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Diversity of small mammals in the Sierra Nevada: filtering by natural selection or by anthropogenic activities?

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Both historical and contemporary factors may influence the structure and composition of biotas. Small mammal faunas in the Sierra Nevada of California, United States, are strongly dominated by generalist species; however, whereas 1 recent study argues that this is a product of recent anthropogenic influences, another provides a deeper evolutionary explanation based on historic fire frequencies. We summarize these patterns and proposed mechanisms, and we integrate data from 2 other studies—1 in the Sierra Nevada and 1 from an evolutionarily related mountain range in Baja California—to provisionally conclude that evolutionary adaptation, and possibly climatic warming in the Holocene, likely are the primary drivers of this faunal structure. However, we agree with work elsewhere in North America that recent anthropogenic filtering likely has amplified the effects of adaptation and climatic warming; one result of this is that the Sierra Nevada currently supports very limited areas of older (decadent) forests, and species dependent on these habitats may require special attention by resource managers.

Tanto factores históricos como contemporáneos pueden influir en la estructura y composición de biotas. Las faunas de micromamíferos en la Sierra Nevada de California, Estados Unidos, son fuertemente dominadas por especies generalistas; sin embargo, mientras que 1 estudio reciente sostiene que este es un producto de las influencias antrópicas recientes, otro estudio ofrece una explicación más profunda y evolucionista basada en las frecuencias de fuegos históricos. Resumimos estos patrones y mecanismos propuestos, e integramos datos procedentes de otros 2 estudios—1 en la Sierra Nevada y 1 de una cordillera evolutivamente relacionada en Baja California—para concluir provisionalmente que la adaptación evolutiva, y posiblemente el calentamiento climático en el Holoceno, son probablemente los conductores primarios de esta estructura de fauna. Sin embargo, estamos de acuerdo con trabajos en otras partes de América del Norte que recientes filtros antropogénicos han amplificado los efectos de adaptación y de calentamiento climático; un resultado de esto es que actualmente la Sierra Nevada tiene muy limitadas áreas de los bosques antiguos (decadentes), y las especies dependientes de estos hábitats pueden requerir atención especial de los administradores de recursos.

Key words: anthropogenic filtering, forest management, frequent-fire habitat, natural selection, small mammal faunal composition

Ecological communities include species whose niches, in the broadest sense, range from narrow to broad, restricted to catholic, specialist to generalist. The evolution of more specialized niches has been a potent topic in the ecological literature since the heyday of community and geographical ecology (e.g., Levins 1968; Roughgarden 1972; Futuyma and Moreno 1988; Van Tienderen 1991) and remains popular yet incompletely resolved today (Devictor et al. 2008; Poisot et al. 2011; Peers et al. 2012). Whereas experimental (Kassen 2002) and theoretical (Ackermann and Doebeli 2004) efforts are able to address underlying mechanisms leading to specialization by virtue of the artificial nature of the landscape within which their study species evolve, studies conducted in natural landscapes may be constrained by confounding factors associated with anthropogenic influences. This is increasingly true in an era of global climate change, which some now refer to as the Anthropocene (Corlett 2015; Lewis and

Maslin 2015), and which may be leading to a decline in specialists regionally (Le Viol et al. 2012) or globally (Clavel et al. 2011).

In western North America, forested ecosystems have been subjected to a variety of anthropogenic impacts since Native Americans arrived by the end of the last ice age (e.g., 10,000–30,000 years ago). In the Sierra Nevada of California, traditional practices emphasized fire to maintain open forest structure and favor prey species such as deer and elk (Blackburn and Anderson 1993). With the arrival of European Americans, however, multiple additional impacts were initiated, most notably livestock grazing, wildfire suppression, timber extraction, and road-building associated with these activities. Timber extraction and fire suppression, in particular, have been amplified since World War II (Ruth 1996), and while the former has been curtailed significantly in the last 25 years, the latter remains a dominant factor in the Sierra. Whereas we are beginning to understand the structure of Sierra Nevada forests prior to these latter impacts (Stephens et al. 2015), the historic fauna here is poorly documented, with the exception of large or economically important species.

Two recent studies in the Sierra Nevada (Kelt et al. 2013; Sollmann et al. 2015) documented highly asymmetric assemblage composition in nonflying small mammals (e.g., < ~500 g), with extreme dominance by a small number of generalist species. To explain this pattern, these authors proposed very different explanations, with implications for faunal assemblage and evolution as well as contemporary management. A third study (Roberts et al. 2015) assessed responses of small mammals to fire in a system in the Sierra Nevada that has not been subject to the same comprehensive fire suppression or logging activities that impact the National Forests studied by Kelt et al. (2013) and Sollmann et al. (2015). Here, we summarize the patterns observed by these authors, outline the explanations provided for these patterns, and discuss the consequences of these differing explanations for understanding the evolution of forest mammal faunas, and for managing them in the face of continued impacts. Finally, we present data on 1 additional fauna in an effort to evaluate which of these explanations appears more likely to explain contemporary faunal structure.

Observed Patterns

Research summarized here was conducted in 3 distinct regions of the Sierra Nevada (Fig. 1). All 3 studies emphasized coniferous forests and included data from numerous sites that spanned broad and overlapping elevational ranges. All 3 studies sampled small mammals with both Tomahawk and Sherman live traps, but Sollmann et al. (2015) used larger Sherman traps (Model XLF15, 10 × 11 × 38 cm) than either Kelt et al. (2013) or Roberts et al. (2015—Model XLK, 7.6 × 9.5 × 30.5 cm). However, captures in these studies were dominated by smaller species readily captured in either trap type, suggesting that results remain comparable in spite of difference in traps used. Additionally, all 3 studies used similar bait in Tomahawk traps (a mix of peanut butter, oats, molasses, and raisins), but while Kelt et al. (2013) and Sollmann et al. (2015) used the same bait in Sherman traps, Roberts et al. (2015) used millet seed. We are not aware of species potentially occurring in this region whose capture would be strongly biased by these differences, however.

