Abstract

The Kenya Long-term Exclosure Experiment (KLEE) was established in 1995 in a semi-arid savanna rangeland on the Laikipia Plateau to examine the separate and combined effects of livestock, wildlife, and megaherbivores (elephants and giraffes) on their shared environment and on each other. The long-term nature of this experiment also allowed us to measure these effects and related questions of stability and resilience in the context of multiple drought-rainy cycles. Here we outline some of the lessons learned over the last 29 years. In particular, we summarize three ways that KLEE exemplifies the value of long-term studies: 1) identifying experimental effects that take a many years to express themselves, 2) quantifying the effects of different years, especially multiple droughts, and 3) capturing time periods long enough to see the signature of systemic, anthropogenic change in the broader landscape. Across all aspects of a long-term study such as this one, there is a need to incorporate both consistency and flexibility to ensure deeper understanding.

Getting better with age: Lessons from the Kenya Long-term Exclosure Experiment (KLEE)

Truman P. Young\(^1,2\)*, Corinna RIGINOS\(^2\), Duncan M. Kimuyu\(^3\), Kari E. Veblen\(^4\), Lauren M. Porensky\(^5\), Wilfred O. Odadi\(^6\), and Ryan L. Sensenig\(^7\)

\(^1\)Department of Plant Sciences, University of California, Davis, CA, USA; and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA
\(^2\)Mpala Research Centre, Nanyuki, Kenya
\(^3\)The Nature Conservancy, Lander, WY, USA
\(^4\)Department of Natural Resources, Karatina University, Karatina, Kenya
\(^5\)Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT, USA
\(^6\)USDA-ARS Rangeland Resources and Systems Research Unit, Fort Collins, CO, USA
\(^7\)Department of Natural Resources, Egerton University, Egerton, Kenya
\(^8\)Department of Biology, University of Notre Dame, South Bend, IN, USA

*Corresponding author: Truman Young (tpyoung@ucdavis.edu)Author contributions: TPY and CR contributed equally the first draft of the manuscript, and all authors contributed substantially to revisions.Data accessibility statement: No new data are reported in this msNumber of words in the abstract: 150, and main text:
2000. Number of cited references: 54, number of tables: 0, number of figures: 2. Key words: year effects, environmental change, drought, mega-herbivores, livestock, herbivore exclosures, delayed responses

Abstract

The Kenya Long-term Exclosure Experiment (KLEE) was established in 1995 in a semi-arid savanna rangeland on the Laikipia Plateau to examine the separate and combined effects of livestock, wildlife, and mega-herbivores (elephants and giraffes) on their shared environment. The long-term nature of this experiment allowed us to measure these effects and related questions of stability and resilience in the context of multiple drought-rainy cycles. Here we outline some of the lessons learned over the last 29 years. In particular, we summarize three ways that KLEE exemplifies the value of long-term studies: 1) identifying experimental effects that take many years to manifest, 2) quantifying the effects of different years, especially multiple droughts, and 3) capturing time periods long enough to see the signature of systemic anthropogenic. Across all aspects of a long-term study such as this one, there is a need to incorporate both consistency and flexibility to ensure deeper understanding.

Long-term Origins

The Kenya Long-term Exclosure Experiment (KLEE) was established in 1995, but has its origins in the 1970s when one of TPY’s graduate mentors recommended to his students: start a long-term project. It did not need to be strongly conceptual or experimental, he said; just pick something, start monitoring it, and keep monitoring. The wisdom of this early advice is clear: the longest duration ecological projects have been some of the most fruitful, particularly in a world experiencing global change (e.g., Likens 1989, Risser 1991, Inouye and Barr 2000, Reinke et al. 2019, Campbell et al. 2022, Prather et al. 2023, Krebs et al. 2023).

KLEE experimentally examines the separate and combined effects of livestock (cattle) and wildlife on each other and their shared environment (Young et al. 1997). The experiment is composed of three blocks of six 4-ha plots assigned to different treatment combinations of large mammalian herbivores, using semi-permeable barriers (Figure 1).

Setting Up the Long-Term

Early decisions regarding site selection had long-lasting effects on KLEE. The project is located on relatively homogenous topography where the plant community of over 100 plant species is dominated by one tree species (Acacia drepanolobium) and a handful of grasses; this has helped us obtain powerful results from a low-replication experiment (n=3 for each treatment – trading off replication for relatively large 4 ha plot size) and has revealed unexpected complexity in this seemingly “simple” system. A further key decision was to designate the inner 1 ha of each plot for long-term monitoring, but no further manipulations. This left space in the outer 3 ha for short-term manipulations, the addition of embedded long-term rodent exclosures, and over time, prescribed fire, heavy grazing and rainfall manipulation experiments – which have resulted in more numerous and rewarding collaborations and findings than originally anticipated (Figure 2).

