pear unlikely, putting the focus on elevational gradients, where range-shift gaps will develop early for the great numbers of narrow-ranged species. The lowland tropics lack a source pool of species adapted to higher temperatures to replace those driven upslope by warming, raising the possibility of substantial attrition in species richness in the tropical lowlands.

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Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA

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We provide a century-scale view of small-mammal responses to global warming, without confounding effects of land-use change, by repeating Grinnell's early–20th century survey across a 3000-meter-elevation gradient that spans Yosemite National Park, California, USA. Using occupancy modeling to control for variation in detectability, we show substantial (~500 meters on average) upward changes in elevational limits for half of 28 species monitored, consistent with the observed ~3°C increase in minimum temperatures. Formerly low-elevation species expanded their ranges and high-elevation species contracted theirs, leading to changed community composition at mid- and high elevations. Elevational replacement among congeners changed because species' responses were idiosyncratic. Though some high-elevation species are threatened, protection of elevation gradients allows other species to respond via migration.

Although human-driven global warming (*1*) has changed phenology of species and contributed to range expansions (*2*–*6*), contractions of species' ranges are less well documented (*7*–*10*). Models of future climate-change scenarios predict large range shifts, high global extinction rates, and reorganized communities (*11*, *12*), but model outcomes are also highly uncertain (*13*, *14*). Most studies of species' responses span only a few decades—typically from the 1960 or 1970s, which was a relatively cool period, to the present. Such results can be confounded by decadal-scale climate oscillations (*15*) and landscape modification (*8*, *16*). Furthermore, range shifts are uncertain when confounded by false absences due to limited historic sampling and inability to control for changes in detectability between sampling periods (*17*, *18*).

We quantified the impact of nearly a century of climate change on the small-mammal community of Yosemite National Park (YNP) in California, USA, by resampling a broad elevational transect (60 to 3300 m above sea level) that Joseph Grinnell and colleagues surveyed from 1914 to 1920 (*19*) (Fig. 1). Their work documented the diversity and distribution of terrestrial vertebrates in California to establish a benchmark for future comparison (*20*), and led to the concept of the ecological niche, the importance of temperature as determinant of range boundaries, and the notion that species respond uniquely to environmental changes (*21*). In contrast to most early–20th century records, the "Yosemite Transect" was densely sampled across elevations (Fig. 1) and is amply documented by specimens (n = 4354), field notes (>3000 pages), and photographs (~700) (*22*), enabling precise identification of both species and sampling sites. From daily trapping records, we estimated detectability of species in historical as well as current surveys, permitting the unbiased estimation of species' "absences" from elevational bands in both periods (*23*). The transect spans YNP, a protected landscape since 1890, and allowed us to examine long-term responses to climate change without confounding effects of land-use change, although at low to mid-elevations there has been localized vegetation change relating to seral dynamics, climate change, or both (*24*). Finally, analyses of regional weather records pointed to substantial increase of the average minimum monthly temperature of 3.7°C over the past 100 years, with notable increases from 1910 to 1945 and from 1970 to the present (*15*, *22*) (fig. S1).

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Future warming is predicted to cause substantial turnover of species within North American National Parks, including Yosemite (*25*). Given marked regional warming over the past century, we predicted that species ranges should have shifted upward (*5*, *10*). This should manifest as upward contraction of the lower range limit for mid- to high-elevation species, upward shift of the entire range or expansion of the upper limit for low- to mid-elevation species, and altered community composition within elevational bands (*9*).

