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Forests in the Sierra Nevada, similar to those across the continent, have been substantially altered by logging, fire exclusion, and other human activities. Current forest management emphasizes maintenance or restoration of resiliency in the face of contemporary disturbance factors that include wildfire, climate change, continued urbanization, and invasive species. We evaluated responses of small mammals to forest management by monitoring a series of 12 replicate trapping grids in compositionally homogeneous forest over 8 years, and implemented 2 levels of canopy thinning. Livetrapping efforts (119,712 trap-nights) yielded 15,613 captures of 2,305 individuals of 13 species, and although forest structure was significantly influenced by canopy treatments, small mammal numbers and assemblage composition were not. To better understand this we assessed habitat associations of small mammals at 599 census points on 75 transects established in a stratified random manner throughout Plumas National Forest. We analyzed these data with 2 complementary forms of constrained ordination (canonical correspondence and canonical correlation) that extract major gradients in 1 data set (e.g., distribution of small mammal captures) and explain these in terms of measured variables from a 2nd data set (e.g., habitat and environmental measurements). Over 3 years and 57,504 trap-nights of effort we captured 1,367 individuals of 11 species. Both forms of ordination exposed significant associations between small mammals and underlying habitat metrics, but they explained remarkably little variation in these data, suggesting that small mammals are responding only modestly to habitat variation as expressed by the available environmental variables measured at each plot. We followed this with stepwise multiple Poisson regression to build models of habitat associations of these species. We applied model-averaging and employed Akaike's information criterion corrected for small sample size (AIC_c) to evaluate candidate models. Reflecting ordination results, competitive models (e.g., those with Akaike differences [ΔAIC_c] < 2.0) cumulatively explained little variation (12–36%) and regression coefficients were very low. Hence, both ordination and Poisson multiple regression suggest that the limited response by small mammals to canopy thinning primarily reflects the generalist habits of the common species in this forest. We propose that anthropogenic influences have led to structural homogenization of these forests, even across > 800 m of elevation, such that habitat specialists (e.g., old-forest–dependent species such as *Myodes* [*Clethrionomys*] *californicus* and *Glaucomys sabrinus*) have become less common due to the lack of suitable habitat. Further efforts should target nonforested habitats (meadows and riparian corridors), but results presented here suggest that managers should strive to increase heterogeneity at large spatial scales and especially to promote the development of mature forest structure.

Key words: forest management, habitat associations, montane small mammals, ordination, Sierra Nevada, stepwise multiple regression

The challenge for sustainable forestry is to define the attributes of forested ecosystems that are ecologically and societally important and to maximize these ecosystem services in the face of change (Chapin et al. 2002:359).

Forests in montane western North America have been subjected to extensive alteration over the past century, reflecting decades of logging, increasing urbanization, and widespread and systematic fire suppression. In spite of their limited area, coniferous forests and associated habitats of the Sierra Nevada, Cascade, and Rocky Mountain ranges support nearly one-half of North American mammal species (Lawlor 2003). A recent review of mammal ecology in these systems (Zabel and Anthony 2003) highlights applied research on the ecology of small mammals in these areas, but underscores an emphasis in the Rocky Mountains and especially the Pacific Northwest (mostly Oregon and Washington). Much less work has been pursued in the topographically and taxonomically diverse Sierra Nevada, where often little more than basic presence–absence data are available to managers. As a result it is unclear how small mammals in this relatively xeric system compare ecologically and in terms of forest and wildlands management with those of the more mesic Cascade Range to the north, and the more interior montane system of the Rocky Mountains.

The topographical and ecological characteristics of the Sierra Nevada have resulted in very diverse forest communities relative to the more uniform conditions of Pacific Northwest forests (Helms and Tappeiner 1996). Northern flying squirrels (*Glaucomys sabrinus*), for example, are more restricted by available soil moisture and presumably the resulting distribution of truffles (Meyer et al. 2005; Smith 2009; see also Lehmkuhl et al. 2006). The extent to which this characterizes other species is not clear. However, the Sierra Nevada supports a diverse mammal fauna (Ingles 1965; Jameson and Peeters 2004), many of which have important ecological roles as key prey for predators, consumers and disseminators of conifer and other seeds, disseminators of fungal spores (many of which are mycorrhizal), or as keystone species (Carey 2000, 2009). Species here range from strongly generalist taxa such as *Peromyscus maniculatus* and *Tamias* species to habitat specialists such as the riparian-associated *Zapus princeps* and *Sorex palustris*, and others dependent on mature forest (e.g., *Myodes* [*Clethrionomys*] *californicus* and *Phenacomys intermedius*). Consequently, anthropogenic impacts are likely to impact some species more heavily than others, and generalists are likely to fare well in the face of such influences.

Forest management in the Sierra Nevada has the multifaceted objectives of sustaining or enhancing diverse ecosystem services, including promoting biodiversity, while simultaneously reducing the risk of wildfire and supporting resource-based employment opportunities (North et al. 2009; North 2012), and within this context our research pursued 2

parallel field efforts over 8 years (2003–2010). We worked in Plumas National Forest (PNF) located in the northern Sierra Nevada. Broadly speaking, our objectives were to document demographic responses to forest management and to characterize small mammal habitat associations across a range of forest types. We initially focused on demographic responses by small mammals to 2 levels of canopy thinning at study sites we sampled both before and after treatment. Reflecting the needs of forest managers in PNF, these efforts focused on forest dominated by white fir (*Abies concolor*), the most widespread forest type in this forest. We predicted that small mammals would respond to these habitat alterations, and that the response would be greater in more heavily thinned sites. Because we anticipated that the mammal fauna here would be dominated by generalist species, we expected differential shifts in relative composition rather than wholesale changes in community composition. To monitor this, we tracked responses by individual species as well as community parameters. Initial evaluations suggested overwhelming dominance by only a few species. To assess responses over a greater range of habitat structure and composition, we expanded our efforts to evaluate mammal assemblage composition across most forest types (using stratified random sampling) in PNF over a 3-year period. We recorded extensive structural and habitat features at all sampling points, and predicted that small mammal species would segregate in ordination space according to structural features segregating preferred forest type or suites of environmental variables. We compiled the most comprehensive sampling regime of which we are aware in the Sierra Nevada, and somewhat unexpectedly the results suggest that the legacy of fire exclusion and timber extraction has led to severe biotic homogenization in the Sierra Nevada; indeed, it is the lack of diversity across both spatial and temporal data sets that we find most impressive, and most informative to conservation biologists and landscape managers.

MATERIALS AND METHODS

Study Area

This study includes spatial and temporal data sets. All data were collected in PNF, located in the vicinity of Quincy, California (39°56′N, 120°57′W), in the northern Sierra Nevada. Topography generally is rugged and montane, with elevations ranging from $< 1,000$ to $> 2,200$ m. Annual precipitation in Quincy is 105 cm ($SD = 28.7$ cm; 1895–2012 [Western Regional Climate Center 2013]). Overall, PNF is dominated by lower and upper montane vegetation such as ponderosa pine (*Pinus ponderosa*)–mixed conifer, white fir–

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mixed conifer, and red fir (*Abies magnifica*) forest types (Fites-Kaufman et al. 2007). Common tree species include red fir, Douglas-fir (*Pseudotsuga menziesii*), mixed ponderosa pine or Jeffrey pine (*P. jeffreyi*), and incense cedar (*Calocedrus decurrens*). Common shrubs in our sites include Woods' rose (*Rosa woodsii*), Sierra gooseberry (*Ribes roezlii*), Utah serviceberry (*Amelanchier utahensis*), bush chinquapin (*Chrysolepis sempervirens*), green-leaf and white-leaf manzanita (*Arctostaphylos patula* and *A. viscida*), mountain dogwood (*Cornus nuttallii*), mountain whitethorn and deer brush (*Ceanothus cordulatus* and *C. integerrimus*), bitter cherry (*Prunus emarginata*), willow (*Salix* spp.), Fremont silk tassel (*Garrya fremontii*), Sierra coffee berry (*Rhamnus californica*), and huckleberry oak (*Quercus vacciniifolia*). Pinemat manzanita (*Arctostaphylos nevadensis*) occurs almost exclusively in red fir forests, and buck brush (*Ceanothus cuneatus*) occurs predominantly in pine–incense cedar forests. The small mammal fauna of this region includes 6 shrews and moles (Soricomorpha), 9 squirrels (Sciuridae), 1 zapodid rodent, and 11 murid rodents (Supporting Information S1, DOI: 10.1644/12-MAMM-A-303.S1).

Long-term Plots

In summer 2003 we established 18 long-term plots in white fir ($n = 9$), red fir ($n = 3$), Douglas-fir ($n = 3$), and pine–incense cedar ($n = 3$) forests; we established 3 additional plots in white fir habitat in 2005. Coppeto et al. (2006) reported on mammal assemblages and habitat relations across all habitat types on the original 18 plots; here we focus on data collected over 8 years on the 12 plots in white fir habitat. These plots were established with the objective of evaluating small mammal responses to experimental canopy thinning, and were placed in 3 blocks established in structurally similar forest with approximately 70% canopy cover (Bigelow et al. 2011). Each block consisted of 4 plots assigned randomly to control, group selection (small-scale clear-cuts, approximately 0.5–1 ha), and 2 levels of canopy thinning (moderate and heavy); treatment resulted in a reduction of canopy cover to 12% (group selection), 49% (heavy thin), and 56% (moderate thin).