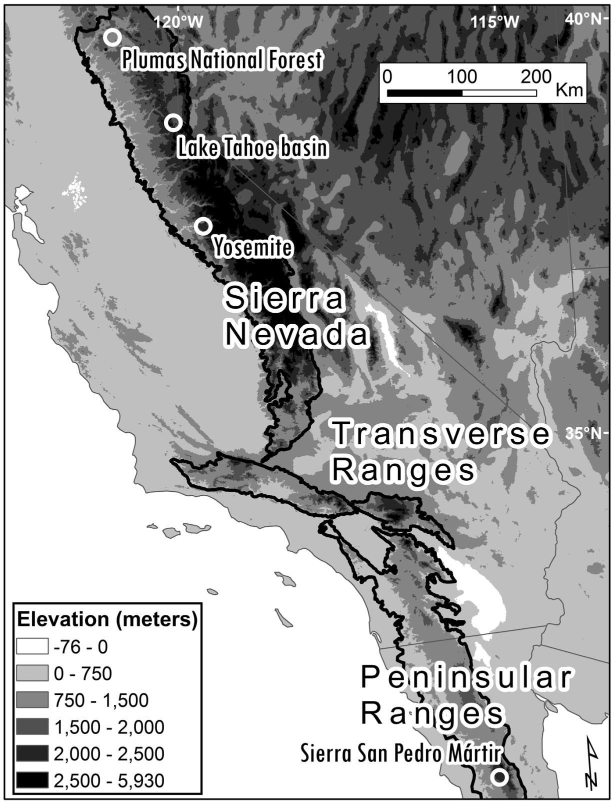

Fig. 1.—Location of sites mentioned in text. This map also illustrates how the Sierra Nevada and both the Transverse and Peninsular ranges are connected.

In the Plumas National Forest (hereafter, PNF), Kelt et al. (2013) pursued 2 complementary studies on small mammals. In the first study, they sampled small mammals at 75 sites ranging from about 1,000 to 2,250 m above sea level (a.s.l.); these sites supported 7–10 small mammal species (operationally defined as species readily captured in the traps used; e.g., smaller sciurids and all muroid rodents in this region) but were overwhelmingly dominated by 1–2 species. Fully 54.2% of individuals captured were deer mice (*Peromyscus maniculatus*), 26.0% were long-eared chipmunks (*Tamias senex*), and 10.2% were Allen's chipmunks (*T. quadrimaculatus*—Kelt et al. 2013; Stephens et al. 2014); no other species exceeded 3% of captures. In their second study, Kelt et al. (2013) surveyed 12 sites 1–6 times annually over 6–8 years; 8 sites were dominated by deer mice (33.4%), and 4 were co-dominated by deer mice and either long-eared or Allen's chipmunk (20.2% and 28.0%, respectively; Fig. 2a; Supplementary Data SD1; Kelt et al. 2013; Stephens et al. 2014). Brush mice (*P. boylii*) comprised another 11.4% of individuals captured, but none of the 9 other species captured at these sites exceeded 3%. Hence, in 2 complementary studies in the PNF, 3 small mammal species comprised fully 90% and 82% of individuals captured.

In the Lake Tahoe Basin Management Unit (hereafter, TB), forests from the lower montane zone (about 1,900–2,250 m a.s.l.) supported 6–12 species (Sollmann et al. 2015) and, while clearly