Elevational ranges of species and their habitats differed markedly between the gradual western and steep eastern slopes of the transect (*19*) (Fig. 1). On the west slope, we trapped small mammals at 121 sites compared to 56 in Grinnell's time (table S1), but overall effort and elevational range (~50 to 3300 m) were comparable (*22*). There were fewer sites on the east side in both time periods (9 for Grinnell, 12 for resurveys) because of limited extent (Fig. 1). Our analyses of richness and turnover focused on species detectable by standardized trapping (37 species) or by observation (6 species; table S2). To test for elevational shifts, we applied occupancy modeling (*22*, *23*) to the 23 west slope taxa with sufficient trapping records to estimate detectability in both periods (tables S1 and S2 and Fig. 2). The best detection model in a set of 36 (table S3) was used to calculate the probability of a false absence (P_{fa}) across trapping sites, where a species was not observed in one sampling period but was in the other (Table 1). Range shifts were significant if $P_{fa} \leq 0.05$. For each species we evaluated eight hypothesized relationships of occupancy, era, and elevation (fig. S2) using the 14 best detection models (table S3) to create model-averaged occupancy-elevation profiles (Fig. 2 and fig. S3). Conservatively, we excluded shifts that were statistically significant but biologically trivial (Fig. 3). In most cases where the P_{fa} test indicated an elevation shift, occupancy models agreed (Table 1 and fig. S3). Exceptions occurred when occupancy models were weak (i.e., insufficient data) or detected changes in occupancy at elevations other than range limits, or when nonstandard data (i.e., records from ad hoc collecting) were included in P_{fa} tests but not in occupancy models.

Elevation limits shifted mostly upward (Table 1 and Fig. 3A), and this occurred more frequently for lower than upper limits ($\chi^2 = 4.26$, df = 1, $P = 0.039$). Twelve of 28 (43%) west slope species showed significant shifts in lower limits, of which 10 increased (mean = +475 m) and two, both shrews, decreased (mean = −744 m). In contrast, upper limits changed significantly in only seven instances, with similar numbers of upward ($n = 4$, mean = +501 m) and downward shifts ($n = 3$, mean = −309 m).

High-elevation species typically experienced range contractions, whereas low-elevation species expanded their ranges upward ($\chi^2 = 8.8$, df = 2, $P = 0.012$), a pattern expected with increased temperature. Lower range limits contracted in 50% of the high-elevation species but in only 10% of low-elevation species, whereas 50% of low-elevation species expanded their upper range compared to none of the high-elevation species (Fig. 3B). High-elevation species contracting (Table 1 and Fig. 2A) included the alpine chipmunk (*Tamais alpinus*), Belding's ground squirrel (*Spermophilus beldingi*), water shrew (*Sorex palustris*), and pika (*Ochotona princeps*). Range collapse—increased lower limits and decreased upper limits—was observed in two high-elevation species: the bushy-tailed woodrat (*Neotoma cinerea*) and the shadow chipmunk (*T. senex*) (Fig. 2B). Parallel trends were observed on the east slope of the Sierra for *N. cinerea* and *S. beldingi* (fig. S3). Range contractions due to increases in lower-elevation limits were also observed for two species formerly at mid- to high elevations [the golden-mantled ground squirrel (*Spermophilus lateralis*) and the long-tailed vole (*Microtus longicaudus*)] (Table 1). Only one lowland species contracted—the kangaroo rat (*Dipodomys heermanni*) showed a modest increase in lower limit and a larger decrease in upper limit since Grinnell's time. Range expansions resulted from either expanded upper limits [the pocket mouse (*Chaetodippus californicus*), the California vole (*M. californicus*), and the harvest mouse (*Reithrodontomys megalotis*)] or expanded lower limits (two shrews: *Sorex monticola* and *S. ornatus*). Finally, the pinyon mouse (*Peromyscus truei*) translocated upward (Fig. 2C); both upper and lower limits increased by ~500 m, but it now also occupies montane conifer habitats on the west slope 800 to 1400 m higher after its east slope population expanded upward by ~1000 m to cross the Sierra crest.

Elevational range shifts resulted in modest changes in species richness and composition at varying spatial scales. Species richness averaged across five estimators (*26*) that account for non-observed species (Fig. 3C, fig. S4, and table S4) declined from the Grinnell era to the present (repeated measures analysis of variance, $F = 32.7$ df = 1, $P = 0.004$). Richness estimators suggest a slight decrease across the whole transect (current-historic mean estimates = −4.4 species, −9%), but not within YNP (+1.3 species, 4%). Species richness was reduced within each life zone, with the largest change in the Lower and Upper Sonoran zones west of YNP. Community similarity between Grinnell's period and the present was high (mean similarity, $S > 0.9$) for the whole transect, the park alone, and most life zones. Species composition was least similar for the Transition and Hudsonian-Arctic zones, as expected given the upward expansions of formerly Sonoran zone taxa and the range shifts of high-elevation species (Table 1).