Small mammal sampling.—All sites were sampled with 100 Sherman live traps (model XLK; H. B. Sherman Traps, Inc., Tallahassee, Florida) placed on the ground in a 10×10 array with 10-m spacing, nested within a larger 6×6 grid of 72 Tomahawk traps (model 201; Tomahawk Live Trap, Tomahawk, Wisconsin; 1 ground trap and 1 arboreal trap) with 30-m spacing. Total sampling effort comprised 120 trap stations, and the area sampled was approximately 3.24 ha (including a one-half intertrap–distance buffer). Ground traps were placed within 1 m of the grid point, and arboreal traps were placed 1.5–2 m above the ground on the largest tree within 10 m of the grid point; we selected larger trees to provide better support for traps, thereby improving trap functionality and capture success (Carey et al. 1991). We are not aware of any species in this region for which such treatment would have resulted in a negative bias, but in any event the functionality of these traps precluded placement on small trees.

Traps were baited with a mix of crimped oats and black oil sunflower seeds lightly coated in peanut butter or with a mixture of rolled oats, molasses, raisins, and peanut butter that was formed into a small, sticky ball (Carey et al. 1991). We placed small nest boxes (plasticized-paper milk cartons) behind the treadle in Tomahawks to minimize stress and provide cover (Carey et al. 1991), and we provided nonabsorbent polyethylene bedding material and cover (e.g., bark, moss, or cover boards) as needed for thermal insulation. Each census was conducted over 4 consecutive nights. Traps were set and baited every evening just before dusk, and checked just after dawn. Sherman traps were then closed, whereas Tomahawk traps were rebaited, then checked and closed at midmorning (≥ 2 h after the 1st trap check).

Captured animals were identified to species, individually marked with numbered ear tags (model 1005-1; National Band & Tag Co., Newport, Kentucky), weighed, aged (based on weight, pelage, and reproductive condition), examined for reproductive status, and released at the point of capture. Total processing time generally was < 2 min. All fieldwork and handling procedures were approved by the University of California, Davis Animal Use and Care Administrative Advisory Committee protocol, and meet guidelines recommended by the American Society of Mammalogists (Kelt et al. 2010; Sikes et al. 2011, 2012).

Most plots were sampled for small mammals 1–6 times annually, May–October, 2003–2010. Changes in frequency of sampling reflected changing objectives and resources, and avoidance of trap damage by black bears (*Ursus americanus*). For the purposes of this study we characterized trapping efforts as spring or early summer (May–June), summer (July–August), or late summer or fall (September–October). When 2 samples were made in a given season we used the mean values across both samples.

We calculated the minimum number known alive for all species because repeated samples were insufficient to warrant application of demographic estimators (Krebs 1966). Because minimum number known alive does not account for nondetection it has the potential to produce biased inferences. However, all sampling efforts were conducted in similar (coniferous forest) habitat so any resulting biases were evenly distributed across samples. Additionally, the overwhelming majority of captures comprised only a few species (see "Results") and we refrain from pursuing detailed assessment of uncommon species. As such, we believe that minimum number known alive is sufficient for the objectives of this study.

Our sampling efforts resulted in capture of 13 species of small mammals, but the distribution of captures was highly asymmetric, as expected for montane forests (Hallett et al. 2003). Four species (*Microtus longicaudus*, *M. montanus*, *Sciurus griseus*, and *Thomomys bottae*) were captured ≤ 3 times each and are not considered further except in metrics of community structure. Fully 88% of all individuals captured in this study were deer mice (*P. maniculatus*) or chipmunks (*Tamias senex* and *T. quadrimaculatus*). An additional 5%

TABLE 1.—Environmental metrics recorded in Plumas National Forest. Ground cover metrics were recorded by ocular estimation and included all vegetation at or below breast height; vegetation above breast height was included in canopy cover measurements using photo analysis. Aspect was recorded with a compass and slope was recorded with a clinometer. Three metrics (denoted with an asterisk [*]) could not be normalized at the station scale and so are not used in analyses at that scale.

Variable	Acronym	Definition
Bare ground cover	Bare	Cover by exposed soil
Fine woody debris cover	FWD	Cover by downed woody debris < 10-cm diameter
Canopy closure	Canopy	Cover of open sky above breast height (1.4 m)
Coarse woody debris cover	CWD	Cover by downed woody debris >10-cm diameter; includes all stumps and snags
Elevation	Elev	Elevation (m)
East–west aspect	EW	Aspect in east–west direction (0 = E, 180 = W)
Mat-forming ground cover	GndCov	Cover by low-growing mat vegetation (e.g., *Ceanothus prostratus*) and by mosses
Hardwood cover	HardCv	Cover by hardwoods (*Quercus kelloggii* and *Cornus nuttallii*)
Herbaceous cover	HerbCv	Cover by graminoids, forbs, and suffrutescent shrubs
Litter cover	Litter	Cover by dead leaves, pine needles, wood chips, and sawdust-like debris
Number of live trees	Tree	Number of live standing trees
North–south aspect	NS	Aspect in north–south direction (0 = N, 180 = S)
Live shrub cover	LiveShrb	Cover by true shrubs and shrubby trees ≤ 5 m
Rock cover	Rock	Cover by exposed rocks and large stones
Number of saplings	Sapling	Number of small trees < 2-m tall
Sapling species richness	SapRich*	Number of species of saplings (transect only)
Shrub species richness	ShRich*	Number of species of shrubs (transect only)
Slope	Slope	Slope (degrees)
Number of large snags	Snag30	Number of snags > 30-cm diameter at breast height (50-m plot)
Snag basal area	SnagBA	Basal area by snags (50-m plot)
Softwood cover	SoftCv	Cover by softwoods (firs, pines, and Douglas-fir)
Tree basal area	TotBA	Basal area by trees (> 5-m tall; 50-m plot)
Tree cover	TreeCv	Cover by trees (> 5-m tall; 50-m plot)
Tree species richness	TrRich*	Number of species of trees (transect only)

comprised northern flying squirrels (*G. sabrinus*) and brush mice (*Peromyscus boylii*).

To assess responses by small mammal species to forest treatments (control, moderate thin, heavy thin, and group selection) we applied a repeated-measures multivariate analysis of variance (rmMANOVA). Because we did not expect data to be normal, and no species numbers can be negative, we used a Poisson mixed-model (Proc GLIMMIX; SAS Institute Inc., 2008); we used a Satterthwaite approximation for the denominator *d.f.*, and the default variance components covariance structure. We developed a binary dummy variable (PrePost) to distinguish samples collected before and after application of thinning treatments. We nested years within PrePost and we nested sites within treatments. We treated sites (within treatment) as random, as well as all interactions involving this variable; all other variables were treated as fixed effects. We only analyzed responses by the 3 most abundant species because the analysis would not converge when additional species were included.

Vegetative measurements.—We recorded habitat metrics at every trapping station before thinning treatments were effected (summer 2005) and after treatments had been in place for a full year (summer 2008); active forestry operations precluded us from making these measurements on group-selection plots prior to treatment. Metrics were selected to characterize structural features of the forest thought to be important to small mammals (Table 1), and include 3 abiotic measures (elevation, slope, and aspect) and 10 cover estimates made at 1,440 ground cover plots (1-m radius) at

our experimental long-term plots ($n = 12$), supplemented with data on trees and snags at a larger (50-m circular plot) scale (Table 1). Additionally, in 2010 we captured and analyzed hemispherical canopy photos at all trapping points, using a digital camera affixed with a hemispherical lens mounted at breast height (1.4 m) on an adjustable tripod. All photos were taken with a 180° azimuth at low-light hours to ensure that the contrast between canopy and sky was not obscured by the reflection of sunlight off vegetation. Photos were analyzed with Gap Light Analyzer 2.0 (Frazer et al. 2000; Bigelow et al. 2011).

Statistics.—Because group-selection plots were established after we had recorded pretreatment habitat metrics, we were able to evaluate temporal variation in the environment (2005 versus 2008) only for control plots and 2 levels of canopy thinning. We accomplished this with a principal component (PC) analysis on 12 environmental variables using a correlation matrix (Table 2). We applied square-root and log transformations as necessary to approach normality. We assessed the number of informative PC axes with a scree plot, and analyzed the distribution of sample plots over time and across treatments using MANOVA on informative PC axes. Segregation of treatments on PC axes was quantified with Scheffé a posteriori tests.

Forest-wide Surveys—Stratified Random Sampling Across Plumas National Forest

To complement data collected at our long-term plots and to incorporate additional habitat diversity in PNF we surveyed

TABLE 2.—Informative eigenvectors from a principal component analysis on habitat metrics from 9 long-term study plots in Plumas National Forest. Larger loadings are indicated in boldface type. These analyses exclude group-selection plots for which pretreatment data were not available. Acronyms are as in Table 1.

	PC1	PC2	PC3	PC4
Eigenvalue (λ)	2.42	1.79	1.64	1.10
Cumulative proportion of variance explained	0.20	0.35	0.49	0.58
Rock	**0.412**	−0.249	0.275	−0.037
Bare	**0.463**	−0.223	0.257	−0.159
Litter	−0.198	−0.129	−0.196	**0.699**
FWD	−0.266	0.167	−0.284	**−0.316**
CWD	−0.080	0.040	−0.052	**−0.386**
LiveShrb	0.134	**0.617**	0.171	0.190
GndCov	0.002	−0.026	0.267	0.147
HerbCv	−0.069	**0.306**	0.094	**−0.369**
Tree	**−0.387**	−0.064	**0.549**	0.009
ShRich	0.173	**0.597**	0.171	0.188
TrRich	**−0.400**	−0.085	**0.538**	−0.004
Canopy	0.371	0.011	0.083	0.083

small mammal communities at up to 8 trapping points at 250-m intervals on 75 transects distributed randomly throughout the forest but stratified by major forest habitat type (e.g., red fir, white fir, etc.), with the exception that the location of transects was constrained to some extent by access and feasibility of sampling (e.g., very steep slopes and inaccessible locations). We divided this effort across 3 field seasons (2006, 2007, and 2009) and we arranged our efforts such that each year we sampled transects throughout the forest. At each census point, we established a 2 × 2 array of live traps in a square arrangement 50 × 50 m, ensuring that all traps resided within a 50-m radius to match plots established for some vegetation measurements (see below). These efforts resulted in placement of trap arrays at 582 points, 521 of which yielded small mammal captures.