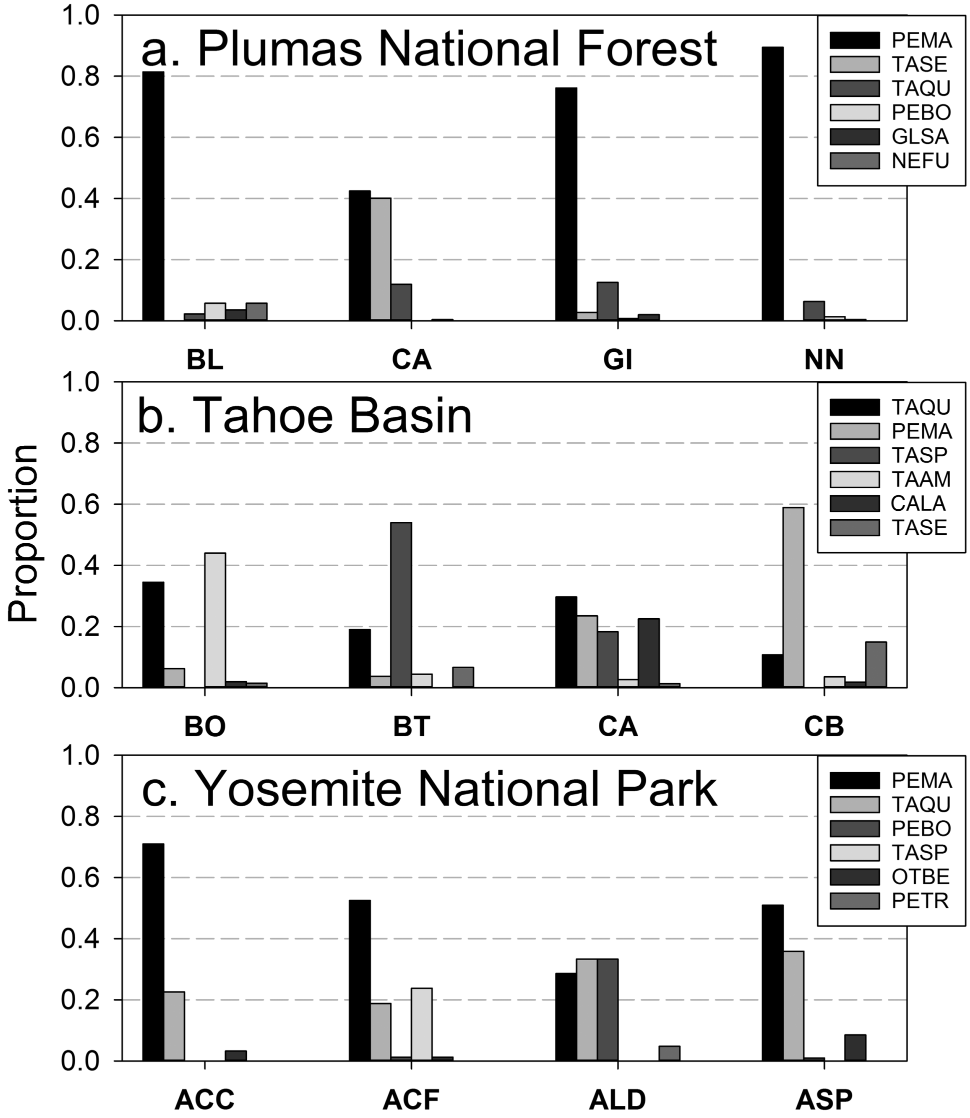

Fig. 2.—Proportion of individuals of 6 dominant species of small mammal captured across 4 sites in 3 regions of the Sierra Nevada, California. a–c) Representative sites from the Plumas National Forest, the Lake Tahoe Basin, and Yosemite National Park, respectively (for illustrations of all sites, see Supplementary Data SD1). Legends on the abscissa refer to trapping sites; for locations and details, see Kelt et al. (2013) for the Plumas National Forest, Sollmann et al. (2015) for the Tahoe Basin, and Roberts et al. (2015) for Yosemite National Park or contact the original authors. CALA = *Callospermophilus lateralis*; GLSA = *Glaucomys sabrinus*; NEFU = *Neotoma fuscipes*; OTBE = *Otospermophilus beecheyi*; PEBO = *Peromyscus boylii*; PEMA = *Peromyscus maniculatus*; PETR = *Peromyscus truei*; TAAM = *Tamias amoenus*; TAQU = *Tamias quadrimaculatus*; TASE = *Tamias senex*; TASP = *Tamias speciosus*.

dominated by 1–3 species, the level of dominance was lower than that documented at the PNF. To some extent, this likely reflects a more sophisticated analysis employed by these authors (e.g., hierarchical capture–recapture modeling versus use of minimum number known alive), but the observation of highly asymmetric assemblage composition remains characteristic of both forests. Sites in the TB were dominated largely by sciurids, in particular chipmunks (*Tamias*). Yellow-pine (*T. amoenus*) and long-eared chipmunks (*T. quadrimaculatus*) were most commonly the dominant species, but deer mice, golden-mantled ground squirrels (*Callospermophilus lateralis*), and lodgepole chipmunks (*T. speciosus*) shared dominance at some sites (Fig. 2b; Supplementary Data SD1), with some turnover among these dominant generalists across years. Across all sites, yellow-pine and long-eared chipmunks were most abundant (26% and 25% of individuals, respectively), followed by deer mice (17%).

A final dataset comes from Yosemite National Park (hereafter, YNP); field efforts here were similar to those used in both the PNF and the TB, although they spanned fewer years, and the range of elevations was somewhat intermediate (1,400 to >2,200 m a.s.l.—Roberts et al. 2015). These authors compared small mammal assemblages in recently burned (1989–2004) and unburned sites within YNP in a system lacking timber removal and with a lower rate of fire suppression. Roberts et al. (2015) recorded a similar diversity of small mammals with results comparable to those of Kelt et al. (2013) in being dominated by deer mice (65% of individuals captured), followed by long-eared chipmunks (16%; Fig. 2c; Supplementary Data

SD1). Other species yielding modest numbers of captures were lodgepole chipmunks (6%) and brush mice (4%).

PROPOSED MECHANISMS—NATURAL SELECTION OR ANTHROPOGENIC FILTERING

To explain the preponderance of generalist species, Kelt et al. (2013; see also Stephens et al. 2014) argued that small mammal assemblages in forests of the Sierra Nevada have been filtered through a century of anthropogenic influences. In particular, fire suppression over the past century (and particularly post-World War II) has resulted in an accumulation of litter and fine woody debris on the forest floor and emergence of abundant sapling and small to medium-sized trees, such that many areas lack mineral soil and sufficient moisture to support ephemeral plants (SNEP 1996b). When combined with forestry practices that favor rapid harvest cycles and trees over shrubs, and additional impacts such as grazing (an important driver of recent change in small mammal faunas of the Great Basin—Rickart et al. 2013; Rowe and Terry 2014), the result is a forest that is structurally relatively homogeneous and most suitable to broadly generalist small mammal species. We expect that grazing likely impacted riparian and meadow systems much more than the forested systems in the Sierra Nevada (Belsky et al. 1999).