Closely related species responded idiosyncratically to climate change (Table 1), but why species vary in response is not clear. For example, some species of *Peromyscus* mice showed elevation range shifts (*P. truei*), whereas others did not (*P. boylii*, *P. maniculatus*). The same is

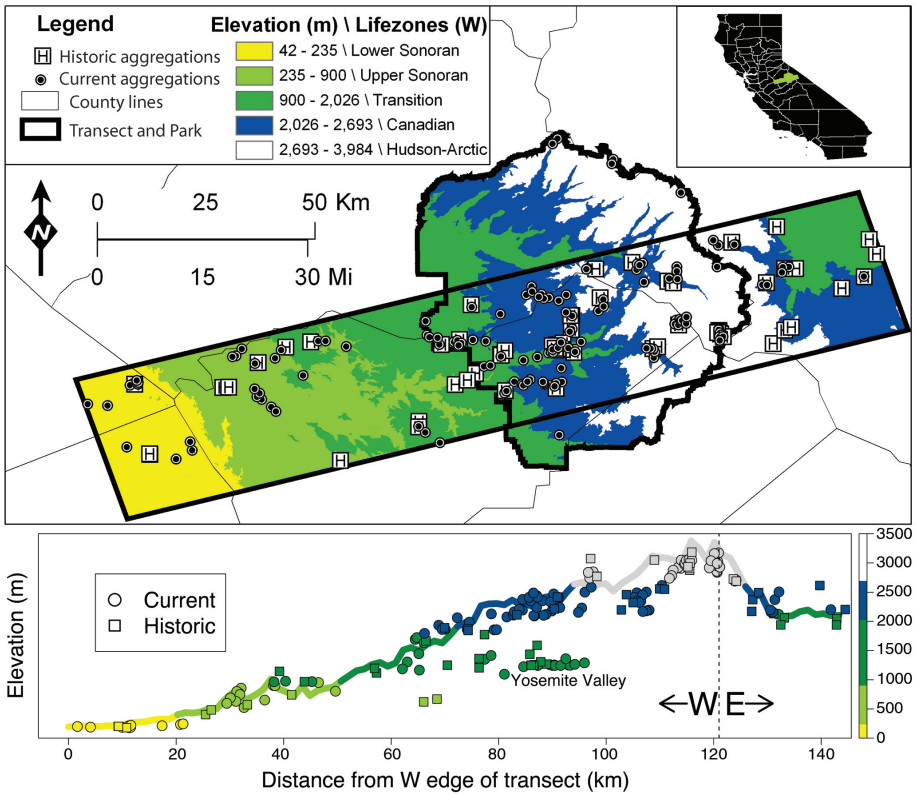

Fig. 1. Map of surveyed sites in Grinnell (Historic) and Current surveys relative to the Yosemite National Park boundary and life zones (upper panel), and to an averaged elevational profile (lower panel).

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true for chipmunks (*Tamias*), ground squirrels (*Spermophilus*), voles (*Microtus*), and shrews (*Sorex*). Beyond original elevation range (high versus low), life history and ecological traits were weak predictors of which species exhibited upward shifts of their range limits (tables S5 and S6). This was especially true for high-elevation species with upward contraction of their lower range limit. However, lowland species that are short-lived and lay more litters per year (so-called fast life-style species) were more likely to expand their range upward than were their long-lived, less fecund counterparts (table S5 and fig. S5). The elevational replacements among congeners, documented so carefully in the early 20th century (*19*), are now quite different.

