the basis of cross-cutting relationships, textural features at Endurance crater suggest relatively late diagenetic events (*24*) that record chemical interaction with a local groundwater table (*21*, *24*). If correct, the observation of comparable vertical trends in sections that may represent distinct stratigraphic levels could imply that a set of depositional and early diagenetic processes recurred through time during regional stratigraphic development. Alternatively, chemostratigraphic trends at Endurance may reflect downward-penetrating diagenesis related to surface exposure (*25*). This would allow chemical trends in both sections to reflect a single alteration event that took place during or after development of the current land surface. In either case, the wettest conditions occurred during deposition and early diagenesis, with drying thereafter (*26*).

Opportunity's investigation of Victoria crater shows that depositional, diagenetic, and erosional processes documented locally at Eagle and Endurance craters acted regionally. These processes include (i) chemical interaction of basalts and acidic water to produce sulfate salts; (ii) production of sands, transport and deposition by wind, and subsequent groundwater-influenced cementation; (iii) later diagenetic alteration of outcrop surfaces under increasingly arid conditions; and (iv) erosion of friable sedimentary rocks by persistent wind action, continuing to the present.

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Bone Assemblages Track Animal Community Structure over 40 Years in an African Savanna Ecosystem

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Reconstructing ancient communities depends on how accurately fossil assemblages retain information about living populations. We report a high level of fidelity between modern bone assemblages and living populations based on a 40-year study of the Amboseli ecosystem in southern Kenya. Relative abundance of 15 herbivorous species recorded in the bone assemblage accurately tracks the living populations through major changes in community composition and habitat over intervals as short as 5 years. The aggregated bone sample provides an accurate record of community structure time-averaged over four decades. These results lay the groundwork for integrating paleobiological and contemporary ecological studies across evolutionary and ecological time scales. Bone surveys also provide a useful method of assessing population changes and community structure for modern vertebrates.

Accurate reconstructions of ancient community ecology depend on how closely fossil assemblages match species richness and relative abundances in the original living communities. Many taphonomic and methodological biases relating to morphology, body size, and life habit can affect the presence or absence of taxa and their relative abundance in fossil assemblages (*1–4*). Vertebrates and shelly invertebrates have durable remains that can accumulate over long periods of time, raising questions about how such remains record properties of the original community, especially during periods of marked population and habitat change (*2–5*). Data quality issues have been addressed through studies of living populations and their death assemblages in marine invertebrates (*3, 4, 6, 7*) and terrestrial vertebrates (*8–10*). These "live:dead" studies show that single-census death assemblages can approximate ecological snapshots but typically include durable remains representing varying intervals of accumulation, or time averaging. Time averaging usually inflates species richness relative to live samples, but under stable population and environmental conditions can accurately represent rank abundances of the dominant species in shelly invertebrate assemblages (*3, 4, 6, 7*).

Earlier, single-census live:dead research in the Amboseli ecosystem demonstrated preburial fidelity of the surface bone assemblage with respect to large (15 to 4000 kg) herbivore populations and their habitat distributions (*8, 11–13*). Birth and death rates among species, and hence the production of skeletal remains, are inversely scaled to species body weight (*12*). Consequently, the greater numbers of dead smaller animals were offset by allometrically scaled bone destruction

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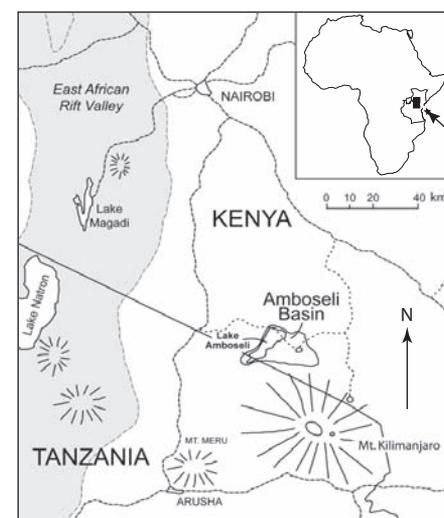
Fig. 1. Regional map of southern Kenya showing the physiographic context of the Amboseli Basin north of Mount Kilimanjaro. Lake Amboseli is a shallow, seasonal playa with wetlands fed by springs from Mount Kilimanjaro.

rates, such that the relative abundances and size-frequency distributions of species in the bone and living assemblages matched (8, 13). The question remains, however, whether cumulative bone assemblages accurately reflect time-averaged community structure, especially during periods of rapid population and environmental change.