In contrast to the relatively short time span over which anthropogenic habitat alteration may have filtered species composition, Sollmann et al. (2015) proposed a much longer-term explanation for the generalist-dominated small mammal faunas of the TB. Noting that Sierra Nevada forests at the elevations of all 3 study sites historically experienced frequent fires (5–20 year return intervals—Kilgore and Taylor 1979; Caprio and Swetnam 1995) and that fire greatly influences vegetation composition as well as structure (Scholl and Taylor 2010), they argued that decadent forest structure in the Sierra Nevada likely has been patchier and more dispersed, and overall less available, than in more mesic (and stable) environments such as the Pacific Northwest. They proposed that "small mammal populations that evolved in frequent-fire forests . . . may be less restricted to specific habitat conditions due to the instability of these resources in time and space" (Sollmann et al. 2015:247). Small mammals certainly track habitat succession (Fox 1990; Gomez and Anthony 1998), but the argument implicit in Sollmann et al. (2015) is that when fire return intervals are sufficiently short, few small mammal species dependent on patchy and transient mature forests will persist, and selection will favor species with broad habitat (and presumably trophic) tolerances. While some insect (Heyborne et al. 2003) and bird species (Meslow 1978; Hagar 2007; Jones et al. 2012) are seral-stage specialists that track preferred habitat or seral stages across a temporally changing landscape, these species either have much more rapid turnover or are volant and therefore more vagile than most small mammals.

Roberts et al. (2015) documented similar species diversity in burned and unburned forests. For the 7 most common small mammal species captured, fire severity was the most important predictor of relative abundances in a nonparametric multiplicative regression model, underscoring the importance of fire on small mammal assemblages here.

None of these studies sampled for shrews (*Sorex* sp.) or moles (*Neurotrichus gibbsii*, *Scapanus* sp.), nor did they sample riparian or mesic habitats, which likely explains the absence of some species from the samples, even though they are present in the regional species pool (determined by the geographic range of all species in each of the regions sampled, as extracted from regional guides—Ingles 1965; Jameson and Peeters 2004; Ceballos 2014; Table 1). However, these studies were notable for what was not captured in forested habitat. In the PNF, red-backed (*Myodes californicus*) and long-tailed voles (*Microtus longicaudus*; 16 and 3 captures, respectively, over the course of the study) were rare, and in the TB, woodrats (*Neotoma fuscipes*, *N. cinerea*) and brush or piñon mice (*P. truei*) were functionally absent, with a single capture each of *N. cinerea* and *P. boylii* over the course of the study. Although these results in the TB may be the result of sampling higher elevation sites, at least some of these species have shifted upslope in the Sierra Nevada over the past century (e.g., *P. truei*, from piñon-juniper to mixed-conifer habitats—Moritz et al. 2008).

An alternative evolutionary explanation merits consideration. While the small mammal fauna of the Sierra Nevada prior to substantial Euro-American influence (e.g., pre-Gold Rush) is not known, studies elsewhere have documented shifts in small mammal assemblage composition over longer time periods, with patterns suggestive of a much deeper loss of ecological specialization among small mammals. In the Great Basin (Rowe and Terry 2014) and in the Klamath Mountains of northern California (Blois et al. 2010), paleo-records of 7000- and 17,000-year periods suggest an inverse relationship between temperature and small mammal species richness. In the Klamath region in particular, Blois et al. (2010) documented a strong increase in abundance of the generalist genus *Peromyscus*, suggesting that the abundance of this taxon in this region, including the Sierra Nevada just to the southeast, may reflect ancient compositional changes and more recently a warming climate. This mechanism is not entirely inconsistent with the fire-return interval argument presented by Sollmann et al. (2015); if fire-return intervals were longer in a cooler Pleistocene world and shorter in a warmer Holocene world then fire could be the proximate mechanism through which a more distal trigger has influenced small mammal assemblages.

Over a shorter time scale (about 100 years), Myers et al. (2009) documented changes in small mammal distributions and local abundances in the Great Lakes regions, with southern species increasing in abundance and extending their ranges northward at an apparent cost to species with more boreal distributions; Terry et al. (2011) showed similar patterns in the Great Basin. These data are indicative of a role for climate change and suggest that a third explanation for the generalist-dominated small mammal fauna of the Sierra Nevada may implicate climatic dynamics through the Pleistocene and Holocene.

IMPLICATIONS OF THESE EXPLANATIONS

Wildlife and resource management, and conservation science in general, are predicated on an adequate characterization and understanding of baseline conditions. Efforts to "restore" a system to conditions that never occurred could waste limited

Table 1.—Small mammal species documented at 3 sites in the Sierra Nevada (Kelt, Sollmann, and Roberts) and 1 in the Sierra San Pedro Mártir (Vander Wall), and occurring in the geographic species pool for these sites based on their geographic ranges in Ingles (1965), Jameson and Peeters (2004), and Ceballos (2014). Species documented at sites or occurring in the species pool are indicated by "X"; bold font indicates species present in pools but not documented at these sites. This table emphasizes taxonomic differences in the latter site relative to those in the Sierra Nevada, but taxa present are closely related and ecologically similar. Shrews (Soricomorpha, Soricidae) and gophers (Rodentia, Geomyidae) have been excluded from analyses as sampling efforts were not appropriate for these species.