By applying occupancy modeling to a thoroughly documented historical record and the resurvey, we provide an unbiased comparison of changes in species' ranges at the centennial scale. Because much of the transect spans a long-protected National Park, confounding effects of land-use change are minimized. Even so, vegetation has changed within YNP over this period, in part due to fire suppression (*22*). The park was hardly pristine in the early 20th century, with ranching of introduced herbivores in Yosemite Valley and the high country recovering from historical overgrazing. As examples, expansion by *C. californicus* and west slope *P. truei* are associated with fire-related conversion of conifer to shrub habitats, whereas the downward shift of *S. monticola* could reflect recovery of their preferred wet meadow habitats. Increased prevalence of mesic small mammals following cessation of grazing has also been reported for an analogous community in the Rocky Mountains (*27*).

The preponderance of upward range shifts, leading to contraction of high-elevation species and expansions of low-elevation taxa, accords with the predicted impacts of climate warming (*5*, *8*, *9*). Although vegetation dynamics have likely contributed to changes at low to mid-elevation, habitat change at higher elevations is limited (*15*) (fig. S6). The ~500-m average increase in elevation for affected species is also consistent with estimated warming of +3°C, assuming a change of temperature with elevation of ~6°C per km. Several small-mammal taxa that responded to changing temperature also showed large range fluctuations during late Quaternary climate fluctuations (*28*), and some have declined regionally (*29*).

Table 1. Analyses of elevation change for 28 west slope species. Given are average detectability per site for Grinnell [*P*(*G*)] and current [*P*(*C*)] periods, original elevation range, changes in upper (U) and lower (L) range limit that are significant by the P_{fa} tests, the best supported form of the occupancy model (Elev, elevation; NA, not analyzed), the cumulative Akaike's Information Criterion weight for all models with those terms (*w*), and original Lifezone classification (*18*), where L and H refer, respectively, to species with mostly low- to mid-elevation ranges (<2000 m) and mid- to high-elevation ranges (>2000 m) in Grinnell's time; *P. maniculatus* covered the entire transect. Values in bold are further supported by occupancy models. See fig. S4 for elevation plots and models of individual species.