Small mammal sampling.—As with long-term plots, we sampled all stations with 1 Sherman (ground) and 2 Tomahawk (ground + arboreal) traps placed at each station in the array; thus, each array (point) consisted of 12 live traps, and each transect of 8 points included 96 traps. Trap placement and trap baiting and setting protocols were similar to those in long-term plots. Surveys consisted of 2 sequential 4-night sessions separated by 2 nights, allowing for a period of rest for animals from the stress of repeated capture and handling (Carey et al. 1991). Hence, assuming no interruptions, each transect was surveyed with 768 trap-nights of effort. For comparability with long-term plots we apply minimum number known alive to estimate small mammal numbers. As with our long-term plots, the vast majority of captures (and individuals) at these transects comprised few species and we refrain from pursuing refined assessments for less common species, such that minimum number known alive should not unduly bias our results.

Vegetative measurements.—We measured habitat characteristics at all trap stations ($n = 2,397$) in the same year that mammals were surveyed, and with the same approach

used in long-term plots to allow for comparability, with the exception that canopy cover was measured with a moosehorn (Garrison 1949) rather than digital photography, and some variables (Table 1) were recorded using 50-m-radius plots centered on each point. As noted, each trap station lay within these 50-m-radius plots. Although we recorded elevation at every point, preliminary analyses indicated that results were similar regardless of whether this parameter was included; model fit was only slightly improved when elevation was included, but correlations between ordination results with and without elevation were very high ($r > 0.9$). We interpret these observations to suggest that elevation is the driving influence underlying the distribution of habitat features (as expected— Grinnell et al. 1930; Moritz et al. 2008). Because we are interested in mammalian responses to environmental variables, however, we include only results from analyses excluding elevation.

Statistics.—We applied complementary approaches to analysis of these data. To evaluate the role of spatial scale, we conducted these both for data at the point level (all unique individuals at 4 stations per point) and at the transect level (data compiled across 8 points within each transect). We began with 2 forms of constrained ordination, canonical correspondence analysis (CCA) and canonical correlation (CanCorr). Constrained ordination extracts major gradients in the data from 1 data set (e.g., distribution of small mammal captures) and explains these in terms of measured variables from a 2nd data set (e.g., habitat and environmental measurements). CCA is an iterative multiple regression between site scores (e.g., mammal captures) and environmental variables, and produces a series of canonical (e.g., constrained) coefficients between these data sets, as well as a multiple correlation of the regression (the species–environment correlation) that is a measure of the association between species and the environment. Because ordinations yielding small eigenvalues may have misleadingly high species–environment correlations, a better metric of this association is the associated eigenvalue, which measures how much variation in the site scores is explained by the corresponding environmental variables (ter Braak 1995). Importantly, CCA assumes that species respond unimodally to environmental variation, which generally seems a reasonable assumption with data sets spanning modest ecological gradients. CanCorr is another eigenanalysis method that aims to find ordination axes that maximally reveal the relationships between 2 related data sets (e.g., small mammal captures and associated environmental variables). Unlike CCA, CanCorr assumes linear responses, which some authors (e.g., Gauch and Wentworth 1976) consider unreasonable. Additionally, ter Braak (1995) notes practical constraints with this method when the number of species analyzed is large; this is not a concern with our study. Other authors (Manly 1994; McGarigal et al. 2000) note that CanCorr is an appropriate and informative method when assumptions are not violated. Because each analysis provides complementary insights to species-environment associations and very different output, we apply both here in an attempt to glean a
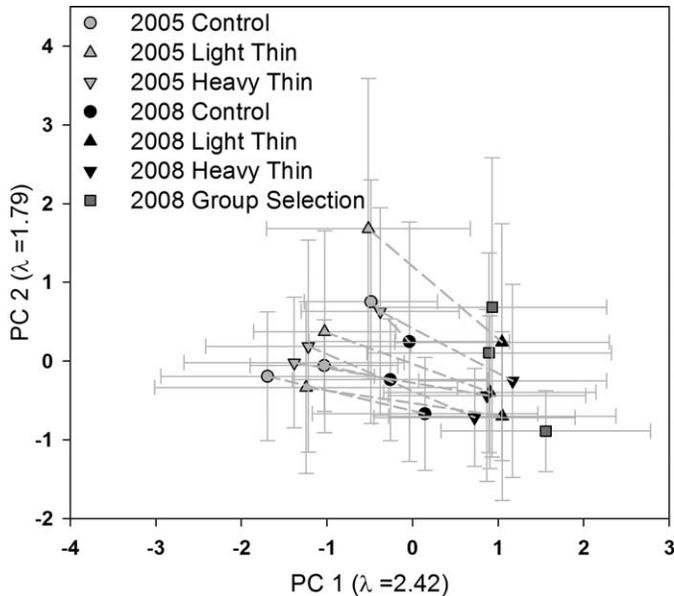
FIG. 1.—Biplot showing vegetative changes in long-term study plots between 2005 and 2008. Lines connect identical plots before versus after thinning. Although we lack pretreatment habitat metrics for group-selection plots, and group-selection plots were not included in analyses discussed in text, we include them here for reference; principal component analysis results are virtually identical when these are excluded.

better understanding of mammalian responses to a gradient in environmental conditions across PNF.

We ran CCA in PC-Ord 6.04 (McCune and Mefford 2011). We standardized row and column scores by centering and normalizing them. Mammal data were log-transformed to prevent domination of the ordination by common species. CCA produces 2 sets of site scores, which either are linear combinations of environmental variables, or are calculated by weighted averaging. Palmer (1993) recommends the use of linear combination scores in CCA but McCune (1997) showed that these are highly sensitive to "noisy" environmental variables. Because environmental noise is inevitable in data such as used here, we used weighted averaging scores and, correspondingly, we used intraset correlations (ter Braak 1986; McCune and Grace 2002). We ran CanCorr in SAS (Proc CANCORR—SAS Institute Inc. 2008), applying log or square-root transformations to environmental variables as necessary to meet assumptions of normality, and standardized all data to a mean = 0, $SD = 1$; we applied log transformations (log (value + 0.05)) to all mammal species. For both analyses we included the following environmental parameters (Table 1): Bare, Canopy, CWD, EW, FWD, GndCov, HardCv, HerbCv, Litter, LiveShrb, NS, Rock, Sapling, Slope, Snag30, SnagBA, SoftCv, and TrRich.

Because our results indicated very low spatial structure as a function of environmental variables, we pursued an exploratory assessment of habitat associations for species and community metrics using Poisson regression. To evaluate community responses across PNF we tallied the total number of individuals

and species captured at sites, and we calculated both Shannon–Weiner evenness ($H' = -\Sigma[p_i \ln(p_i)]$) and Simpson's evenness ($D = \Sigma \, p_i^2$), where p_i is the proportional contribution to the community by mammal species i (Magurran 1988). Because SAS does not provide a means of selecting among competing models with Akaike's information criterion corrected for small sample size (AIC_c) scores in stepwise regression, we conducted separate analyses (Proc REG—SAS Institute Inc. 2008) to select the best 1, 2, 3, …, 21-variable models; we then combined these in a single data set and ranked them by AIC_c. By running separate analyses for each step in model complexity, results (based on MAXR model selection) were identical to that that would be obtained using AIC_c. SAS Proc REG also does not allow for stepwise Poisson regression, which would be appropriate for count data used here. However, Poisson regression employs a log-link function, and we log-transformed all mammal data for these analyses, reducing the disparity between these approaches. Nonetheless, we then accepted all resulting models with Akaike differences (ΔAIC_c) < 2.0 and subjected these to Poisson regression (Proc GLIMMIX—SAS Institute Inc. 2008). We ranked the resulting models by AIC_c and calculated both relative importance (e.g., $\Sigma \, w_i$) and model-averaged parameter values ($\overline{\beta} = \Sigma(\beta \times w_i)/\Sigma \, w_i$) for environmental variables across all models (Burnham and Anderson 2002). We consider environmental variables to be informative when they exhibit both high relative importance (e.g., $\Sigma \, w_i >$ approximately 0.8) and large mean parameter coefficients.

RESULTS

Long-term Plots

Principal component analysis documented significant vegetative responses to canopy thinning, whereas small mammal assemblages exhibited no such response. PC analysis on 12 habitat and environmental variables yielded 6 PC axes with eigenvalues (λ) > 1.0, of which at most 4, and likely only 2, were particularly informative (based on a scree plot; Table 2). The 1st axis explained 20% of the variance in the data; was negatively weighted by tree species richness, number of trees, and cover by fine woody debris; and was positively weighted by canopy openness and cover by rock and bare ground. The 2nd axis explained an additional 15% of the variance, and comprised a gradient from sites with high cover by rocks and bare ground to those with abundant herbaceous cover and especially greater shrub species richness and cover. The 3rd and 4th axes explained another 13% and 9% of variance, respectively, and generally are not considered further.

