

Scaling up from site-based research to a national research and monitoring network: lessons from Tierberg Karoo Research Centre and other design considerations

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South Africa is in the process of setting up a national environmental observatory system (SAEON) to monitor and gain a predictive understanding of the effects of climate change and land use on biodiversity, carbon and nutrient fluxes, soils and sediments, primary and secondary productivity, hydrology and disturbance regimes. It is intended that the data should be archived, analysed and translated into information accessible to decision-makers. We present a case that illustrates the infrastructural needs and challenges for long-term research and then discuss optimal designs and collaborations required to detect change in many variables, land-use types and geographical areas of South Africa.

Introduction

There is a global need for long-term environmental observation as well as research to detect, understand, and predict environmental change as a basis for decision making at local, national and global levels. The observatory approach is generally not primarily research orientated, but involves the monitoring of physical, biological and socio-economic variables to detect changes arising from natural or anthropogenic factors. In contrast, the research approach to understanding change is based on hypothesis testing. Recognition of the need for research to answer ecological questions that cannot be addressed within the timeframe of short-term funding cycles led to the establishment of Long-term Ecological Research (LTER) sites in the US¹ and South Africa² in the 1980s, and the German Biodiversity Monitoring Transect Analysis (BIOTA) programme in southern Africa³ in the year 2000. As these sites are expensive to establish and maintain, it was economically desirable to use them for many different types of research, such as pattern analysis and long-term manipulations to test hypotheses concerning drivers of ecosystem dynamics over decades. Much insight was gained from such studies, but extrapolation from one or a few possibly unique sites was of dubious reliability because of the confounding variables caused by pseudo-replication.

The US National Ecological Observatory Network (NEON) (see www.neoninc.org) and the new South African Environmental Observation Network (SAEON) (see www.saeon.ac.za) grew from the recognition that the value of LTERs was constrained by site-specificity and that drivers of change

occurred at scales beyond site boundaries.^{4,5} The objectives of NEON and SAEON are broader than those of LTERs. Their focus is on environmental change rather than ecology, and both explicitly aim to generate information required to alert decision-makers to widespread ecosystem change and its causes.⁶ It is intended that SAEON should achieve an understanding of change through investment in a sampling design that incorporates replication and land type representivity, and combines research and monitoring approaches to investigate key variables.

In this paper we distinguish between long-term ecological research and networks of environmental observatories and explain why elements of both are needed to inform South Africa's decision-makers about present and possible future effects of climate and land-use change. Long-term research requires an institutional framework, infrastructure and mechanisms for ensuring continuity, including the maintenance and accessibility of databases. We discuss these issues using the Tierberg Karoo Research Centre as a case study, and then consider the elements required for a national sampling system that will both detect and improve understanding of long-term change. The optimal design should achieve representative coverage of natural and anthropogenic ecosystems in South Africa and include experiments to explore mechanisms of change.

Long-term research lessons from Tierberg Karoo Research Centre

The challenges for all LTERs were clearly described by Strayer *et al.* in their report on long-term ecological research in the United States¹—the problem of funding facilities and personnel as governments and national priorities change, the brevity of careers, changing methods for field sampling, and data storage, dissemination and retrieval. Here we review the history, strengths and weaknesses of a single South African LTER (Tierberg Karoo Research Centre, TKRC), to identify the key requirements for LTER success, indicators of its performance, and limitations of site-based research that are relevant to the design of a network of LTER and observatory sites in South Africa.

Context of Tierberg Karoo Research Centre

The National Programme for Ecosystem Research (NPER), established by the Council for Scientific and Industrial Research in 1972, was modelled, in its interdisciplinary, collaborative and long-term scope, on the International Biological Programme initiated in the 1960s as a response to global awareness of environmental issues. The central goal of the National Programme for Ecosystem Research was to 'develop a predictive understanding of the structure, functioning and dynamics' of South African ecosystems. The programme was subdivided into well-funded Savanna, Fynbos, Grassland, Forest and Karoo

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long-term^{2,7} biome projects. Cooperative ecological research was fostered and interaction between researchers and managers promoted, to enable young scientists to compete for research funds and encourage international collaboration. LTER sites were established in savanna at Nylsvley Nature Reserve near Naboomspruit, in fynbos at Riverlands Nature Reserve near Cape Town, and in the karoo on Tierberg farm near Prince Albert. Although the programme was officially closed down in the early 1990s, some of these projects continue through interdisciplinary forums (Fynbos, Arid Zone), and further site-based research.