No.	Species	*P*(*G*)	*P*(*C*)	Original elevation range (m)	Range limit change (m)	Best occupancy model	*w*	Original life zone (H, L)
					Range expansions			
1	*Microtus californicus*	0.81	0.58	57–1160	+505 U	Elev	0.36	Lower–Upper Sonoran (L)
2	*Reithrodontomys megalotis*	0.99	0.87	57–1160	+112 U	Elev	0.50	Lower–Upper Sonoran (L)
3	*Peromyscus truei**	0.99	0.93	183–1220	**+589 U**, **+468 L**	Era*(Elev + Elev^2)	0.99	Upper Sonoran (L)
4	*Chaetodippus californicus*	0.28	0.19	193–914	**+800 U**	Era*(Elev + Elev^2)	0.32	Upper Sonoran (L)
5	*Sorex ornatus*	0.32	0.93	549–914	**−485 L**	Era *(Elev + Elev^2)	0.74	Upper Sonoran (L)
6	*Sorex monticolus*	0.99	0.97	2212–3287	**−1003 L**	Era + Elev + Elev^2	0.37	Canadian–Hudsonian (H)
					Range contractions			
7	*Dipodomys heermanni*	0.16	0.98	57–1025	+63 L, **−293 U**	Era*Elev	0.48	Lower–Upper Sonoran (L)
8	*Microtus longicaudus*	0.99	0.98	623–3287	**+614 L**	Era + Elev + Elev^2	0.74	Transition–Hudsonian (H)
9	*Zapus princeps*	0.98	0.90	1291–3185	+159 L, −64 U	Era + Elev + Elev^2	0.53	Transition–Hudsonian (H)
10	*Tamias senex*	0.95	0.71	1402–2743	+1007 L, −334 U	Elev +Elev^2	0.48	Canadian (H)
11	*Spermophilus lateralis*	0.70	0.89	1646–3200	**+244 L**	Era*(Elev + Elev^2)	0.78	Transition–Hudsonian (H)
12	*Sorex palustris*	0.39	0.23	1658–3155	**+512 L**	Era + Elev + Elev^2	0.39	Canadian–Hudsonian (H)
13	*Neotoma cinerea**	0.90	0.71	1798–3287	**+609 L**, **−719 U**	Era*(Elev + Elev^2)	0.83	Canadian–Arctic-Alpine (H)
14	*Spermophilus beldingi**	0.98	0.98	2286–3287	+355 L	Elev	0.32	Canadian–Arctic-Alpine (H)
15	*Tamias alpinus*	0.92	0.95	2307–3353	**+629 L**	Era + Elev	0.56	Hudsonian–Arctic-Alpine (H)
16	*Ochotona princeps*†	NA	NA	2377–3871	+153 L	NA	NA	Canadian–Arctic-Alpine (H)
					No change			
17	*Peromyscus maniculatus**	0.99	0.99	57–3287	No change	Era*(Elev + Elev^2)	0.72	Lower Sonoran–Arctic-Alpine (H)
18	*Thomomys bottae*†	NA	NA	57–1676	No change	NA	NA	Lower Sonoran–Transition (L)
19	*Spermophilus beecheyi*	0.50	0.82	61–2734	−250 U	Era*(Elev + Elev^2)	0.89	Lower Sonoran–Canadian (L)
20	*Neotoma macrotis*	0.90	0.91	183–1646	+67 U	Elev + Elev^2	0.62	Lower Sonoran–Transition (L)
21	*Peromyscus boylii*	0.98	0.97	183–2469	−122 L	Elev + Elev^2	0.60	Upper Sonoran–Transition (L)
22	*Sorex trowbridgii*	0.71	0.88	1160–2286	No change	Elev + Elev^2	0.40	Transition–Canadian (H)
23	*Microtus montanus**	0.81	0.98	1217–3155	No change	Elev + Elev^2	0.36	Transition–Hudsonian (H)
24	*Tamiasciurus douglasi**†	NA	NA	1229–3185	No change	NA	NA	Transition–Hudsonian (H)
25	*Tamias quadrimaculatus*	0.95	0.85	1494–2210	+50 U	Era*(Elev + Elev^2)	0.78	Transition–Canadian (H)
26	*Tamias speciosus**	1.00	1.00	1768–3155	+128 L, +65 U	Era*(Elev + Elev^2)	1.00	Canadian–Hudsonian (H)
27	*Thomomys monticola*†	NA	NA	1905–3155	No change	NA	NA	Canadian–Hudsonian (H)
28	*Marmota flaviventris*†	NA	NA	2469–3353	No change	NA	NA	Canadian–Arctic-Alpine (H)

* Similar trends are observed for east-side populations (see fig. S4). †These species were encountered by observation and/or specialized trapping and were not subject to occupancy analyses.

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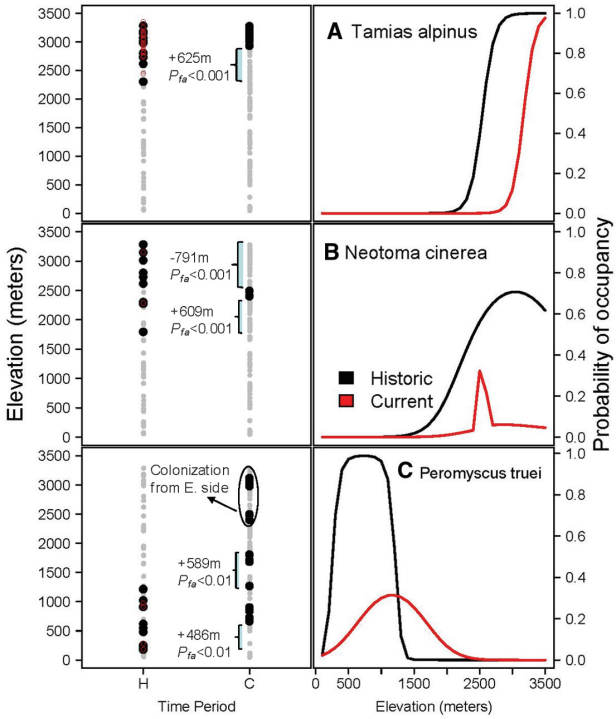

Fig. 2. Example elevation plots from the west slope transect of upward range expansion (*T. alpinus and P. truei*) (**A** and **C**), and range collapse (*N. cinerea*) (**B**). Shown are occupied (black) and unoccupied (gray) sites, probability of false absence (P_{fa}), and model-averaged occupancy-elevation profiles (table S3 and fig. S2). *P. truei* colonized high elevations west of the Sierra crest from the eastern slope. Red marks for historical elevation profile of *T. alpinus* refer to ad hoc records.