Repeated-measures MANOVA on the first 4 PC axes demonstrated effects both of year (2005 versus 2008) and treatment (control and 2 levels of thinning) as well as an interaction between these. Scheffé's a posteriori tests on least-squared means indicated that control plots differed from both moderate and heavy thinning on PC1, whereas the 2 thinning treatments differed from each other on PC2 (but neither

TABLE 3.—Repeated-measures MANOVA on small mammals in long-term experimental plots using the 3 most common species (*Peromyscus maniculatus*, *Tamias senex*, and *Tamias quadrimaculatus*; 92% of individuals captured). PrePost = dummy variable distinguishing years before and after application of thinning treatments; Trt = canopy treatments; Sp = species; Yr(PrePost) = year nested within PrePost.

Effect	d.f.	F	P
Season	2, 100.1	1.05	0.354
PrePost	1, 30.27	3.29	0.080
Trt	2, 11.34	0.65	0.539
Sp	2, 20.13	8.95	0.002
Yr(PrePost)	6, 174	17.46	< 0.0001
PrePost × Season	2, 59.7	0.28	0.755
Season × Trt	4, 53.1	1.48	0.221
Season × Sp	4, 174	4.07	0.004
PrePost × Sp	2, 42.1	8.87	6E−04
PrePost × Trt	2, 24	0.85	0.439
Trt × Sp	4, 22.18	1.41	0.263
Season × Yr(PrePost)	5, 174	3.21	0.009
Trt × Yr(PrePost)	10, 174	0.61	0.807
Sp × Yr(PrePost)	12, 174	5.89	< 0.0001
PrePost × Season × Trt	3, 43.91	1.45	0.240
PrePost × Season × Sp	4, 174	2.79	0.028
Season × Sp × Trt	7, 174	1.98	0.061
Season × Trt × Yr(PrePost)	6, 174	2.39	0.030
Season × Sp × Yr(PrePost)	10, 174	0.78	0.643
Trt × Sp × Yr(PrePost)	17, 174	1.87	0.023
PrePost × Trt × Sp	4, 43.5	0.20	0.939
Season × Trt × Sp × Yr(PrePost)	5, 174	1.31	0.262
Season × Trt × Sp × PrePost	3, 174	1.13	0.339

differed from controls). When this was parsed to include a year effect, we found that thinning treatments generally were similar to each other before as well as after treatment, but they both shifted in the same direction in ordination space (Fig. 1); this was true of control plots as well but to a lesser extent (circles in Fig. 1). In general, plots shifted to higher values on PC1 and lower values on PC2, suggesting a general reduction in forb, shrub, and canopy cover and an increase in bare ground and rock cover, as expected. The roughly parallel temporal shift in control plots, however, likely reflects substantial interannual variation in abiotic drivers in this system (a conjecture supported by the strong temporal changes in small mammal numbers documented below).

Small mammal assemblages did not respond to forest thinning treatments. Over 8 years, 119,712 trap-nights of effort on these plots yielded 15,363 captures of 2,305 individuals representing 13 species of small mammals. Of these, 88% comprised only 3 species—*P. maniculatus* (53%), *T. senex* (25%), and *T. quadrimaculatus* (10%). *G. sabrinus* and *P. boylii* were the 4th and 5th most commonly captured species, and together comprised an additional 3%. We applied rmMANOVA to the 3 most common species, and because light and heavy thinning did not separate clearly in PC space (see above) we combined these into a single treatment; hence, these analyses evaluate small mammals in control, thin, and group-selection treatments. The effect of season was not important (Table 3), but models failed to converge if we removed this effect so a simpler set of models was not analytically possible. Captures varied by species and across years, and we documented a significant interaction between species and the imposition of treatments (PrePost × Sp) but this was not associated with the thinning treatments themselves (e.g., did not include Trt) so likely was merely a function of univariate effects of species over time. Parameters of particular interest here are those that reflect differential temporal changes across treatments (e.g., those that include an interaction between the treatments and the imposition of these treatments; Trt × PrePost). Our analysis included 4 such interactions, none of which were significant (Table 3).

Forest-wide Surveys

Over 3 years we sampled 582 points on 75 transects. A total of 57,504 trap-nights of effort yielded 1,367 individuals of 13 species; 4 species were sufficiently uncommon that they were excluded from further consideration (*M. californicus*, *Z. princeps*, *M. longicaudatus*, and *M. montanus*). We analyzed these data with 2 forms of constrained ordination (CCA and CanCorr) and with multiple Poisson regression. In general, small mammals exhibit little if any compositional responses to spatial variation in habitat structure.

TABLE 4.—Results of canonical correspondence (CC) analyses at 2 spatial scales. Significant eigenvalues (λ) and correlations are indicated by an asterisk (*).

|	CC axis 1	CC axis 2	CC axis 3
Transect scale; total inertia 0.729			
Eigenvalue (λ)	0.153*	0.048	0.042
Randomization of eigenvalues	0.075 (0.038–0.132)	0.041 (0.025–0.064)	0.030 (0.018–0.051)
% variance explained	21.0	6.6	5.8
Species–environment correlations	0.816*	0.697	0.694
Randomizations of species–environment correlations	0.606 (0.442–0.763)	0.635 (0.409–0.732)	0.571 (0.390–0.732)
Station scale; total inertia 2.491			
Eigenvalue (λ)	0.141*	0.063*	0.040*
Randomization of eigenvalues	0.032 (0.017–0.060)	0.023 (0.013–0.042)	0.017 (0.010–0.028)
% variance explained	5.6	2.5	1.6
Species–environment correlations	0.556*	0.409*	0.355*
Randomizations of species–environment correlations	0.296 (0.213–0.385)	0.262 (0.188–0.345)	0.235 (0.171–0.298)
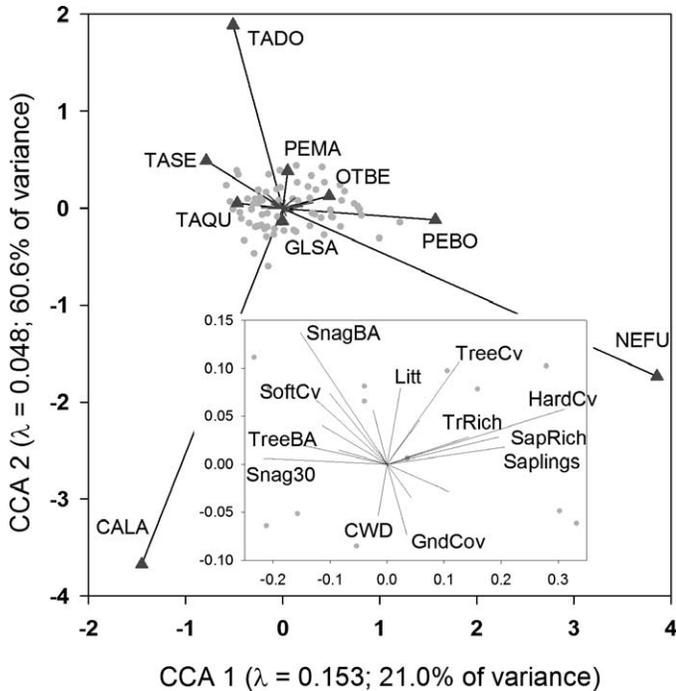
FIG. 2.—Biplot scores for first 2 axes of canonical correspondence analysis on data from forest-wide transects in Plumas National Forest. Light gray symbols present location of sampling points in ordination space. Inset shows vectors for environmental measurements. Acronyms are as in Supporting Information S1 and Table 1.

Canonical correspondence analysis.—At both spatial scales CCA produced 3 ordination axes, although not all of these were significant. At the broader (transect) scale ordinations had low inertia that explained only modest proportions of variance in our data. Axes reached tolerance after 14, 105, and 15 iterations. The 1st axis (Table 4) explained 21% of the variance in these data ($\lambda = 0.153$) and yielded significant correlations between small mammal species and environmental variables ($P < 0.0005$ based on 1,999 randomizations). Only 2 among-variable correlations exceeded 0.60 (sapling versus sapling richness, 0.76; and litter versus softwood cover, 0.62). Although the 2nd canonical correspondence (CC) axis fell within the range of randomized values (and therefore is not statistically significant), we include this to the extent that it allows us to present these results in bivariate ordination space.

Canonical correspondence analysis produces several types of coefficients but these yielded a consensus in terms of the limited importance of environmental variables on CC axes. Standardized canonical coefficients were modest and indicated that the 1st axis was negatively influenced only weakly by softwood cover (−0.11), polarized modestly against hardwood cover (0.23) and number of saplings (0.12). Interset correlations polarized the 1st CC axis by number of large snags (−0.45) and basal area by both snags (−0.32) and trees (−0.31) contrasted against hardwood cover (0.65) as well as sapling abundance (0.43) and sapling species richness (0.41). Finally, biplot scores (Fig. 2) were generally weak, polarizing number of large snags (−0.22) against hardwood cover (0.31). Hence,

this axis presents a gradient from sites with abundant hardwoods and saplings to those characterized by numerous and large snags.

The 2nd and 3rd CC axes were markedly smaller and were not significant (Table 4). Perhaps reflecting this, no canonical coefficients or biplot scores exceeded |0.15|. Interset correlations suggested a negative influence of mat-forming ground cover (−0.23) and positive influences of snag basal area (0.43) and canopy cover (0.34).