In a discussion document on science research policy, Ellis⁸ wrote of the Karoo Biome Project (KBP) as follows,

The project was initiated in 1987 and terminated in 1989. In developing this project an attempt was made to learn from the mistakes of other projects. A study site [TKRC] was identified in the southern Karoo [in 1987] for long-term research required to understand processes in arid lands. Despite truncation, the projects initiated under the KBP have made significant advances in our understanding of southern African arid lands. These have been translated into explicit guidelines for range management. The KBP had lively interaction between researchers, managers and farmers.

This paragraph succinctly contextualizes the reasons for the success of the Tierberg Karoo Research Centre, which was the central component of the KBP.

Karoo Biome Project planning, site selection and human resource management

The planning and implementation of the all biome projects followed a similar format. A committee was appointed to guide research, which then drew up criteria for a research site to be secured for at least 10 years. As most of the Karoo land surface is used as rangeland for domestic livestock, contrasts in land-use history, as well as site homogeneity to facilitate replication, representative vegetation, security, proximity to accommodation, supplies and transport, and aesthetics of the site were considered in the selection of the TKRC.

The centre lies inland of the Swartberg in the arid transition zone between summer rainfall Nama Karoo and winter rainfall Succulent Karoo. The site is part of the privately owned, 12 000 ha ranch 'Tierberg', which has been grazed by merino sheep since 1900, and shares one boundary with the historically overgrazed ranch 'Argentina'. The 100 ha TKRC enclosure was established in 1987 to exclude domestic livestock, and research has focused on comparison of processes and patterns within this enclosure and outside it on adjacent commercial ranches. Project coordinators, both of whom were doctoral candidates, managed the site facilities. Delegation of responsibilities ensured smooth running of the field site and avoided conflicts among researchers or with landowners.

New research was stimulated through carefully planned workshops, where practical and theoretical aspects of ecology could be freely debated by researchers and users.² Small group size, innovative thinkers from a variety of disciplines, and a published product, ensured that such workshops advanced understanding. Student researchers and supervisors were accommodated in a farmhouse close to the study sites. The interaction among groups of young researchers and their supervisors at the field site led to synergy and amicable competition which, doubtless, motivated innovation, dedication and publication. Being based on a working sheep ranch also gave the researchers opportunities to share ideas informally with land users as well as interacting with this group at the annual Karoo Biome Project Forum (later the Arid Zone Ecology Forum).

The Karoo Biome steering committee maintained quality and productivity of research at TKRC partly through mentorship and personal involvement by the site champions (particularly Roy Siegfried and Richard Cowling), partly through appointment of external reviewers with LTER experience, such as W.G. Whitford,⁸ and partly by facilitating frequent interaction of students and personnel with a stream of international visitors to the site.

Empirical foundation for asking appropriate questions

Before any research was started, existing literature on the biome was synthesized by established and new researchers, to identify research gaps and needs⁹⁻¹¹ and to provide the foundation for developing appropriate hypotheses and formal questions to guide new research. The vegetation maps and writings of John Acocks¹² were the paradigm for understanding the changes in Karoo vegetation in response to grazing by domestic livestock. The long-term experiments of Piet Roux and other researchers, at the Middelburg and Carnavon agricultural research stations,¹³⁻¹⁵ provided data and conceptual models of shorter-term responses of plant communities to grazing and to variation in rainfall. Enthusiastic young researchers, such as Timm Hoffman,¹⁶ stimulated Ph.D. studies on the processes underlying the observed dynamics and threshold behaviour, and the relevance of improved understanding to policy and management. As a result of initial close coordination through the NPER, all studies sought to contribute to a predictive understanding of the structure, functioning and dynamics of the Karoo ecosystem. Research was thus question based.

Hypothesis testing through observation, manipulation, serendipity and persistence

A single small study site clearly has both advantages and disadvantages for understanding land use and climate effects on plant and animal communities. Despite the fact that the site is in a rainfall seasonality transition zone, the narrow range of soil and vegetation variation made it unsuitable for monitoring differences in grass and community responses to changes in rainfall or grazing parameters. On the other hand, the relative homogeneity of the vegetation and the dominance of a single mammalian herbivore (sheep) at two levels of abundance on adjacent ranches, reduced the number of agents of change and the response variables to be measured, increasing confidence in experimental results.