KLEE is predicated on the conceptual understanding that rainfall, wild herbivores, livestock and fire are the dominant forces in both short-term and long-term savanna dynamics. Time and layered additional manipulations have collectively contributed to our understanding of how herbivore guilds affect community ecology, trophic dynamics, species coexistence, disease ecology, tree-grass interactions, fire ecology, mutualisms, spatial heterogeneity, and other core topics in ecology (see Supplement 1, and https://tpyoung.ucdavis.edu/kleepubs).

Below, we summarize three ways that KLEE exemplifies the value of long-term studies:

1. Identifying experimental effects that take a long time to manifest, either because they are slow to accumulate, or because the response is delayed.
2. Recognizing and capturing “year effects”, especially through multiple rainy vs. drought periods.
3. Capturing the effects of systemic anthropogenic changes and shifting baselines.

Long-term and unexpected findings
Some treatment responses within KLEE were immediate and rapid. For example, within < 1 year, there were large increases in herbaceous biomass and a doubling of rodent numbers in plots from which large herbivores had been excluded (Keesing 1998, 2000) indicating indirect suppression of rodents by large herbivores. These rodent results formed the basis of a diverse set of studies examining disease vectors and pathogens (McCausley et al. 2008, Keesing et al. 2013, Young et al. 2016, Weinstein et al. 2017, Keesing et al. 2018, Tchouassi 2021) – an exemplar of how KLEE has contributed to emerging disciplines, such as disease ecology.

Within the first few years, there was clear evidence for the predicted competition between cattle and grazing wildlife (mostly zebras), but also a surprising finding that elephants mitigated this competition (Young et al. 2005). Later work, taking advantage of multiple droughts, provided stronger evidence for competition during dry seasons – but unexpected facilitative effects of wildlife on cattle during wet seasons (Odadi et al. 2011, Kimuyu et al. 2017). Long-term data also revealed, surprisingly, a high degree of functional similarity between wildlife and moderately- (but not heavily-) stocked cattle in their effects on plant community composition and primary productivity (Veblen et al. 2016, Charles et al. 2017, Wells et al. 2022). These results highlight conservation opportunities for lands shared by livestock and wildlife.

Other responses were delayed. Herbaceous community composition did not shift across treatments until 5 to 10 years into the experiment, whereupon it began to make more pronounced shifts (Figure 4 in Veblen et al. 2016; Figure 1 in Riginos et al. 2018). This delay is perhaps not surprising in a disturbance-adapted system dominated by (shorter-lived) perennials (Lv et al. 2023), but even a decade-long study would have ended before profound patterns attributable to herbivore community composition were revealed. Similarly, differences in soil chemistry across herbivore treatments only became apparent many years into the experiment (Sitters et al. 2020). Often, plant compositional shifts can take even longer (e.g., > 30 years in shortgrass prairie, Porensky et al. 2017), representing a challenge to even multi-decadal experiments (Cusser et al. 2012).

2) Long-term responses to interannual variation, including multiple drought-rainy periods

Many, if not most, ecological processes vary substantially among years (often called “year effects”), due to temporally variable environmental and anthropogenic influences as well as internal dynamics (Vaughn & Young 2010, Werner et al. 2020). Thus, data from any one or few years generally provide an incomplete picture of ecological and evolutionary processes or the effects of intensifying global change. Results from single droughts revealed in shorter-term studies run a greater risk of being idiosyncratic; if consistent across multiple droughts, true drought effects become more clear.

Long-term data through periods of below- and above-average rainfall (Figure 1) have helped us to illuminate and separate dynamics that are periodic but consistent, versus those that are accelerating. For example, the competition-facilitation balances between cattle and wildlife (Odadi et al. 2011, Kimuyu et al. 2017), between different grass species (Veblen 2008) and between grasses and trees (LaMalfa et al. 2021), are all contingent upon rainfall. Similarly, tick abundance varies with presence of cattle and amount of rainfall (Keesing et al. 2018). In contrast to these oscillating patterns, we have also found that drought-release years (the first rainy year after a drought) are important inflection points for directional – or accelerating – changes in plant community composition, contingent upon herbivore treatment (Porensky et al. 2013, Veblen et al. 2016, Riginos et al. 2018, LaMalfa et al. 2021, Wells et al. 2024). For example, in less-grazed treatments, successive post-drought periods widen the dissimilarity in community composition over time via rapid increases in certain grasses, at the expense of others (Riginos et al. 2018).