Rodent group	Species	Acronym	Species observed				Species pool			
			Kelt	Sollmann	Roberts	Vander Wall	Kelt	Sollmann	Roberts	Vander Wall
Sciuridae	*Callospermophilus lateralis*	CALA		X	X		**X**	X	X	
	Glaucomys sabrinus	GLSA	X	X	X		X	X	X	
	Otospermophilus beecheyi	OTBE	X	X	X	X	X	X	X	X
	Sciurus griseus	SCGR	X		X		X	**X**	X	
	Tamias amoenus	TAAM		X			**X**	X	**X**	
	Tamias minimus	TAMI		X				X		
	Tamias obscurus	TAOB				X				X
	Tamias quadrimaculatus	TAQU	X	X	X		X	X	X	
	Tamias senex	TASE	X	X			X	X	**X**	
	Tamias speciosus	TASP		X	X		**X**	X	X	
	Tamiasciurus douglasii	TADO	X	X	X		X	X	X	
	Tamiasciurus mearnsi	TAME								**X**
Heteromyidae	*Chaetodipus californicus*	CHCA			X				X	
Cricetidae, Neotominae	*Neotoma bryanti*	NEBR								X
	Neotoma cinerea	NECI					**X**	**X**	**X**	
	Neotoma fuscipes	NEFU	X				X	**X**		
	Neotoma macrotis	NEMA			X				X	**X**
	Peromyscus boylii	PEBO	X		X		X	**X**	X	**X**
	Peromyscus californicus	PECA								**X**
	Peromyscus crinitus	PECR								**X**
	Peromyscus fraterculus	PEFR								**X**
	Peromyscus maniculatus	PEMA	X	X	X	X	X	X	X	X
	Peromyscus truei	PETR			X	X	**X**	**X**	X	X
Cricetidae, Arvicolinae	*Microtus californicus*	MICA								**X**
	Microtus longicaudus	MILO	X	X	X		X	X	X	
	Microtus montanus	MIMO	X		X		X	**X**	X	
	Myodes californicus	MICA	X				X			
Dipodidae, Zapodinae	*Zapus princeps*	ZAPR			X		**X**	**X**	X	
	Total number of species		12	11	15	4	18	18	18	12

financial resources toward irrelevant goals and could even result in an ecologically unbalanced system. Given this potentiality, the dichotomy in causal factors proposed by Kelt et al. (2013) and Sollmann et al. (2015) is more than academic.

Under anthropogenic filtering (Kelt et al. 2013), a century of habitat alterations may have greatly impacted species composition, favoring species tolerant of degraded forests, but leaving managers with an unclear target for restoration efforts. Changes in forest structure at mid- and high elevations in the Sierra Nevada include reductions in abundance and basal area by large trees and increases by small trees, as well as changes in relative cover of key species (Dolanc et al. 2014; McIntyre et al. 2015; Stephens et al. 2015). Selective timber harvesting has targeted large trees, while fire suppression, grazing, and a historic lack of active restoration efforts have precluded development of late successional or decadent forest conditions, impacting species known to require forest cover, such as northern flying squirrels (*Glaucomys sabrinus*). Lack of mature forest with large woody debris also would select against species that forage on fungi (e.g., red-backed voles, northern flying squirrels) or litter-dwelling arthropods. Fire suppression also has led to an accumulation of litter and fine woody debris (Weatherspoon and Skinner 1996; Stephens et al. 2009; Banwell and Varner 2014), which would disfavor species requiring open patches on the ground or access to mineral soil. Hence, this scenario predicts the differential loss of species with more restrictive habitat or dietary needs (via reduced population density and subsequent stochastic influences), to the benefit of more generalist species that can tolerate current conditions. It further suggests that management should target species known to favor mature or decadent forest structure, such as northern flying squirrels, red-backed and montane voles, and American shrew-moles (*Neurotrichus*), as well as sensitive riparian species that may be impacted by changes to adjacent forest (e.g., jumping mice [*Zapus*], water shrews [*Sorex palustris*], etc.).

In contrast, both natural selection through fire (Sollmann et al. 2015) and Holocene warming-related diversity loss (Blois et al. 2010; Rowe and Terry 2014) imply that the extant mammal fauna reflects, at least to some extent, a temporally deeper response to the frequency of fire in this system, to historic climate changes, or both. Either scenario would predict that prior to human colonization of this area, and certainly prior to the arrival of European Americans, the small mammal fauna would comprise primarily generalist species because these have the breadth of tolerance to persist in the face of relatively rapid environmental changes. Additionally, species dependent on mature forest conditions would be predicted to be more spatially restricted and adapted to immigrate to new areas as fire modified the landscape, leading to a metapopulation structure. Under this scenario, the patterns observed in our studies may not be as deviant from historic composition as suggested by hypotheses of anthropogenic filtering (Kelt et al. 2013). This does not negate the fact that the Sierra Nevada fauna was heavily impacted by unmanaged timber harvest and grazing in the Gold Rush era (Elliott-Fisk et al. 1996), nor that current anthropogenic impacts pose threats to the extant small mammal fauna. Indeed, both scenarios likely have influenced the contemporary fauna of this region in a synergistic and possibly a multiplicative manner, as observed in the Great Basin (Rowe 2007; Rowe and Terry 2014).

Roberts et al. (2015) shed some light on the importance of disturbance for the small mammal community, as they compared sites with a recent history of fire against control (unburned) sites within a national park that has been largely protected from logging activities since 1890. They documented similar species richness, and nearly identical species diversity (*H′*), in burned and unburned sites, but the relative abundance of the most common species was markedly different in burned and unburned forest. In particular, 2 of the 6 most common species (deer mice and Douglas squirrels [*Tamiasciurus douglasii*]) were 77% and 380% more abundant in unburned forests, whereas 4 other species (long-eared chipmunk, lodgepole chipmunk, California ground squirrel [*Otospermophilus beecheyi*], and brush mouse) were 44–575% more abundant in burned sites. However, indicator species analysis showed that none of these species was significantly more common in either habitat; only 1 species (northern flying squirrel) was significantly more likely to occur in unburned forests than burned forests, and no species was significantly more likely in burned sites. Of course, it is well documented that fire influences small mammal assemblages (e.g., Fox 1982; Diffendorfer et al. 2012; Letnic et al. 2013), and assemblages of small mammals studied by Roberts et al. (2015) differ across a major seral gradient, even if both habitat types studied remain dominated by generalist species. However, the data provided by Roberts et al. (2015) cannot shed light on the *origins* of a generalist-dominated fauna here.