The over-arching paradigm for research at TKRC was that selective grazing by sheep differentially affected the seed production, survival and recruitment of plant species, leading to changes in vegetation structure and animal communities. All studies were conducted within the same landscape and vegetation type and used the same set of fence-line contrasts for distinguishing the effects of grazing from those of weather on the response variables for soils, plants, invertebrates, and mammals. Researchers assisted one another with identification of plants and animals and shared data for weather, soils and vegetation cover. Studies of plant physiology,¹⁷ population dynamics¹⁸ and plant and animal community response to rainfall, grazing,^{19,20} and competition²¹ were comparable in terms of site and scale, and could later be combined to model community dynamics.

The leased status of TKRC made it possible to conduct manipulative studies such as vegetation clearing, wildlife enclosures, and food supplementation, and to erect infrastructural facilities such as buildings and a weather station. The presence of the research coordinator at the site, daily in the first two years and weekly over the next eight years, provided excellent opportunities for serendipity and detection of rare events such as insect

outbreaks, hail storms, flowering and seedling emergence.^{22,23} Long association with the sites led to a new and well-documented understanding of plant and animal community responses to weather. For example, regular counts made it possible to categorize TKRC bird species as resident, migratory or nomadic²⁴ (Fig. 1) and thus gain some understanding of bird community responses to land use.^{25,26} Collaboration of field ecologists with ecological modellers enabled empirical findings from research at TKRC to be extrapolated over longer time scales^{27,28} and stimulated new field research to test ideas generated by models.

Indicators of LTER performance

The strengths of an LTER facility can be measured in products including number, quality and relevance of the research outputs, academic and public use of the research products, and data quality, security and accessibility.

Types and numbers of publications can be expected to vary with the age and vitality of an LTER. As indicated in Fig. 2, theses and journal papers are relatively early products of research programmes, but show lags of 2–3 years. Journal paper production peaks as the project matures, and may then rise and fall with cycles of senescence and revitalization, which are closely linked to career paths and project leadership.¹ Books are the mature product of a successful project and few are likely to be produced within the first five years of an LTER study. In terms of publication indicators, TKRC has performed fairly well (4 books, 15 book chapters, 104 journal papers; see supplementary material online). This success can be attributed to planning and financial support, initially by the National Scientific Programmes, and later by the FitzPatrick Institute under the direction of Professor Roy Siegfried, which minimized the administrative load for local coordinators, and provided intellectual stimulation. Success of long-term research is typically linked to project coordinators, land tenure, financial support for research activities, infrastructure maintenance and management of data. The possible effects of such externalities as funding on the publication output from TKRC are indicated in Fig. 2. Other factors contributing to LTER success were enthusiastic local coordinators, sharing of information through research meetings (such as the Arid Zone Forum) and the energy, skill and commitment of local and foreign researchers.

Long-term observation of socio-ecological systems serves little purpose unless the results are communicated to researchers, managers and policy makers. Academic awareness of research at TKRC was achieved through peer-reviewed papers in high profile journals, and via the multi-authored book, *The Karoo – Ecological patterns and processes*,²⁹ edited by Dean and Milton in 1999. Building on the foundation of the 1986 National Scientific