Small mammals correlated strongly with environmental variables on the 1st CC axis ($r = 0.82$; $P = 0.0005$ based on 1,999 randomizations; Table 4). *Neotoma fuscipes* and *P. boylii* were negatively associated with 1st CC axis (and *Otospermophilus beecheyi* weakly so; Fig. 2), whereas *Callospermophilus lateralis* and to a lesser degree, *T. senex*, *T. quadrimaculatus*, and *Tamiasciurus douglasii* were positively associated (albeit only moderately so; Table 5). Although patterns on the 2nd CC axis are less readily interpreted, it was roughly polarized by *N. fuscipes* and especially *C. lateralis* (negative) and *T. douglasii* (positive).

Graphical representation of this ordination (Fig. 2) suggests an association of *T. douglasii* with abundant snags and against mat-forming vegetation, and of *C. lateralis* with coarse woody debris and possibly with mat-forming vegetation, while avoiding sites with heavy tree cover or litter. *N. fuscipes* occurs at sites with numerous and diverse saplings and trees, and high cover by hardwood species, while avoiding sites with abundant softwoods, large snags, and high basal area by trees or snags. Few other generalizations emerge from this analysis.

At the smaller (point) spatial scale the total variance explained by our environmental variables ("inertia") was nearly 3 times that for the transect levels (although to our knowledge there is no heuristic rationale for directly comparing inertia across separate analyses). In part this may reflect the increase in sample locations (494 versus 73). CCA at the point scale produced 3 axes and reached tolerance after 23, 23, and 12 iterations. All 3 axes fell well outside the range of expected values based on 1,999 randomizations of our data (Table 4), but cumulatively explained less than 10% of the variance in the species data. Hence, although point-scale analyses resulted in higher inertia (variance) than did transect-level analyses, the proportion of this variance that was explained by the resulting CC axes was much lower.

Correlations between small mammal species and environmental variables were significantly greater than expected (based on 1,999 randomizations) on all 3 axes, and as with the larger-scale analyses, correlations among variables were low to modest; only 1 exceeded 0.48 (sapling versus sapling richness, 0.67). In general this ordination was polarized by hardwood cover (canonical coefficient 0.24, interset correlation 0.42, and biplot score 0.28), and steeper slopes (0.06, 0.19, and 0.13), opposed weakly by tree basal area (−0.13, −0.27, and −0.18, respectively) and snag basal area (−0.10, −0.23, and −0.16).

The 2nd axis was relatively weakly polarized but all 3 metrics were qualitatively similar. Tree cover (−0.20, −0.30,

TABLE 5.—Canonical correspondence (CC) scores and correlations for small mammals on the 1st and 2nd CC axes calculated at the transect and point scales. Species acronyms are as in Supporting Information S1.

| | Transect scale | | | | | | Point scale | | | | | |
| | Final scores | | CC axis 1 | | CC axis 2 | | Final scores | | CC axis 1 | | CC axis 2 | |
Species	CC axis 1	CC axis 2	Pearson's r (r²)	Kendall's tau	Pearson's r (r²)	Kendall's tau	CC axis 1	CC axis 2	Pearson's r (r²)	Kendall's tau	Pearson's r (r²)	Kendall's tau
GLSA	−0.002	−0.132	−0.113 (0.013)	−0.077	−0.031 (0.001)	−0.006	0.257	−0.896	−0.011 (0)	0.003	−0.056 (0.003)	−0.037
NEFU	3.856	−1.733	0.582 (0.338)	0.384	−0.173 (0.030)	−0.109	4.044	−1.357	0.298 (0.089)	0.196	−0.067 (0.004)	−0.061
PEBO	1.573	−0.119	0.565 (0.319)	0.397	−0.041 (0.002)	−0.02	2.188	0.828	0.368 (0.135)	0.222	0.156 (0.024)	0.109
PEMA	0.051	0.384	−0.336 (0.113)	−0.226	0.236 (0.056)	0.204	−0.072	−0.853	−0.22 (0.049)	−0.142	−0.237 (0.056)	−0.157
OTBE	0.479	0.126	0.033 (0.001)	0.037	0.014 (0)	0.012	0.660	0.963	0.032 (0.001)	0	0.093 (0.009)	0.065
CALA	−1.452	−3.673	−0.407 (0.165)	−0.342	−0.494 (0.244)	−0.327	−0.580	3.188	−0.094 (0.009)	−0.068	0.254 (0.064)	0.211
TADO	−0.512	1.891	−0.171 (0.029)	−0.173	0.219 (0.048)	0.186	0.147	−0.906	−0.014 (0)	−0.022	−0.034 (0.001)	−0.009
TAQU	−0.467	0.050	−0.430 (0.185)	−0.273	0.006 (0)	0.013	−0.404	1.119	−0.175 (0.031)	−0.138	0.229 (0.052)	0.164
TASE	−0.788	0.490	−0.590 (0.348)	−0.400	0.141 (0.020)	0.115	−0.822	−0.090	−0.358 (0.128)	−0.28	0.031 (0.001)	0.021
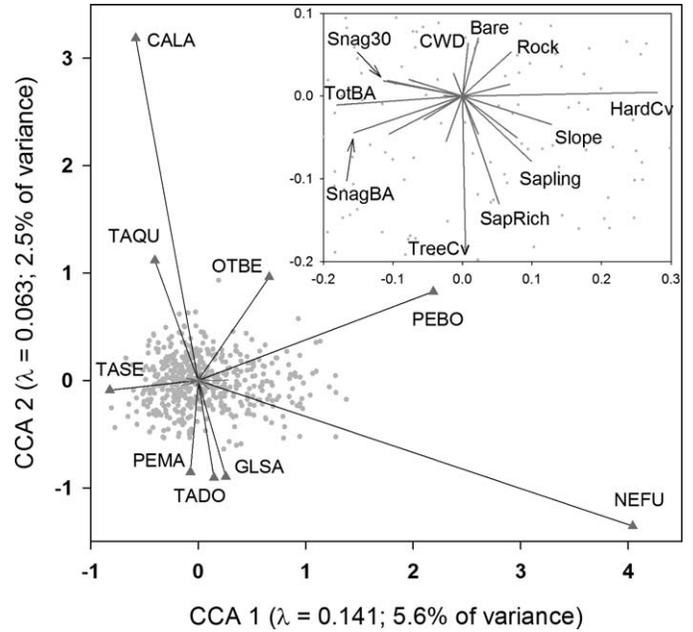
FIG. 3.—Canonical correspondence analysis on point-scale data, without elevation. Gray dots represent trapping stations (points). Vectors represent biplot scores. Acronyms are as in Supporting Information S1 and Table 1.

and −0.19) and sapling richness (−0.13, −0.21, and −0.13) were associated with sites low on this axis, and more coarse woody debris (0.05, 0.10, and 0.07) and bare ground (0.04, 0.12, and 0.07) at sites high on this axis.

At this scale, *N. fuscipes*, *P. boylii*, and to a lesser extent, *O. beecheyi*, were strongly positively loaded on the 1st CC axis, whereas *T. senex* exhibited modest negative scores (Table 5). On the 2nd CC axis, *C. lateralis* was positively associated, whereas *N. fuscipes* and to a lesser extent *T. douglasii*, *G. sabrinus*, and *P. maniculatus* were negatively so. Linear correlations of small mammal species with CC axes yielded low R^2-values (all < 14%) and so are not interpreted. A plot of this ordination (Fig. 3) reflects many features observed at the transect scale, although at this scale there appears to be a strong influence of slope and hardwood cover on the distribution of *N. fuscipes*, and tree cover and sapling richness appear to be associated with *P. maniculatus*, *T. douglasii*, and *G. sabrinus*; we reiterate, however, that this ordination explains relatively little variation in small mammal distributions, and the very low correlations between small mammals and these axes makes any interpretation little more than a hypothesis.

Canonical correlation analysis.—At the transect scale only 2 pairs of species were moderately correlated (*T. quadrimaculatus* and *T. senex*, $r = 0.70$; *P. maniculatus* and *T. quadrimaculatus*, $r = 0.57$); no other species or habitat variables exhibited strong correlations at either spatial scale, and so none were removed from analyses. Bivariate plots of species × habitat metrics in ordination space suggested that our data did not suffer from outliers. Most small mammal species were significantly associated with habitat metrics (Table 6), but these

TABLE 6.—Squared multiple correlations of small mammal species on canonical correlation axes for analyses at the transect and point scales. Species acronyms are as in Supporting Information S1.

Species	Transect scale ($d.f. = 20, 47$)				Point scale ($d.f. = 18, 433$)			
	R^2	Adjusted R^2	F	P	R^2	Adjusted R^2	F	P
PEMA	0.468	0.257	2.22	0.0133	0.162	0.127	4.64	< 0.0001
PEBO	0.412	0.180	1.77	0.0557	0.123	0.087	3.39	< 0.0001
TASE	0.600	0.441	3.78	< 0.0001	0.165	0.130	4.75	< 0.0001
TAQU	0.416	0.185	1.80	0.0509	0.136	0.101	3.80	< 0.0001
GLSA	0.305	0.029	1.11	0.3746	0.073	0.035	1.90	0.0142
NEFU	0.494	0.293	2.46	0.0061	0.072	0.033	1.86	0.0174
TADO	0.397	0.158	1.66	0.0789	0.046	0.006	1.16	0.2917
CALA	0.380	0.132	1.54	0.1158	0.106	0.068	2.84	< 0.0001
OTBE	0.397	0.158	1.66	0.0785	0.089	0.051	2.36	0.0014

explained relatively low proportions of variance in small mammal data (1 $R^2 = 0.60$; all others < 0.50).

Canonical correlation indicated that 2 axes were informative (Table 7), and together explained 56% of the variance in the data. Redundancy analysis (Table 7) indicated that only 44% of the variation in the distribution of small mammal captures was explained by all canonical habitat axes; 55% of this was explained by these 2 axes.