The 8500 km² Amboseli ecosystem straddling the Kenya-Tanzania border (Fig. 1) lies at an altitude of 1200 m and receives an annual rainfall of 250 to 300 mm, distributed in two seasons (14, 15). The ecosystem encompasses the migrations of the large ungulates and pastoral livestock that concentrate seasonally around permanent swamps in the Amboseli Basin (11, 16, 17) [supporting online material (SOM) text S1]. In the 1960s, the ecosystem was dominated by dense woodlands and bushland interspersed with grasslands and swamps. By the 1990s, woodlands had given way to open grassland and scrubland and the swamps had doubled in size (18). Amboseli's ungulate populations have fluctuated widely in response to drought cycles and human impact over the past four decades (18) (table S1). Overall, the abundance of grazers increased relative to browsers, and species richness declined in response to the habitat changes (18).

Amboseli thus provides a test of the response of a large vertebrate community to decadal-scale ecological changes and the fidelity of bones in reflecting these changes. The large herbivore counts and vegetation maps give a continuous picture of the changing numbers and distribu-

tions of animals in relation to habitat from 1967 to 2004 (SOM text S1.1). The bone sampling protocol (8, 13) targeted the main areas and habitats used by the living vertebrate species. Bones of vertebrate species were recorded along 96 ground transects in 1975 to 1976, and a subset of 44 of these transects in 2002 to 2004 (SOM text S1.2). Bone survey data for 15 regularly censused abundant wild ungulates (14 mammals and ostrich) were used for comparison with the live population counts (Table 1 and table S1).

We tested how well recent bone assemblages represent abundances of the parent populations by tracking correlations between dead and living populations of large herbivores over 40 years (1964 to 2004) that span some of the most rapid habitat changes and herbivore population fluxes recorded in the African savannas (16, 18) (table S1). We use live population counts versus bone surveys to test three hypotheses: (i) bone surveys accurately track community structure through successive time intervals and record the time-averaged structure for all intervals combined, (ii) bone surveys accurately record live species abundance distributions in different habitats, and (iii) ecological properties of the living community can be deduced from its bone assemblage.

Counts of individuals for each bone sampling period include identifiable remains of animals dying up to ~10 years before the sampling years (19) (SOM text S1.3). Sampling was done in two phases (1975 to 1976 and 2002 to 2004); thus, the surveys recorded fresh to weathered bones representing time intervals of 11 to 12 years before these dates, that is, 1964 to 1976 and 1993 to 2004. Based on established bone weathering stages (WS) in Amboseli (19), each of these two intervals can be divided into two subintervals. Bones in WS 0 to

2 (~5 years since death) represent animals that died in 1970 to 1976 and 1998 to 2004, and WS 3 and 4 (~6 to 12 years since death) represent deaths in 1964 to 1969 and 1993 to 1998 (SOM text S1.3 and table S2). The bone survey data thus are grouped in four time intervals: 1964 to 1969, 1970 to 1976, 1993 to 1998, and 1999 to 2004 (table S2), representing ~25 out of 40 years or ~60% of the total time span (SOM text S1.3). Live census data were selected to match these same multiyear intervals (table S2). Counts of live and dead individuals of each species are expressed as a proportion of all individuals in each habitat and time interval (table S1).

Spearman's rank order coefficient (r_s) and reduced major axis (RMA) regressions (SOM text S2.1) show highly significant correlations of species abundances in live populations and bone counts for each time interval separately, and for the time-averaged counts over the entire study (Table 1, Fig. 2, and fig. S1). These results show that the bone assemblage closely tracks population changes in the parent community and also gives an accurate averaged record of herbivore community structure over time. The match of live:dead abundances confirms that size-related death (turnover) rates among species in Amboseli herbivores are nearly balanced by size-related bone destruction rates (8, 12). The time-averaged live:dead RMA regression (Fig. 2), as well as each of the four time-interval samples, have slopes slightly (but insignificantly) below 1 (Table 1 and table S1). Body size frequency distribution of species in the living large herbivore community is therefore retained by the bone assemblage, although the cluster of large-bodied species to the left of the regression line in Fig. 2 suggests a slight bias in the survival of their larger, more durable bones (SOM text S2.3).
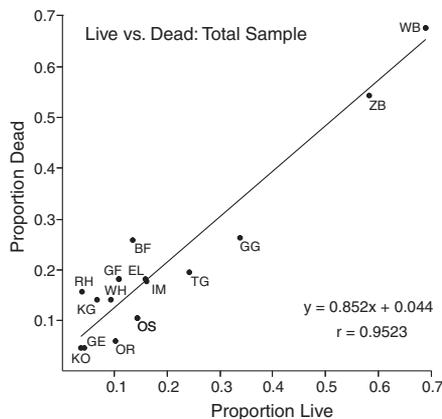