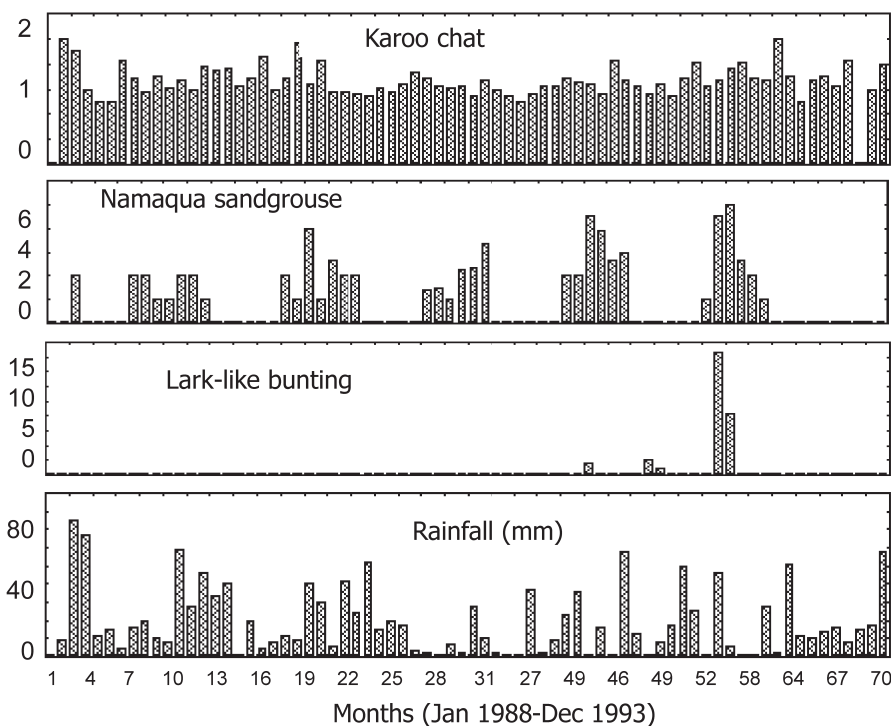


Fig. 1. Bird counts on 4 km × 1 km transects, once weekly over seven years (1023 transects), show temporal changes in abundance of selected bird species in relation to rainfall patterns. These data were used to categorize their status as resident, summer migrant or nomadic on TKRC.²⁴

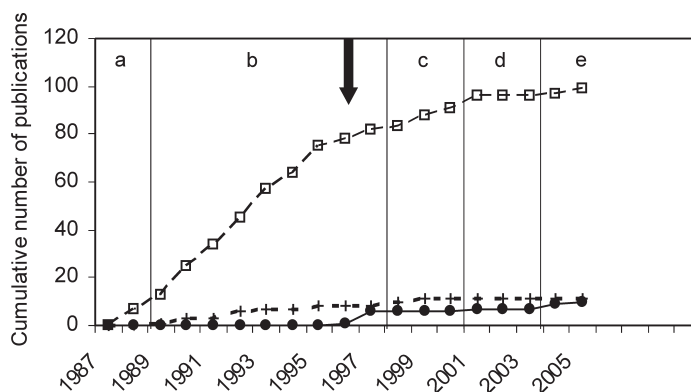


Fig. 2. TKRC project life-cycle showing the cumulative number of theses (dashed line), journal papers (open symbol) and books or book chapters (closed symbol) produced over 19 years. Phases a–e indicate differing external influences on the project: (a) 'long-term' funding via NSP; (b) research funding through Percy FitzPatrick, University of Cape Town; (c) *ad hoc* funding through the University of Stellenbosch; (d) no funding or personnel; (e) temporary funding via international science liaison between German BIOTA programme and South African Department of Science and Technology. The arrow indicates the end of the 10-year lease agreement and start of a rent-free agreement with the landowner.

Programmes reports,^{10–12} this synthesized research on all aspects of Karoo biome ecology and made it accessible to an international readership. General public awareness of the research issues addressed by TKRC was achieved mainly through *Karoo Veld Ecology and Management*,³⁰ a handbook written expressly for farmers. The revised and expanded version, published in 2006,³¹ generated considerable interest and debate on rangeland assessment, management and restoration among land management agencies, educators and land users. Public awareness of LTER research objectives was also achieved by the use of TKRC facilities for environmental education at school, on university field courses and as a showcase for visiting academics.

Arguably the most important products of long-term research are well-archived data with sufficient meta-data to be accessible and useful beyond the lifespan of the original researchers or the

Table 1. The most influential agents of change and response measures identified for SAEON (adapted from Van Jaarsveld and Biggs⁴). Every response variable can potentially be influenced by every agent of change.

Agents of change	Response variables						
	Biodiversity	Carbon fluxes	Nutrient fluxes	Soils and sediments	Primary and secondary productivity	Disturbance regime	Hydrology
Climate change	***(O)	***(O)	***(O)	***(O)	***(O)	** (O)	***(O)
Land transformation	***(O)	***(O)	***(O)	***(O)	***(O)	***(O)	***(o)
Land use (+ management)	** (O)	** (o)	** (o)	** (O)	** (O)	***(O)	** (O)
Nutrient loading	** (o)	** (o)	*** (o)	* (o)	*** (o)	* (o)	** (o)
Rare events	*** (o)	**/*** (.)	**/*** (.)	**/*** (.)	**/*** (.)	** (.)	*** (o)
Soil erosion	** (o)	*** (.)	*** (.)	*** (O)	*** (.)	*** (.)	**Scale?
Geomorphological change	*** (.)	*** (.)	*** (.)	*** (.)	*** (.)	*** (.)	** (.)
System configuration	* (o)	* (.)	* (.)	* (o)	* (.)	** (o)	* (.)
Alien plants and animals	** (o)	** (o)	** (o)	* (o)	*** (o)	*** (o)	** (o)
Pollution/poisons	** (o)	* (o)	** (o)	* (o)	** (o)	* (o)	* (o)