Can This Dichotomy Be Tested?

While establishing a field experiment to evaluate the relative importance of evolutionary-scale selection relative to more immediate filtering by human activities is not possible, we can envision 2 means of assessing these alternatives. The first of these would be to characterize long-term temporal patterns in small mammal assemblages in this region using a taphonomic approach (cf. Blois et al. 2010; Rowe and Terry 2014); unfortunately, we are not aware of any such records or locations with such materials. The alternative is to compare small mammal assemblage compositions in other frequent-fire systems; if frequent-fire forests that have been relatively undisturbed by humans were dominated by generalist species then we might conclude—albeit cautiously—that this also is true for the Sierra Nevada.

The most comparable frequent-fire system that we are aware of and for which some data on small mammals are available is the Sierra San Pedro Mártir (SSPM) in northern Baja California (Fig. 1). While an imperfect comparison that must be treated cautiously—SSPM is an isolated range at a lower latitude and closer to the ocean—the key point is that this is a frequent-fire system within the California Floristic Province, and as such shares a common evolutionary history with the Sierra Nevada flora (Minnich et al. 2000). Although the mammal species found in the SSPM are different from those at our 3 Sierra Nevada sites (Table 1), they are closely related congeners to species present in the Sierra Nevada. Forests in the SSPM and the Sierra Nevada have similar fire frequency, although the seasonality of fire may differ (Stephens et al. 2003). Unlike the Sierra Nevada, however, forests in the SSPM have only recently been subjected to fire suppression activities and have not been commercially harvested for timber (Minnich et al. 2000; Stephens et al. 2003). The small mammal fauna of Baja California is well known (Huey 1964; Ceballos 2014), but to our knowledge no comprehensive surveys have characterized small mammal assemblages in the SSPM. Fortunately, Vander Wall et al. (2012) assessed seed dispersal in Jeffrey pine (*Pinus jeffreyi*) forests in this range and provided an initial glimpse of the local diversity and abundance of small mammals. Unlike our studies, Vander Wall et al. (2012) used only Sherman traps (Model SFAL, 5.2×6.4×22.9 cm) and baited with sunflower seeds, but all of the species known for this region are readily sampled with Sherman traps (see Table 1) and we do not believe this impacts the comparability of our results. Their limited sampling in the SSPM over 2 years yielded only 4 species (Table 1), all of which were habitat generalists, similar to the patterns observed in our studies in the Sierra Nevada. Hence, to the extent that the SSPM can be considered a control for recent anthropogenic impacts in western North America (an assumption we accept with caution), these observations suggest that the generalist nature of the small mammal fauna here may, at least in part, be a long-term legacy of nonanthropogenic factors.

Conclusions and Management Recommendations

The generalist-dominated small mammal fauna of the Sierra Nevada appears to have deep origins in Holocene climate warming, frequent fire-return intervals, or both. The extent to which these drivers have inhibited the development or establishment of more specialist species is unclear, but the past century of anthropogenic activities likely has further eroded niche diversity in this biota. These conclusions are suggestive, albeit preliminary. Long-term records such as those employed by Blois et al. (2010) and Rowe and Terry (2014) would be highly informative. Whereas these data are not available, the small mammal species found in at least 1 ecologically similar range, the SSPM, reflects that of the Sierra Nevada in being dominated by species with relatively broad ecological niches, which would support a hypothesis of evolutionary selection for generalist habits. Further sampling in the SSPM, using effort and sampling methodology similar to that applied in the Sierra Nevada, could provide further insight to the generality of these observations. Efforts in additional frequent-fire systems (e.g., Australia—Bradstock et al. 2002) could be pursued to assess whether similar patterns of generalist dominance emerge.

Further efforts in the Sierra Nevada also would be productive; the 3 papers emphasized here focused almost exclusively on forested habitats. In this relatively xeric forest system, mesic habitats such as meadows and riparian corridors may be critical foci for more specialized species such as jumping mice, shrews, and mesic-adapted voles (*Myodes*, *Microtus*, *Phenacomys*). Evidence from the southern Sierra suggests that northern flying squirrels are constrained to riparian corridors, perhaps because these provide moisture to support the truffles that these squirrels favor (Meyer et al. 2005).

If a climate warming, fire-frequency hypothesis is valid then it should apply to other taxa as well, and we encourage parallel research to assess this for other groups of animals as well as plants. However, regardless of the origin of generalist dominance in this system, it is clear that these relatively xeric forests exhibit a strong bias toward hyper-generalist taxa such as deer mice and chipmunks, and a virtual absence of species with more exacting trophic or habitat requirements that are known to occur in Sierra Nevada forests (such as the mesic-adapted voles and northern flying squirrel noted above). We agree with Sollmann et al. (2015) that this pattern comprises a call to managers to emphasize both spatial and temporal heterogeneity to maintain and promote faunal diversity. For example, abundance of many generalist small mammal species in the Sierra Nevada correlates negatively with canopy closure (Coppeto et al. 2006; Sollmann et al. 2015), whereas northern flying squirrel densities elsewhere in the Sierra Nevada showed the opposite pattern (Coppeto et al. 2006; Sollmann et al. 2016). Only a heterogeneous forest can accommodate the ecological requirements of such a diverse fauna.