Canonical correlation, like CCA, produces multiple types of coefficients; among these are standardized canonical coefficients (comprising the canonical pattern) and correlations between variables and their canonical variates (structure coefficients). Because the latter are not affected by relationships with other variables, they reflect the true relationship between variables and their respective canonical variates, and McGarigal et al. (2000) recommend these whenever they differ qualitatively from standardized canonical coefficients. This was the case with our analyses so we emphasize structure coefficients.

The 1st CanCorr axis was negatively influenced by snag, live shrub, softwood cover, and total basal area, and positively by hardwood cover and sapling abundance. The 2nd axis was negatively influenced by herbaceous cover and positively by mat-forming vegetation, litter cover, and to a lesser extent cover by softwoods and by total basal area. Cross-correlations (e.g., between small mammals and environmental metrics [Fig. 4]) indicated that *N. fuscipes* and *P. boylii* favored sites with hardwood cover and abundant samplings, and with fewer snags and lower total basal area and softwood cover. *O. beecheyi* and *P. maniculatus* occurred at sites with greater herbaceous cover and lower litter and mat-forming vegetation. Both *Tamias* species and to a lesser extent, *C. lateralis*, favored sites with large snags and higher basal area of both snags and trees, with more softwoods, while disfavoring sites with abundant saplings and higher cover by hardwoods. *T. douglasii* appears to avoid sites with steep slopes, abundant saplings, and rocky cover, while occurring at sites with fine woody debris and high cover by softwoods.

TABLE 7.—Canonical correlation at the transect and point scales. Note that McGarigal et al. (2000) consider the canonical R^2 to be the eigenvalue (λ); both this and the eigenvalue produced by SAS (SAS Institute Inc. 2008) are presented, followed by the percentage of variance explained by each axis and the cumulative percentage explained. The hypothesis tested (H$_0$: $R_{x..n} = 0$) is that the canonical correlation (R) in this and all subsequent axes = 0. Redundancy analysis indicates the proportion of the raw variance in the small mammal variables that is explained by habitat metrics; relative redundancy is the proportion of the total redundancy explained by a given axis. Significant axes ($P < 0.05$) are in boldface type.

| Canonical correlation (R)	Canonical R^2	λ	Proportion	Cumulative	H$_0$: $R_{x..n} = 0$			Redundancy analysis		
					F	$d.f.$	P	Redundancy	Cumulative	Relative
Transect scale										
0.851	**0.724**	**2.62**	**0.366**	**0.366**	**1.55**	**171, 344.92**	**0.0003**	**0.1999**	**0.1999**	**0.4522**
0.763	**0.583**	**1.40**	**0.195**	**0.560**	**1.28**	**144, 315.26**	**0.0384**	**0.0449**	**0.2447**	**0.5535**
0.677	0.458	0.84	0.118	0.678	1.12	119, 283.81	0.2234	0.0404	0.2852	0.6451
. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	
0.305	0.093	0.10	0.014	1.000	0.45	11, 48	0.9262	0.0062	0.4421	
Point scale										
0.513	**0.263**	**0.36**	**0.343**	**0.343**	**2.63**	**162, 3,459.4**	**< 0.0001**	**0.0666**	**0.0666**	**0.4944**
0.453	**0.205**	**0.26**	**0.248**	**0.591**	**2.09**	**136, 3,118.5**	**< 0.0001**	**0.0308**	**0.0974**	**0.7231**
0.359	**0.129**	**0.15**	**0.142**	**0.734**	**1.61**	**112, 2,770.3**	**< 0.0001**	**0.017**	**0.1144**	**0.8493**
0.273	**0.074**	**0.08**	**0.077**	**0.811**	**1.32**	**90, 2,413.5**	**0.0266**	**0.0064**	**0.1208**	**0.8968**
0.258	0.066	0.07	0.068	0.879	1.20	70, 2,046.5	0.1231	0.0043	0.1251	0.9287
. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	
0.121	0.015	0.02	0.014	1.000	0.65	10, 4,323	0.7724	0.0009	0.1347	
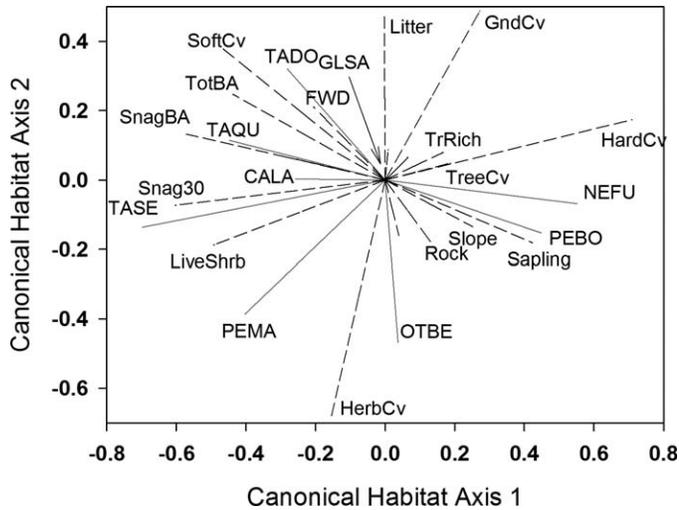
Fig. 4.—Graphical representation of the canonical structure for habitat metrics (correlations and cross-correlations with the canonical habitat axes) for transect-level data. Mammal data presented here represent cross-correlations of the small mammal capture records on habitat-based ordination axes. Acronyms are as in Supporting Information S1 and Table 1.

At the finer (point) scale of analysis, 4 canonical axes were significant and these explained 81% of the total variance in our data. Canonical correlations were notably lower than at the transect scale (Table 7), suggesting a less rigorous association between canonical variates (e.g., between environment- and small mammal-based axes). This is supported by redundancy analysis, which indicated that just over 13% of the variance in small mammal data was explained by canonical habitat axes (Table 7); however, half of this was explained on the 1st canonical axis, and 90% across the 4 significant axes.

At this spatial scale, hardwood cover was strongly negatively associated with the 1st axis, whereas east–west exposure, abundance of large snags, basal area by snags, and shrub cover all were positively associated, albeit not strongly (Fig. 5). The 2nd axis was negatively influenced by tree cover and basal area, and to a lesser extent by softwood cover, litter, and saplings, and positively influenced by cover of shrubs, rocks, and bare ground. Cross-correlations (Fig. 5) suggest few strong associations at this scale (perhaps reflecting the low redundancy reported above), but some associations are apparent in bivariate space (Fig. 5). *O. beecheyi*, *C. lateralis*, and *T. quadrimaculatus* appear to favor sites with low tree cover and little cover by litter, and with exposed rock or bare ground cover. *N. fuscipes* appears positively influenced by hardwood cover (albeit not strongly), whereas *T. senex* and *P. maniculatus* are negatively associated with this variable. Only 4–6 mammal species exhibit large vectors in bivariate space (4 have vectors > 0.3 in bivariate space whereas 2 others have vectors > 0.2); the remaining species do not appear to be influenced by any particular environmental features at this spatial scale.

Multiple regression.—We conducted multiple Poisson regression on 9 species and 4 community metrics (Supporting
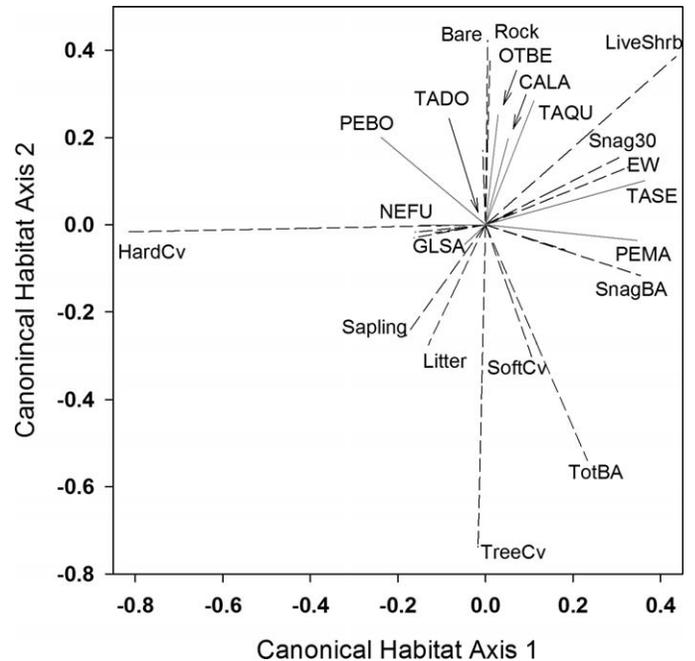

Fig. 5.—Graphical representation of the canonical structure for habitat metrics (correlations and cross correlations with the canonical habitat axes) for point-level data with and without elevation. Small mammal data presented here represent cross-correlations of capture records on habitat-based ordination axes. Acronyms are as in Supporting Information S1 and Table 1.

Information S2, DOI: 10.1644/12-MAMM-A-303.S2). Across species and metrics, 12–219 and 19–238 stepwise multiple regression models were competitive (i.e., $\Delta AIC_c < 2.0$) at the point and transect scales, respectively, and were entered into Poisson regression. This yielded 1–3 competitive models for species, and 2–5 for community metrics, at the point scale, and 1–4 and 1 or 2 models, respectively, at the transect scale. Resulting models displayed strong bimodality in relative importance values at both spatial scales (21% of models at the transect scale yielded $\Sigma \, w_i > 0.8$, whereas 66% yielded $\Sigma \, w_i < 0.3$; similar values at the point scale were 52% and 40%, respectively). Additionally, models generally had low regression coefficients. At the transect scale the largest coefficients were only −0.38 and 0.47 (Supporting Information S2). The finer scale of analysis yielded a greater number of larger coefficients, but only 17 of 162 coefficients exceeded |0.5|. For community metrics the regressions were less informative, with only 2 coefficients exceeding |0.20| at the transect scale, and none exceeding |0.16| at the point scale. Several species appear to exhibit very different associations at the 2 spatial scales studied.

