186.5	0.27 ± 0.33	0.405	181.4	5.1

the inclusion of spatial autocorrelation conceivably give rise to a different interpretation of the results when comparing  $P$  values. The effects of spatial autocorrelation should be taken into account when interpreting the results of the  $P$  test. The inclusion of spatial autocorrelation in the  $P$  test may lead to subtle biases in the effects of early versus late season prescribed burning, with late season burning resulting in the greater consumption of total fuel, lesser reductions in graminoid cover and greater reductions in shrub cover.

## DISCUSSION

Results of the Sierra Nevada, that there is little evidence of spatial autocorrelation in the effects of early versus late season prescribed burning, with late season burning resulting in the greater consumption of total fuel, lesser reductions in graminoid cover and greater reductions in shrub cover. We do not, however, take this as evidence that spatial autocorrelation should be ignored in the analysis. Higher fuel moistures in early season burns likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity. High patch scale heterogeneity is similar to that commonly observed at the landscape scale. Higher fuel moistures in early season burns likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity. High patch scale heterogeneity is similar to that commonly observed at the landscape scale. Higher fuel moistures in early season burns likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity. High patch scale heterogeneity is similar to that commonly observed at the landscape scale.

ple rules concerning the presence or absence of spatial autocorrelation should be taken into account when interpreting the results of the  $P$  test. The inclusion of spatial autocorrelation in the  $P$  test may lead to subtle biases in the effects of early versus late season prescribed burning, with late season burning resulting in the greater consumption of total fuel, lesser reductions in graminoid cover and greater reductions in shrub cover. We do not, however, take this as evidence that spatial autocorrelation should be ignored in the analysis. Higher fuel moistures in early season burns likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity. High patch scale heterogeneity is similar to that commonly observed at the landscape scale. Higher fuel moistures in early season burns likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity. High patch scale heterogeneity is similar to that commonly observed at the landscape scale.

Qwertzuiopkornjvhtguvneqpfkvpqpu before and after burning have a high degree of small, patch scale spatial heterogeneity. Knapp cpf" Mggng{ " \*4228+ " cnuq" hqwpf" gxkfgpeg" hqt jki j" rvej" uecng" jgvgtqj gpgkv{ "kp" Ltg" ugxgtkv{. " as measured by scorch heights and area burned, which they attributed to variation in topography, fuel characteristics and forest structure. Higher fuel moistures in early season burns likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity. High patch scale heterogeneity is similar to that commonly observed at the landscape scale. Higher fuel moistures in early season burns likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity, thereby likely inhibit effective fuel continuity. High patch scale heterogeneity is similar to that commonly observed at the landscape scale.

The presence of high patch scale variability is an important consequence for the management of Sierra Nevada forests. Bonnicksen and Upton (2003) and Upton (2003) argue that prescribed fire in heterogeneous forests, and application of prescribed fire to maintain unnaturally uniform forest conditions. This view has been challenged on several occasions (e.g., Upton 2003, Upton and Fiebert 2003) and our results also demonstrate that even following prescribed fire, forest conditions are far from homogeneous either before or after treatment. Encouraging stand heterogeneity either in fuels or vegetation is likely unnecessary in Sierra Nevada mixed conifer forests.

The lack of strong spatial autocorrelation also has implications for the interpretation and use of spatial autocorrelation. If spatial autocorrelation is generally weak, it is doubtful that one or even several small monitoring plots within a burned area will provide a general description of overall effects of a given fire. Evidently, the lack of strong spatial autocorrelation is generally weak, it is doubtful that one or even several small monitoring plots within a burned area will provide a general description of overall effects of a given fire.

with only a single plot established within each fire. The potential to support satellite-based observations might be best used when individual plot data are assembled together across a particular vegetation type. This approach might be best used when individual plot data are assembled together across a particular vegetation type.

We conclude that the conditions and results are certainly more variable than is sometimes suggested for an area as simply burned or unburned, as conditions combine to create heterogeneous conditions. We do not, however, possess a mechanistic understanding of what drives this complexity. Some factors are obvious, such as variation in slope or vegetation types within a burned area. Understanding these mechanisms is becoming increasingly important in fire management. Understanding these mechanisms is becoming increasingly important in fire management.

## ACKNOWLEDGEMENTS

We thank J. Keeley and E. Knapp for their management of the Sequoia National Park Fire and two anonymous reviewers for helpful comments on the manuscript; and J. Yee for statistical assistance. Any use of trade names is for descriptive purposes only and does not imply endorsement by the US government.

## LITERATURE CITED

- Dcvckpgj."C0N0."D0R0"Qu y cnf."O0"Dcvckpgj."F0"Wpigt."K0"Jwpi."cpf"F0"Ueqipcoknnq0"42280"Urcvkcncwvqeqtgtgncvkqp"cpf"rugwftqgrnkecvkqp"kp"Łtg"geqni {"0"Hktg"Geqni {"4<"329/33:0
- Dqpf."Y0L0."cpf"L0G0"Mggng{"0"42270"Hktg"cu"cinqdcn":jgtdkxqtgø<"vjg"geqni {"cpf"gxqnvkqp"qh"İc o-mable ecosystems. *Trends in Ecology & Evolution* 20: 387-394.
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