Long-term data have helped to verify oscillation versus inflection dynamics, as we have seen these two patterns play out repeatedly. As we move into a future with more extreme rainfall dynamics, long-term data may reveal where these patterns hold or break – for example, we may see that more prolonged droughts lead to more inflection patterns rather than oscillations or resilience. Particularly in arid and semi-arid ecosystems – and especially those in the tropics where seasons are less defined – long-term data are necessary to be able to tease out the signature of a changing climate from inherent interannual variability.

3) Long-term system change
KLEE was set up in part to improve our understanding of how to manage a complex system with multiple land-use objectives – most notably, livestock husbandry and wildlife conservation. Typical of many ecological communities in the Anthropocene, long-term studies like KLEE can capture shifting sociological and ecological baselines, which in this setting included (unexpected) increases in elephant numbers, changes in livestock composition, and the introduction of invasive species. These changes have spurred adjustments in experimental design and created space for new, unanticipated learning – highlighting the need for flexibility as well as consistency in such a long-term study.

For example, an initial motivation for KLEE was to study ecological dynamics outside of parks and protected areas that include rising livestock numbers, declining wildlife numbers, fire suppression, and woody encroachment (du Toit & Cumming 1999, Reid 2012). The origins of KLEE did not anticipate a later shift to sheep/goats over cattle and heavy wood harvesting for charcoal in many communally-managed lands – changes that have made KLEE less representative of many unprotected areas than we expected. Adding a heavily-grazed area within each plot in 2008 was an experimental adjustment that produced new insights about moderate versus heavy livestock grazing and its compatibility with wildlife (Wells et al. 2022a,b). A 2008 tree thinning and clearing experiment simulated woody losses to elephants and/or charcoal production (e.g., Riginos et al. 2009). The addition of fire treatments in 2014 assists in understanding the effects of fire exclusion on community dynamics (e.g., Werner et al. 2021, Masudi et al. 2024).

Additionally, while a major initial hypothesis was that excluding cattle grazing without browsing herbivores would result in rapid woody encroachment, this has not been the case (Young et al. 2021). Unexpectedly, elephants have increased throughout our 30-year study period as local land managers have become more tolerant of them and other areas have become less hospitable. As a result, the increased woody cover we have observed in some of the KLEE treatments has been driven by both experimental exclusion of elephants and a shifting baseline of increasing elephant numbers outside the plots. In this way, KLEE provides more insights on the dynamics of a wildlife safe-haven than originally expected.

As we move into the fourth decade of the study, KLEE is poised to capture the effects of additional shifting baselines, most notably, invasive species. Non-native Opuntia plant species have spread (Wells et al. 2023), and pantropical invasive big-headed ants (Pheidole megacephala) are projected to reach the KLEE plots soon, with potentially devastating effects on trees, as has been documented nearby (Riginos et al. 2015; Hays et al. 2020). These changes, past and future, underscore the value of long-term data; the rich and extensive baseline makes it possible to learn from and adapt to these changes as they occur.

Long-term funding and the pressure for expanding horizons

It takes a certain amount of faith and optimism to start a project with the knowledge (or at least suspicion) that the greatest values may be well into the future. Funding, even just to maintain infrastructure and core data collection, is a major challenge. Although the value of the dataset(s) increases with each year of a long-term project, there is also pressure from funders to come up with new questions and conceptual approaches to justify continued funding, not merely to continue to monitor in the context of the original questions (see also Alber et al. 2021). This results in a motivating – but at times challenging – need to continually produce compelling results and explore new horizons. Fortunately, long-term studies like KLEE often yield unexpected results that open new lines of inquiry and can host collaborations that expand the project’s scope as the field of ecology itself evolves (see Supplemental Materials). In our case, for example, it is only now, with multiple rainy/drought cycles, that we can carry out powerful analyses of ecosystem stability and resilience in the face of multiple interacting stressors (Ebel et al. 2022, Masudi et al. 2024, Wells et al. 202x) – a conceptual topic that has become integral to recent inquiry and funding cycles.

Conclusion: Long-term and intimate knowledge/deep understanding

Lastly, we note that perhaps the greatest value of long-term studies is the opportunity to get deeply immersed in a system, to learn it well enough to recognize even its more subtle patterns, and departures from them. One could call this a “feeling for the ecosystem.” The authors are indebted not only to the duration of the study but also to the long-term Kenyan field assistants in developing the “feeling for” – and deep knowledge
of – the ecosystem has so greatly enriched the project. As suggested by TPY’s mentor a half century ago, it is not merely spending time with a system, but also the act of consistently and systematically gathering information from it, that provides some of the most surprising insights. As KLEE enters its fourth decade, we continue to discover new layers of subtlety and complexity, new conceptual approaches, and new phenomena that elucidate the ecology of this savanna rangeland, and ecology in general. We encourage fellow researchers and funding sources to benign and to enable more long-term studies.