For the most common species (*P. maniculatus*; 1,381 individuals), 5 variables occurred in all Poisson regressions at the transect scale, and although the associated coefficients were not strong, they suggested avoidance of sites with abundant snags, herbaceous cover, and steep slopes, and preference of sites with dense tree cover. At the finer spatial scale, 7 variables were important but none of these had model coefficients greater than 0.1 and so are not considered

ecologically informative. *P. boylii* was moderately common (304 individuals) but regression results were less compelling than for *P. maniculatus*. At the transect scale, 2 variables appear to be important ($\Sigma\ w_i > 0.7$) but the associated coefficients were very small; this species may avoid sites with high tree basal area and hardwood cover, while favoring sites with more herbaceous cover. At the point scale no variables were important (all $\Sigma\ w_i < 0.002$) or strongly associated (all $\overline{\beta} < |0.18|$).

Neotoma fuscipes was not common. At the transect scale 5 variables appeared to be important ($w_i > 0.9$) and 3 of these were associated with strong model coefficients ($\overline{\beta} < |0.2|$), indicating modest avoidance of sites with heavy tree cover and numerous large snags, and preference for sites with abundant downed woody debris and numerous saplings. At the point scale most (12 of 18) variables were consistently entered in models and a relatively large number of these yielded large coefficients, some of which suggest scale-dependence; large snags and dense tree cover were consistently disfavored at the broader spatial scale yet favored at the finer scale, whereas downed woody debris was favored at the larger scale and avoided locally.

Two chipmunk species were the 2nd and 3rd most abundant species, and both species appear to exhibit stronger patterns of selection at the finer scale of analysis. At the transect spatial scale, shrub cover, herbaceous cover, and hardwood cover were important to *T. quadrimaculatus* but the strength of these associations was generally weak; the mean coefficient for shrub cover was −0.15, and that for hardwood cover was 0.08. Locally, a number of variables were important for this species although the strength of these relations was similarly low, with mean coefficients $< |0.17|$. *T. senex* provided similar results, albeit qualitatively different. At the transect scale, cover by softwoods, hardwoods, shrubs, and both cover and basal area of all trees were important, but none of these yielded particularly strong associations; in fact, softwood cover was avoided ($\overline{\beta} = -0.15$) and hardwood cover was roughly neutral ($\beta = 0.04$) but tree cover was the strongest positive influence on the distribution of this species ($\overline{\beta} = 0.12$). At the point scale, 8 habitat metrics were important, but other than an apparent mild avoidance of sites with extensive litter ($\overline{\beta} = -0.13$) all coefficients were < 0.11, suggesting limited selection of these habitat metrics.

For *T. douglasii* at the transect scale, 8 variables were important, with mean coefficients from −0.21 to 0.47. Results suggest that this species avoided sites with heavy tree cover and large snags while favoring sites with abundant litter cover, numerous snags, and steeper slopes. Other variables (e.g., shrub or sapling richness, and tree basal area) yielded positive coefficients but were not highly important in model results. At the point scale, 14 variables were highly important, and indicated that this species avoided sites with extensive herbaceous or hardwood cover, high basal area, and steep slopes, while favoring sites with abundant fine woody debris, high tree cover, and abundant cover by rocks and litter. The disparity in the sign of slope (favored at large scales, avoided at

smaller scales) suggests that this species was encountered at local sites of low relief within a matrix of steeper terrain.

Glaucomys sabrinus was modestly represented in our data set; we argue elsewhere that this reflects low density in the relatively xeric forests of the northern Sierra Nevada (Smith et al. 2011). Models were inconsistent across scales, with the exception that dense saplings were avoided at both scales. At the larger scale *G. sabrinus* exhibited mild preference for forests with sparse coarse woody debris and a mild avoidance of southern slopes. Locally this species favored sites with more snags and abundant litter cover, but avoided those with high tree basal area, dense saplings, and extensive cover by rocks and fine woody debris.

Ground squirrels tended to exhibit stronger habitat relations at finer spatial scales. *C. lateralis* was not common and only a couple of habitat metrics were important at the transect scale; this species was not captured at sites with high cover by hardwood trees and tended to avoid sites with abundant snags. Locally, the avoidance of hardwoods was even more compelling, as was evidence that this species avoids sites with high tree cover. Six other metrics were highly important but all had low mean regression coefficients ($\overline{\beta} < |0.09|$). *O. beecheyi* was modestly represented in our data set but at both spatial scales avoided sites with high tree basal area. Locally, this species avoided sites with abundant saplings and litter cover, while favoring sites with abundant fine woody debris, exposed rock, and west exposure.

Neither total captures nor species richness were well explained by regressions at the transect scale; both variables were negatively influenced by shrub cover and hardwood tree cover, but coefficients were small and not compelling. Many more variables were important in regressions at finer spatial scales, but regression coefficients were even lower at this scale; tree cover was modestly avoided ($\overline{\beta} = 0.12$ and −0.16, respectively). Diversity and evenness also yielded limited insight, with 2 and 4 important variables, respectively, and generally low coefficients. Shannon–Weiner *H′* was negatively associated with tree cover and possibly with shrub cover, whereas Simpson's index was lower at sites with large snags and mat-forming vegetation. Locally, more metrics were important but they yielded low coefficients, suggesting limited influence of these metrics.

DISCUSSION

To better understand the responses of small mammals to forest management in the northern Sierra Nevada we pursued 2 parallel and complementary field efforts. We sampled 12 replicate plots in homogenous white fir forest over 8 years to assess mammalian responses to 2 levels of canopy thinning as well as to small but more intensive harvesting (group-selection plots). Canopy treatments were imposed in year 4, and although vegetation changed significantly in all treatments (including controls) over time (Fig. 1), small mammals were not markedly influenced (Table 3). Indeed, fully 88% of the individuals captured were generalists (deer mice and chipmunks) with

sufficiently broad habitat and dietary requirements that they presumably were able to thrive across the range of forest conditions represented in these treatments. We argue below that the lack of response by small mammals is a legacy of more than a century of human impacts on this system that have resulted in a fauna dominated by generalist species in a process suggestive of biotic homogenization via differential success of some native species over others (McKinney and Lockwood 1999; Olden and Rooney 2006; Le Viol et al. 2012).

We assessed habitat associations and predictability of small mammals throughout PNF by surveying a large number of sites placed randomly throughout the forest and stratified by forest stand characteristics, allowing us to characterize the fauna across the available range of vegetation. We subjected these samples to 2 sophisticated and complementary ordination techniques at 2 spatial scales. All ordinations yielded qualitatively similar results—relatively little variation in small mammal distributions and abundances were explained by underlying vegetative characteristics. Underscoring this, Poisson multiple regression on each small mammal species at either spatial scale failed to extract compelling signatures of environmental influences driving the distribution of small mammals. Small mammals in PNF do not appear to be markedly constrained by current forest characteristics.

And yet, small mammals do segregate in ordinations. *N. fuscipes* and *P. boylii* fall in the same general region of ordination space in both analyses on transect-scale data, and these appear to be positively associated with hardwood trees, and negatively with large snags, softwood trees, and high basal area; these features correspond with the lower-elevation distribution of these taxa, and for *Neotoma* mirror results of Innes et al. (2007). Contrasting with these species was *T. senex*, for which environmental associations were nearly the opposite of those of *N. fuscipes* and *P. boylii*. This likely reflects the higher-elevation habitat preferences of *T. senex* (generally > 1,500 m—Gannon and Forbes 1995); in ordination space this species appears to avoid hardwood cover (less abundant at higher elevations) while favoring large and abundant snags, softwood cover, and high tree basal area (e.g., mature coniferous forest).

The other set of species for which ordination appears to effectively indicate ecological segregation is *C. lateralis* and *T. quadrimaculatus*, which contrast clearly with *P. maniculatus* in CCA (but not in CanCorr). Canonical correspondence suggests that *C. lateralis*, and to a lesser extent *T. quadrimaculatus*, occur at sites with lower tree and herb cover but greater mat-forming ground cover and more coarse woody debris. This concurs with our understanding of habitat associations for *C. lateralis* (e.g., open and shrubby sites—Bartels and Thompson 1993). *T. quadrimaculatus*, like most chipmunks, also favors shrubby sites but is not otherwise known for associating with mat-forming vegetation; we suspect the latter is a correlate of the preference of the species for open mature forests, which is where mat-forming vegetation occurs in the northern Sierra Nevada. Finally, *P. maniculatus* polarized CCA against the preceding 2 species, but not in CanCorr. In general, CCA

appears to yield more reasonable interpretations of our fauna than CanCorr, although it is worth reiterating that both analyses were consistent in highlighting the limited amount of variation in these species that was explicable by environmental features.