Fig. 2. RMA regression of total live (N = 169,235 counted individuals) against the total dead (N = 1502 individuals), using transformed {ASIN[SQRT(Proportion)]} relative abundances of 15 herbivore species between 20 and 4000 kg (14 mammal species and ostrich). Codes for species: BF, Cape buffalo; EL, elephant; GE, gerenuk; GF, giraffe; GG, Grant's gazelle; IM, impala; KG, kongoni; KO, waterbuck; OR, oryx; OS, ostrich; RH, black rhino; TG, Thomson's gazelle; WB, wildebeest; WH, warthog; ZB, Burchell's zebra. This relationship is significant at the P < 0.001 level (Table 1) (29). ArcSin transformation equalizes variances of proportional data and thus is appropriate for RMA analysis. See table S1 for numerical data and fig. S1.
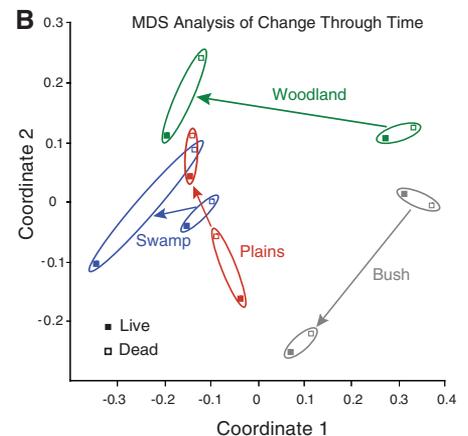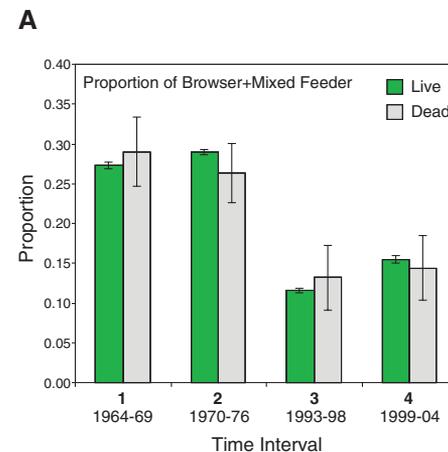

Fig. 3. (**A**) Change through time in Amboseli's browser+mixed feeder guild (N = 7 species) as shown by the live versus dead abundance data. Proportions are based on the total sample of 15 species; the relative abundance of grazers (N = 8 species) increased as the browsers declined, reflecting the loss of wooded habitats since the 1960s. See table S3 for numerical data. The 95% confidence limits are based on the normal approximation to a binomial distribution. (**B**) Results of a nonmetric MDS analysis of transformed relative abundance data for live and dead data sets, using the lower weathering stage subset (bone weathering stages 0 to 2), i.e., time intervals 1970 to 1976 and 1999 to 2004 (table S4). Live:dead pairs are connected by ovals; habitat samples are connected by arrows to show shifts through time. Calculated stress for this analysis using Euclidean distances = 0.1617.

Spearman *r* tests (Table 2) of living versus bone census data in four different habitats are significant for live:dead correlations in all but 3 of the 16 habitat cells and when time-averaged over four decades for each of these habitats. Nonmetric multidimensional scaling (MDS) analysis shows differing herbivore subcommunities in the four habitats, with similar shifts through time in both the live and dead samples (Fig. 3B and SOM text S2.1). These results show that Amboseli's bone assemblages distinguish habitat differences among living populations and tracked population changes during the transition from woodland to open grasslands.

Given the highly significant correlation between the relative species abundance in the live:dead censuses for the four discrete time periods and time-averaged over four decades, the bone assemblage also should accurately predict ecological properties of the Amboseli community. We tested this prediction using standard ecological measures of community structure (Table 3). Ecological indices are similar for live versus dead data sets through the four time

intervals (SOM text S2.2 and fig. S3) but show slightly higher diversity (greater evenness) for the bone survey data. The Shannon H and Simpson D indices are slightly higher for the bone samples but accurately track the living population through time despite 2 orders of magnitude smaller sample size for bone versus live survey data (SOM text S1 and S2.2, Table 3, table S1, and fig. S3). Bone data also closely track changes in guild composition (Fig. 3A) that resulted from woodland collapse (*18*).