Acknowledgements

This research was carried out under Government of Kenya research clearance permit No. NCST/RCD/12B/012/42. We would like to thank Frederick Erii, John Lochikuya, Mathew Namoni, Jackson Ekadeli, Stephen Ekale, Julius Lengais and the fire crew teams for their invaluable assistance in the field. Essential logistical support was provided by Mpala Farm (David Hewett, Michael Littlewood, and David Hewitt) and Mpala Research Centre (in particular Nick Georgiadis, Margaret Kinnaird, Dino Martins, Winnie Kiiru, Alick Roberts, Antony Ngaina, and Julius Nakalonyo). The KLEE exclosure plots were built and maintained and the fire treatments funded by grants from the James Smithson Fund of the Smithsonian Institution (to A.P. Smith), The National Geographic Society (Grants 4691-91, 9106-12, and 9986-16), The National Science Foundation (LTREB DEB 97-07477, 03-16402, 08-16453, 12-56004, 12-56034 and 19-31224) and the African Elephant Program of the U.S. Fish and Wildlife Service (98210-0-G563), UC Davis, and Goshen College. The burns were designed and carried out by Duncan Kimuyu, Ryan Sensenig, and Eric LaMalfa.

References


Inouye, D. & B. Barr. 2006. Consequences of abrupt climate change for hibernating animals and perennial wildflowers at high altitude in the Colorado Rocky Mountains, USA. Pages 166-168 in: Global Change in Mountain Regions (M. F. Price, ed.). Sapiens Publishing, U.K.


illustrate A) cattle grazing in a O plot, with entry gate in lower right, B) cattle and plains zebras in a recently "Glades" are treeless anthropogenic patches arising from long-abandoned cattle enclosures ("bomas"). Photos letters inside each plot represent the (combinations of) large mammalian herbivores allowed access: C = showing the layout of the different herbivore treatment plots and the multiple embedded experiments. The 13: e3980. large mammalian herbivory, previous fire, and year of burn on fire behavior in an African savanna. Ecosphere Kimuyu, E. LaMalfa, C. Werner, C. Jones, P. Masudi, R. Ang’ila, and R.L. Sensenig. 2022. The effects of Management 71:281-291. Young, T.P., D.M. Kimuyu, W.O. Odadi, H.B.M. Wells & A.A. Wolf. 2021. Naive plant communities and individuals may initially suffer in the face of reintroduced megafauna: an experimental exploration of rewilding from an African savanna rangeland. PLOS One 16(4):e0248855. Young, T.P., D. Kimuyu, E. LaMalfa, C. Werner, C. Jones, P. Masudi, R. Ang’ila, and R.L. Sensenig. 2022. The effects of large mammalian herbivory, previous fire, and year of burn on fire behavior in an African savanna. Ecosphere 13: e3980. Figure captions: Figure 1: Schematic of the Kenya Long-term Exclosure Experiment (KLEE), showing the layout of the different herbivore treatment plots and the multiple embedded experiments. The letters inside each plot represent the (combinations of) large mammalian herbivores allowed access: C = cattle, W = meso-herbivores (25-500 kg), M = megaherbivores (>1000kg), O = no large herbivores allowed. "Glades" are treeless anthropogenic patches arising from long-abandoned cattle enclosures ("bomas"). Photos illustrate A) cattle grazing in a O plot, with entry gate in lower right, B) cattle and plains zebras in a recently
burned WC plot. C) KLEE crew conducting a controlled burn in one of the plots. Figure 2: Timeline of the Kenya Long-term Exclosure Experiment (KLEE), highlighting some key developments and funding (the latter does not include multiple NSF GRF, DDIG, REU and ROU grants). Herbivore treatments include separate and combined exclusions of meso-herbivores, mega-herbivores, cattle, and rodents. Dung counts are the mechanism to estimate species-specific plot use. Drought events are highlighted in orange. Brown dots are soil surveys. An adjacent rainfall manipulation experiment was initiated in 2017. The numbers in blue beneath each date are the cumulative numbers of peer-reviewed publications from the project. These totals do not include 33 outreach publications, or 30 American and Kenyan graduate dissertations.

In addition to the mega-authored papers from these collaborative databases, KLEE has hosted collaborators from the U.S., Kenya, South Africa, Canada, Netherlands, Belgium, Cameroon, Germany, Finland, Mexico, and Great Britain. These collaborations were fostered in no small part by the collegial climate provided by the shared infrastructure of the Mpala Research Centre. We note that although some of these collaborations could have been completed in a shorter-term KLEE experiment, they never would have happened if there had not been time for the experiment to become known and draw the attention of other ecologists who had new ideas of things to test within KLEE.

Even before the recent mandates of funding sources and journals, KLEE was making its datasets publicly available, as a way of encouraging and facilitating collaboration.