If ordinations suggest ecologically reasonable associations among small mammals and habitat metrics, why do they explain so little of the underlying variation? One hypothesis is that the habitat data we collected either are not important or are not relevant to small mammals in this region. This seems unlikely, because the parameters we included are typical habitat and microhabitat features measured by many other authors. Additionally, other work in this region (e.g., Coppeto et al. 2006; Innes et al. 2007; Smith 2009) has documented the importance of some of these features to small mammal species here. An alternative to this is that although some of these species do in fact exhibit habitat preferences, most areas in this forest provide these features in sufficient abundance to be acceptable for many of these species—from the perspective of a small mammal PNF is more homogeneous than we initially believed. This would be somewhat surprising because our samples spanned 850 m in elevation (1,000–1,850 m) and included multiple forest types (e.g., white fir–mixed conifer, Douglas-fir–mixed conifer, ponderosa pine–mixed conifer, and red fir, among others). However, small mammals generally focus on structural rather than compositional features, and in the eyes of a deer mouse or chipmunk, red fir forest and white fir–mixed conifer forest may differ primarily in the fact that the former dominates higher-elevation forests and the latter is more prevalent at lower elevations; other than temperatures (to which small mammals can readily adapt—Merritt 2010) these may be less distinct than perceived by humans. Nonetheless, these typically are structurally distinct forests (Fites-Kaufman et al. 2007), which begs the question of why they may be perceived similarly by small mammals in our study area. Key candidate mechanisms in the Sierra Nevada include the legacy of a century of fire exclusion and timber extraction, as well as their interaction (Naficy et al. 2010). Fire has obvious impacts on wildlife habitat and may substantially influence small mammal assemblage composition (Converse et al. 2006c; Amacher et al. 2008; Zwolak 2009). Fire suppression was standard policy through most of the 20th Century (Kauffman 2004; Stephens and Ruth 2005), wheras extractive efforts amplified greatly after the 2nd World War (Ruth 1996). Further research on this issue seems warranted; if fire suppression, logging, or both have created a more-homogenous forest structure then efforts to counter this might promote greater biodiversity (see also Safford et al. 2012).

Unfortunately, the composition and relative abundances of small mammals prior to the onset of extensive human activities in this region are poorly documented. Consequently, we do not know if the patterns documented in this report represent normal conditions for this system or if they reflect a small mammal fauna that has deviated from historic conditions, as alluded to above. Relatively few species in this region are dependent upon mature forest conditions. Some such species include *M.* (*C.*) *californicus*, *G. sabrinus*, *P. intermedius*, and some sorico-

morphs such as *Neurotrichus*; 2 of these (*Myodes* and *Neurotrichus*) reach the southern edge of their ranges here, and both typically favor closed-canopy forest or mesic conditions (Carraway and Verts 1991; Alexander and Verts 1992) so it is reasonable that human activities that open these forests to more xeric conditions could select against these taxa (Maser et al. 1981). Other species of interest in this region generally are more mesic in habitat preferences, and would be expected in meadows or riparian zones rather than the forest conditions reflected in our efforts (e.g., *Z. princeps*, *Sorex monticolus*, *S. palustris*, *Scapanus latimanus*, and *M. montanus*). Further efforts to characterize the distribution and status of such mesic species could enlighten forest management (Anthony et al. 2003). Limited evidence suggests that changes have occurred in the small mammal fauna of forests in this region. Jameson (1951, 1952, 1953) studied small mammals of PNF in the 1940s and 1950s. He expressed surprise to one of us (E. W. Jameson, pers. comm. to DAK) that our trapping efforts were not yielding more *M. californicus*, and that this species was abundant in many forested areas there in the 1950s. Unfortunately, no records exist to quantify this further.

The Sierra Nevada lie within a Mediterranean climate region and as such experiences moderate to heavy winter precipitation (rain and snow) and warm, dry summers. Most research on small mammal responses to forest thinning has occurred in more mesic forests of the Pacific Northwest. In the Oregon Cascades, *G. sabrinus* declined in density following thinning in Douglas-fir forests; this species favored sites with numerous large, standing, dead trees and disfavored sites with high cover by low understory vegetation (Manning et al. 2012). Similarly, in British Columbia, Canada, this species was more abundant in mature stands (Ransome et al. 2004). Voles (*Microtus*) tend to increase in abundance or capture frequency in thinned sites (Sullivan and Sullivan 2001; Suzuki and Hayes 2003; Gitzen et al. 2007), whereas *Peromyscus* may respond to thinning by increasing in abundance (Suzuki and Hayes 2003; Gitzen et al. 2007) or with no discernible change (Ransome et al. 2009). In the southern Washington Cascades, small experimental canopy gaps had positive influences on most forest species, likely reflecting an increase in low vegetative cover (Gitzen and West 2002). In contrast, red-backed voles (*M. californicus* and *Myodes gapperi*) generally decline following thinning treatments (Suzuki and Hayes 2003; Gitzen et al. 2007; Sullivan et al. 2008; Ransome et al. 2009). Chipmunks often respond positively to thinning (Carey 2001; Carey and Wilson 2001), likely reflecting increased shrub development and associated cover and food. Although few studies have addressed small mammal responses in xeric forests, both *P. maniculatus* and *Tamias* responded positively to forest thinning in ponderosa pine forests of Arizona and New Mexico (Converse et al. 2006a, 2006b), similar to results reported here.

Forest management in the Sierra Nevada traditionally emphasized lumber extraction and fuel reduction, although interest in ecological restoration and biodiversity management has increased (North et al. 2009; North 2012). The lack of compelling responses by small mammals to current forest

structure in PNF suggests that further heterogeneity may be needed. Because of their role as key prey species (*N. fuscipes* and *G. sabrinus*) or as reservoirs for disease (*P. maniculatus*) we have contributed previously to the spatial ecology and habitat associations of these and other species (Coppeto et al. 2006; Innes et al. 2007; Smith et al. 2011). We believe that further work should be developed to assess habitat requirements of specialist species in this region, and to evaluate the potential importance of mesic habitats such as riparian corridors (Cockle and Richardson 2003), meadows, and patchy vegetation types such as aspen (*Populus tremuloides*) stands (Oaten and Larsen 2008). Additionally, we find it notable that several species in PNF evidently favored sites with steeper slopes. Whether this reflects differential forest features on steeper sites (e.g., in response to different soil types, drainage, etc.) or is a function of differential timber removal such that sites with shallower slopes have fewer features of mature forest is not clear to us; further clarification of the mechanism underlying this apparent preference would be insightful.

Overall, results presented here suggest that management for small mammal biodiversity in the northern Sierra Nevada would benefit from an emphasis on reducing fine woody debris (accumulated over decades due to fire exclusion), retention and recruitment of hardwoods, and preservation of mature stands for species requiring large trees, snags, and other features of older forests (see also Zielinski et al. 2005), and management promoting broadscale structural heterogeneity (North et al. 2009; North 2012). Cover by hardwoods occurred in models for many species, suggesting an important role of hardwoods in the ecology of many small mammal species here. This appears to be a recurring theme in the Sierra Nevada (Zielinski et al. 2004a, 2004b; Innes et al. 2007; Smith 2009) and merits ongoing consideration. Finally, emphasis on broadscale heterogeneity both of forest structure and understory (shrub) habitats (Maguire et al. 2008; North et al. 2009; North 2012) seems likely to foster greater small mammal diversity while simultaneously serving to reduce the impact of system-wide disturbances such as wildfire or drought, reflecting similar recommendations in the Pacific Northwest (Carey and Wilson 2001).

The Specter of Climate Change

Although logging and fire exclusion have been the dominant influences on the biota of the Sierra Nevada through recent history, this could be eclipsed by climate change (Hannah et al. 2011; Mastrandrea et al. 2011; Shaw et al. 2011; Safford et al. 2012), and if past climatic change provides any indication of regional responses, dramatic changes may be forthcoming (Hadly and Maurer 2001; Blois and Hadly 2007; Blois et al. 2010). In particular, the western United States is warming relatively rapidly (Saunders et al. 2008) and in the northern Sierra Nevada both temperature and rainfall have increased while snowpack has declined (summarized in Safford et al. 2012). Unfortunately, wildlands managers can do little to prepare for climate change; if conditions change such that a given species is no longer viable in the northern Sierra Nevada we can only hope that suitable conditions elsewhere are

accessible and provide refuge. Given the challenges associated with managing locally for climate change, we believe that further efforts in the northern Sierra Nevada would be most productive if focused on assessing postfire recovery (by small mammals as well as on how they influence vegetative recovery) and increasing emphasis on more mesic and patchy habitats, including meadows and riparian zones where species reported here as uncommon to rare might find local environmental conditions favorable.

Forests in western North America are biologically diverse but are increasingly impacted by anthropogenic activities. The Sierra Nevada, in particular, has had a long history of human activities ranging from active forest management by Native Americans to unprecedented human immigration in the mid-1800s to extensive timber management and increasing urbanization in the late 20th Century (Sierra Nevada Ecosystem Project 1996). The pulse of impact following the discovery of gold in California may have resulted in one of the most rapid exploitative events in western North America, with a massive influx of miners and associated industries, rapid and extensive deforestation, and unregulated market hunting. Unfortunately we lack insight into much of the biota of the Sierra Nevada prior to the Gold Rush; exceptions to this general assertion typically pertain to larger species such as grizzly bear (*Ursus arctos*—Storer and Tevis 1955), tule elk (*Cervus elaphus nannodes*—McCullough 1969; Blum 2012), bighorn sheep (*Ovis canadensis*—Monson et al. 1980), and others. Small mammals have received the attention of ecologists only relatively recently. The consequence of this is that placing the results of contemporary studies into a deeper context is challenging; given the roles small mammals play in forest dynamics (Zabel and Anthony 2003) they merit much additional investigation.

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Small mammal species found in the Plumas National Forest, California.
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SUPPORTING INFORMATION S2.—Results of model-averaging over multiple regression models for small mammals in the Plumas National Forest, California.
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