Our results show that relative abundance and habitat distribution of species in a modern bone assemblage accurately represent the composition and changes in large herbivore community structure over intervals as short as 5 years and reflect aggregate structure over four decades of rapid ecological change (SOM text S2.3). A subsample of partially buried bones (SOM text S2.4) shows that the prefossil assemblage also records accurate information on species abundances.

Amboseli provides a reasonable facsimile for live:dead fidelity preserved in a fossil assemblage

time-averaged over decades to millennia through continual burial of surface bones in a land-surface soil (SOM text S2.3 and S2.4). The vertebrate record includes many fossil bone assemblages preserved in strata representing buried land surfaces or floodplain paleosols (*20*, *21*), and these assemblages could retain ecological information similar to that captured in the Amboseli live:dead study. Broad application of our results to the vertebrate fossil record depends on how initial high live:dead fidelity survives additional taphonomic processes such as fluvial reworking of surface-accumulated bone assemblages and long-term diagenesis.

The close tracking of community structure shown by the bone assemblages in this study enriches the range of ecological inferences that can be drawn from both ancient and modern vertebrate communities. Evidence of high fidelity in species relative abundance and habitat tracking in bone assemblages makes it possible to use a common framework for inferring the ecological properties of both contemporary and paleontological bone

Table 1. Sample sizes, Spearman's *r* and probability (*P*) values, and RMA results for comparisons of relative abundances of the living population and bone assemblage data for 15 ungulate species sampled in the Amboseli Basin. Proportional abundance data were transformed using ASIN[SQRT(Proportion)] for each species to equalize variance for residuals for the RMA (*29*). Slope 95% confidence interval (C.I.) estimated using the ±2* (least-squares) SE (*29*). See also table S1 and fig. S1.

Time interval	Years	N live	N dead	Spearman r_s	Spearman P	RMA r	RMA Slope	RMA 95% C.I.	RMA P (slope = 1)
1	1964–1969	36,326	417	**0.666**	**0.008**	0.8617	0.8682	0.624–1.113	**0.2674**
2	1970–1976	72,741	535	**0.682**	**0.006**	0.9420	0.9405	0.765–1.116	**0.4782**
3	1993–1998	35,597	265	**0.664**	**0.008**	0.9072	0.8950	0.686–1.104	**0.3000**
4	1999–2004	24,571	285	**0.880**	**<0.0001**	0.9513	0.9174	0.761–1.074	**0.2785**
1 + 2 + 3 + 4	1964–1976 + 1993–2004	169,235	1,502	**0.823**	**0.0002**	0.9523	0.8951	0.744–1.047	**0.1609**

Table 2. Probability (*P*) values from correlation tests using Spearman's *r* comparing live and dead survey data for the four major habitat types in Amboseli in the four different time intervals and the total sample, based on proportions of a maximum possible 15 species per habitat and time interval. Significant values (*P* ≤ 0.05) in bold. See table S3 for live and dead abundances by habitat.

Time Interval	Years	Spearman P values Swamp	Plains	Bush	Woodland	r_s Values Swamp	Plains	Bush	Woodland
1	1964–1969	0.529	**0.002**	**0.029**	0.093	−0.0253	**0.9669**	**0.8890**	0.6890
2	1970–1976	**0.012**	**<0.001**	**0.026**	**0.001**	**0.9720**	**0.9061**	**0.9618**	**0.9616**
3	1993–1998	**0.022**	**0.002**	0.110	**0.006**	**0.7472**	**0.8586**	0.4804	**0.9766**
4	1999–2004	**0.006**	**0.003**	**<0.001**	**<0.0001**	**0.8487**	**0.9892**	**0.9292**	**0.8950**
1 + 2 + 3 + 4	1964–1976 + 1993–2004	**<0.001**	**<0.001**	**0.011**	**<0.001**	**0.9683**	**0.9725**	**0.9675**	**0.9419**

Table 3. Comparison of diversity indices, evenness, and feeding guild structure (proportions of total *N*) based on live versus dead census data of the Amboseli large herbivore community between 1964 and 2004. See also table S1 and fig. S3.