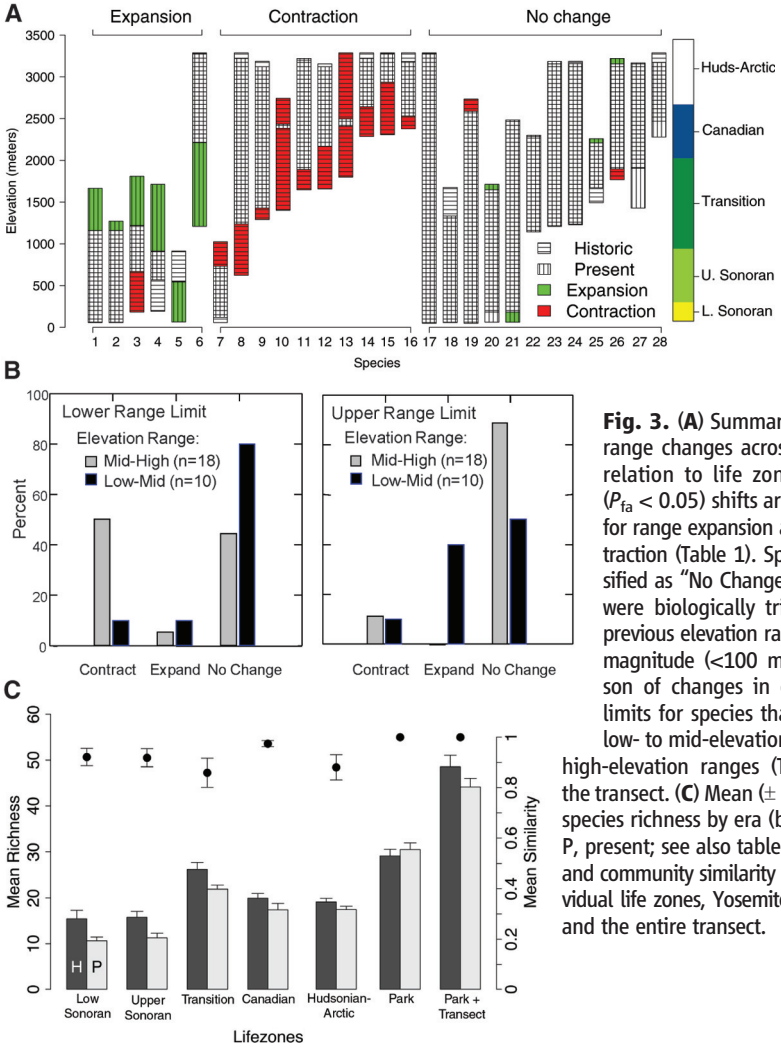

Fig. 3. (**A**) Summary of elevational range changes across all species in relation to life zones. Significant (P_{fa} < 0.05) shifts are colored green for range expansion and red for contraction (Table 1). Species were classified as "No Change" if range shifts were biologically trivial (<10% of previous elevation range) or of small magnitude (<100 m). (**B**) Comparison of changes in elevation-range limits for species that formerly had low- to mid-elevation versus mid- to high-elevation ranges (Table 1) across the transect. (**C**) Mean (± SE) estimates of species richness by era (bars: H, historic; P, present; see also table S4 and fig. S4) and community similarity (points) for individual life zones, Yosemite National Park, and the entire transect.

Recent trends do not bode well for several mid- to high-elevation species, including some endemic to the high Sierra (e.g., *T. alpinus*) (Fig. 3A). Nevertheless, species diversity within Yosemite has changed little, because range expansions compensated for retractions. Our results confirm that protecting large-scale elevation gradients retains diversity by allowing species to migrate in response to climate and vegetation change. The long-recognized importance of protected landscapes has never been greater.

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