Numerous studies in recent years have emphasized the importance of landscape-scale management promoting heterogeneity and diverse ecological interactions, and recent work promoting large-scale spatial and temporal heterogeneity in forest structure and composition (e.g., North et al. 2009; North 2012) provide constructive steps in this direction. In spite of unprecedented forces impacting the Sierra Nevada (SNEP 1996a), concerted efforts and greater insight to the ecological needs of species there have the potential to promote a sustainable future for biodiversity.

SUPPLEMENTARY DATA

Supplementary Data SD1.—Proportion of individuals of 6 dominant species of small mammal captured at all sites in 3 regions of the Sierra Nevada, California.

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LITERATURE CITED

Ackermann, M., and M. Doebeli. 2004. Evolution of niche width and adaptive diversification. Evolution 58:2599–2612.

Banwell, E. M., and J. M. Varner. 2014. Structure and composition of forest floor fuels in long-unburned Jeffrey pine-white fir forests of the Lake Tahoe Basin, USA. International Journal of Wildland Fire 23:363–372.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419–431.

Blackburn, T. C., and K. Anderson. 1993. Before the wilderness: environmental management by native Californians. Ballena Press, Menlo Park, California.

Blois, J. L., J. L. McGuire, and E. A. Hadly. 2010. Small mammal diversity loss in response to late-Pleistocene climatic change. Nature 465:771–774.

Bradstock, R. A., J. E. Williams, and A. M. Gill (eds.). 2002. Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge, United Kingdom.

Caprio, A. C., and T. W. Swetnam. 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. Pp. 173–179 in Proceedings: symposium on fire in wilderness and park management (J. K. Brown, R. W. Mutch, C. W. Spoon, and R. H. Wakimoto, technical coordinators, eds.). General Technical Report INT-GTR-320. USDA Forest Service, Intermountain Research Station, Ogden, Utah.

Ceballos, G. 2014. Mammals of Mexico. Johns Hopkins University Press, Baltimore, Maryland.

Clavel, J., R. Julliard, and V. Devictor. 2011. Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecology and the Environment 9:222–228.

Coppeto, S. A., D. A. Kelt, D. H. Van Vuren, J. A. Wilson, and S. Bigelow. 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. Journal of Mammalogy 87:402–413.

Corlett, R. T. 2015. The Anthropocene concept in ecology and conservation. Trends in Ecology & Evolution 30:36–41.

Devictor, V., R. Julliard, and F. Jiguet. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117:507–514.

Diffendorfer, J., G. M. Fleming, S. Tremor, W. Spencer, and J. L. Beyers. 2012. The role of fire severity, distance from fire perimeter and vegetation on post-fire recovery of small-mammal communities in chaparral. International Journal of Wildland Fire 21:436–448.

Dolanc, C. R., H. D. Safford, J. H. Thorne, and S. Z. Dobrowski. 2014. Changing forest structure across the landscape of the Sierra Nevada, CA, USA, since the 1930s. Ecosphere 5:101. doi:10.1890/es14-00103.1:101.

Elliott-Fisk, D. L., et al. 1996. Lake Tahoe case study. Pp. 217–276 in Sierra Nevada Ecosystem Project: final report to Congress, Addendum. University of California, Centers for Water and Wildland Resources, Davis.

Fox, B. J. 1982. Fire and mammalian secondary succession in an Australian coastal heath. Ecology 63:1332–1341.

Fox, B. J. 1990. Changes in the structure of mammal communities over successional time scales. Oikos 59:321–329.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematics 19:207–233.

Gomez, D. M., and R. G. Anthony. 1998. Small mammal abundance in riparian and upland areas of five seral stages in Western Oregon. Northwest Science 72:293–302.

Hagar, J. C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: a review. Forest Ecology and Management 246:108–122.

Heyborne, W. H., J. C. Miller, and G. L. Parsons. 2003. Ground dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA. Forest Ecology and Management 179:123–134.

Huey, L. M. 1964. The mammals of Baja California, Mexico. Transactions of the San Diego Society of Natural History 13:85–168.

Ingles, L. G. 1965. Mammals of the Pacific States: California, Oregon, and Washington. Stanford University Press, Stanford, California.

Jameson, E. W., and H. J. Peeters. 2004. Mammals of California. University of California Press, Berkeley.

Jones, J. E., A. J. Kroll, J. Giovanini, S. D. Duke, T. M. Ellis, and M. G. Betts. 2012. Avian species richness in relation to intensive forest management practices in early seral tree plantations. PLoS One 7:e43290. doi:10.1371/journal.pone.0043290.

Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. Journal of Evolutionary Biology 15:173–190.

Kelt, D. A., et al. 2013. Small mammals exhibit limited spatiotemporal structure in Sierra Nevada forests. Journal of Mammalogy 94:1197–1213.

Kilgore, B. M., and D. Taylor. 1979. Fire history of a sequoia mixed-conifer forest. Ecology 60:129–142.

Letnic, M., M. Tischler, and C. Gordon. 2013. Desert small mammal responses to wildfire and predation in the aftermath of a La Niña driven resource pulse. Austral Ecology 38:841–849.

Levins, R. 1968. Evolution in changing environments; some theoretical explorations. Princeton University Press, Princeton, New Jersey.

Le Viol, I., et al. 2012. More and more generalists: two decades of changes in the European avifauna. Biology Letters 8:780–782.