Time interval	Years	Simpson live	Simpson dead	Shannon H live	Shannon H dead	Evenness _e^H/S live	Evenness _e^H/S dead	Browser+mixed Prop. live	Browser+mixed Prop. dead	Grazer Prop. live	Grazer Prop. dead
1	1964–1969	0.7577	0.7967	1.73	1.951	0.4029	0.4692	0.273	0.290	0.727	0.710
2	1970–1976	0.7441	0.7661	1.74	1.862	0.3798	0.4290	0.289	0.264	0.711	0.736
3	1993–1998	0.6372	0.6624	1.291	1.542	0.2597	0.3339	0.116	0.132	0.884	0.868
4	1999–2004	0.6869	0.7301	1.458	1.623	0.3071	0.4606	0.154	0.144	0.846	0.856
1 + 2 + 3 + 4	1964–1976 +1993–2004	0.7269	0.7627	1.657	1.862	0.3496	0.4290	0.230	0.225	0.770	0.775

assemblages. Given that body size is a unifying concept in macroecological theory (22), a preserved size-frequency distribution of species in a modern or fossil bone assemblage provides a quantitative basis for reconstructing population and community structure. Measures of ecological properties such as species richness, diversity, productivity, turnover, guild composition, resilience, and resistance can be deduced from allometrically scaled history traits (22, 23). Species size-frequency structure therefore offers a common metric for calculating the ecological and energetic properties of both fossil and contemporary communities (12, 22–25).

Amboseli and other similar taphonomic studies (10, 26–28) demonstrate that bone surveys can be used to monitor modern vertebrate populations and community structure, document unusual mortality levels, and correct bias in habitat use patterns resulting from diurnal live population counts. Bone assemblages also can give a baseline against which to measure disruptions to contemporary animal communities caused by human impact (4).

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Regulators of PP2C Phosphatase Activity Function as Abscisic Acid Sensors

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The plant hormone abscisic acid (ABA) acts as a developmental signal and as an integrator of environmental cues such as drought and cold. Key players in ABA signal transduction include the type 2C protein phosphatases (PP2Cs) ABI1 and ABI2, which act by negatively regulating ABA responses. In this study, we identify interactors of ABI1 and ABI2, which we have named regulatory components of ABA receptor (RCARs). In *Arabidopsis*, RCARs belong to a family with 14 members that share structural similarity with class 10 pathogen-related proteins. RCAR1 was shown to bind ABA, to mediate ABA-dependent inactivation of ABI1 or ABI2 in vitro, and to antagonize PP2C action in planta. Other RCARs also mediated ABA-dependent regulation of ABI1 and ABI2, consistent with a combinatorial assembly of receptor complexes.

The phytohormone abscisic acid (ABA) serves as an endogenous messenger in biotic and abiotic stress responses (1–4). ABA responses include a redirection of gene expression, reduced transpiration, protection of photosynthesis, and control of plant growth (2, 4–6). A variety of proteins has been reported to function as ABA receptors (7–9), but their ability to bind to ABA, to transduce the ABA signal, and thereby to regulate diverse ABA responses has not been unequivocally established (10–15).

Major players in ABA signaling are a subclass of Mg^{2+}- and Mn^{2+}-dependent serine-threonine phosphatases type 2C (PP2Cs) (16–21). Prototypes of these PP2Cs are ABI1 and its close structural homolog ABI2, which act in partially overlapping ways to repress ABA responses (22). ABI1 has emerged as a hub in the network of ABA signal transduction (23–25). The link between ABA perception and the regulation of ABI1 and ABI2 has not been elucidated.

As key regulators of ABA responses, the ABI1 and ABI2 protein phosphatases are of central importance for elucidating the integrative network of ABA signaling. We used the yeast two-hybrid system to screen for *Arabidopsis* proteins interacting with ABI2 (18). One of the interacting proteins (At1g01360.1) had no annotated function, and we named it regulatory component of ABA receptor 1 (RCAR1). The RCAR1 protein shares 75% and 74% amino acid identity to poplar and grape vine homologs, respectively, and its predicted structure is similar to the protein Bet v 1 of birch pollen (Fig. 1, A and B). RCAR1 belongs to a protein family with 14 members in *Arabidopsis* (Fig. 1C).

The interaction between RCAR1 and ABI2 (Fig. 2A) was almost completely abolished by the single–amino acid exchange present in abi2 (ABI2^{G168D}) (26). The mutations in abi2 and abi1 (ABI1^{G180D}) confer dominant ABA insensitivity. The single point mutation present in abi1 also impaired RCAR1 binding, and the interaction was abrogated with a carboxyl terminally truncated ABI1$^{1-180}$. There are more than 50 PP2Cs in *Arabidopsis*. Of these, HAB1, a PP2C involved in ABA signaling and structurally related to ABI1/2 (19), physically interacted with RCAR1 in the yeast assay. In contrast, two additional PP2Cs we

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