Lewis, S. L., and M. A. Maslin. 2015. Defining the Anthropocene. Nature 519:171–180.

McIntyre, P. J., et al. 2015. Twentieth-century shifts in forest structure in California: denser forests, smaller trees, and increased dominance of oaks. Proceedings of the National Academy of Sciences of the United States of America 112:1458–1463.

Meslow, E. C. 1978. The relationship of birds to habitat structure–plant communities and successional stages. Pp. 12–18 in Proceedings of the workshop on nongame bird habitat management in the coniferous forests of the western United States. USDA Forest Service General Technical Report PNW 64, Albany, California.

Meyer, M. D., M. P. North, and D. A. Kelt. 2005. Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada. Canadian Journal of Zoology 83:1581–1589.

Minnich, R. A., M. G. Barbour, J. H. Burk, and J. Sosa-Ramirez. 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Mártir, Baja California, Mexico. Journal of Biogeography 27:105–129.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science (Washington DC) 322:261–264.

Myers, P., B. L. Lundrigan, S. M. G. Hoffman, A. P. Haraminac, and S. H. Seto. 2009. Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. Global Change Biology 15:1434–1454.

North, M. 2012. Managing Sierra Nevada forests. USDA Forest Service Technical Report PSW-GTR-237, Albany, California.

North, M., P. Stine, K. O'Hara, W. Zielinski, and S. Stephens. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. USDA Forest Service Technical Report PSW-GTR-220, Albany, California.

Peers, M. J. L., D. H. Thornton, and D. L. Murray. 2012. Reconsidering the specialist-generalist paradigm in niche breadth dynamics: resource gradient selection by Canada lynx and bobcat. PLoS One 7:e51488. doi:10.1371/journal.pone.0051488.

Poisot, T., J. D. Bever, A. Nemri, P. H. Thrall, and M. E. Hochberg. 2011. A conceptual framework for the evolution of ecological specialisation. Ecology Letters 14:841–851.

Rickart, E. A., K. G. Bienek, and R. J. Rowe. 2013. Impact of livestock grazing on plant and small mammal communities in the Ruby Mountains, northeastern Nevada. Western North American Naturalist 73:505–515.

Roberts, S. L., D. A. Kelt, J. W. van Wagtendonk, A. K. Miles, and M. D. Meyer. 2015. Effects of fire on small mammal communities in frequent-fire forests in California. Journal of Mammalogy 96:107–119.

Roughgarden, J. 1972. Evolution of niche width. The American Naturalist 106:683–718.

Rowe, R. J. 2007. Legacies of land use and recent climatic change: the small mammal fauna in the mountains of Utah. American Naturalist 170:242–257.

Rowe, R. J., and R. C. Terry. 2014. Small mammal responses to environmental change: integrating past and present dynamics. Journal of Mammalogy 95:1157–1174.

Ruth, L. 1996. Conservation and controversy: National Forest management, 1960–95. Pp. 145–162 in Sierra Nevada Ecosystem Project: final report to Congress. Vol. II. Assessments and scientific basis for management options. Center for Water and Wildland Resources, University of California, Davis.

Scholl, A. E., and A. H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecological Applications 20:362–380.

SNEP. 1996a. Sierra Nevada Ecosystem Project: final report to Congress: status of the Sierra Nevada. Centers for Water and Wildland Resources, University of California, Davis.

SNEP. 1996b. Sierra Nevada Ecosystem Project: final report to Congress. Vol. 1. Assessment summaries and management strategies. Wildland Resources Center Report No. 36, Davis, California.

Sollmann, R., A. M. White, B. Gardner, and P. N. Manley. 2015. Investigating the effects of forest structure on the small mammal community in frequent-fire coniferous forests using capture-recapture models for stratified populations. Mammalian Biology 80:247–254.

Sollmann, R., A. M. White, G. L. Tarbill, P. N. Manley, and E. E. Knapp. 2016. Landscape heterogeneity compensates for fuel reduction treatment effects on northern flying squirrel populations. Forest Ecology and Management 373:100–107.

Stephens, S. L., et al. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. Ecological Applications 19:305–320.

Stephens, S. L., et al. 2014. California spotted owl, songbird, and small mammal responses to landscape fuel treatments. BioScience 64:893–906.

Stephens, S. L., J. M. Lydersen, B. M. Collins, D. L. Fry, and M. D. Meyer. 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the southern Sierra Nevada. Ecosphere 6:79. doi:10.1890/ES14-00379.1.

Stephens, S. L., C. N. Skinner, and S. J. Gill. 2003. Dendrochronology-based fire history of Jeffrey pine - mixed conifer forests in the Sierra San Pedro Mártir, Mexico. Canadian Journal of Forest Research 33:1090–1101.

Terry, R. C., C. Li, and E. A. Hadly. 2011. Predicting small-mammal responses to climatic warming: autecology, geographic range, and the Holocene fossil record. Global Change Biology 17:3019–3034.

Vander Wall, S. B., M. S. Enders, S. Barga, C. Moore, A. Seaman, and R. Perea. 2012. Jeffrey pine seed dispersal in the Sierra San Pedro Mártir, Baja California, Mexico. Western North American Naturalist 72:534–542.

Van Tienderen, P. H. 1991. Evolution of generalists and specialist in spatially heterogeneous environments. Evolution 45:1317–1331.

Weatherspoon, C. P., and C. N. Skinner. 1996. Landscape-level strategies for forest fuel management. Pp. 1472–1492 in Sierra Nevada Ecosystem Project: final report to Congress. Vol. II. Assessments and scientific basis for management options. University of California, Centers for Water and Wildland Resources, Davis.

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