Table entries indicate whether an agent of change is expected to exert a main***, intermediate**, or minor* impact on the response variable, and the spatial scale at which this impact is most conspicuous: country (O), regional (o), or local (.)

projects. There are gaps in TKRC data sets and deficiencies in the ways in which the data are archived. Problems with the automatic weather station, and lack of funds or expertise to maintain it, resulted in incomplete weather data sets. Data collected by the coordinators were initially stored on 'stiffy' discs and have had to be transferred to new software as old programs became redundant. Data collected by other researchers are held by them or, in some cases, are lost. There was and is no facility for central archiving of the data so as to make it available beyond the lifespans of the researchers. Good data management will be central to success of an environmental observatory network in South Africa.

Weaknesses of TKRC and limitation of site-based research

Twenty years of research at TKRC have certainly generated new paradigms for Karoo ecology. Some of these are now being challenged because of gaps in research coverage and because of the research approaches taken. For example, although coverage of plant, animal and grazing ecology was fairly good (99 published papers), studies of physical processes, such as spatial aspects of infiltration, nutrient turnover, biomass production, and litter decay, was poor (5 papers). Soil microorganisms and their response to erosion, vegetation cover or composition were not investigated at TKRC. Comparisons between the single TKRC livestock enclosure and the surrounding grazing land are pseudo-replicated. A better design (although with its own problems) would be to have the LTER as part of the working ranch, and to embed replicated livestock enclosures within the matrix used. An additional weakness was the limited numbers of other land-use types available for comparison with the LTER, although this gap also simplified research. Social and economic factors were largely ignored.

The restricted scale and limited complexity (sheep grazing) of the system for which questions were posed and models developed was a key advantage for gaining insight, but obviously a major constraint in extrapolating to open-ended systems. Investigation of more complex Karoo systems would need to include multiple herbivore species, wide fluctuations in herbivore density, multiple land uses, land-use interactions including groundwater abstraction, nutrient addition and severed links among landscape units. This would include greater complexity relating to hierarchical questions concerning populations, communities, and ecosystem functioning at different spatial scales.

What facilities are needed for asking bigger questions?

From this analysis, focal LTER sites are seen to have the advantages of reducing funding and research complexity and encouraging collaboration, but do not provide the geographical coverage and replication needed to detect and understand change at national level. Nor do they necessarily capture changes occurring in the agricultural and urban landscapes covering 80% of the country. At a time of heightened global interest in monitoring the drivers of change and response variables, many nations are investing in networks of observation and research facilities. Here we consider the spatial scales at which agents of change or response variables operate and then discuss the importance of tracking change in landscapes used for agriculture and industry as well as in protected areas. We finally review existing network designs in relation to their cover, replication and representativeness.

Understanding and detecting and long-term change at multiple scales

Agents of change are all expected to show substantial spatial variation in their impact (Table 1). This means that an extensive observation network is required for reliable detection (Table 2). For example, detection of local impacts (rare events, soil erosion) requires a sampling design specific for each type of impact, and one that accommodates its pattern of spatial variability with a high sampling intensity. A similar conclusion emerges from considering observation of response variables. For example, carbon and nutrient fluxes, soil properties and processes, as well as productivity vary substantially over all spatial scales in relation to biophysical influences.³² Hydrological responses depend on the defined size of catchment, which can vary from countrywide to local landscape. Characteristically, many severe hydrological impacts are distant from the specific local catchment; for example, impairment of estuaries from altered flow and sedimentation.

All agents of change may potentially contribute towards a trend in a response variable but at different spatial scales (Table 1). Using biodiversity as an example, the impact of climate change will depend on whether geographic shifts in the range of a given species can match the rate of displacement, whether new areas of appropriate climatic regime offer suitable habitat,³³ and the extent of system disintegration resulting from cascading effects on interacting species.^{34,35} Changes in land use would

Table 2. Characteristics of the main agents of long-term ecological change and the corresponding monitoring requirements for effective assessment of their impact.

Agent of change	Characteristics and spatial scale of impact	Monitoring requirement
Climate change	Directional, spatially variable, strong interaction with other agents of change (e.g. land transformation, nutrient loading)	Countrywide—impact expected everywhere
Land transformation	Directional and spatially non-uniform; geoclimatic influence—concentrated in areas of high rainfall, gentle terrain, and deep soils	Countrywide, remote-sensing
Land use	Regional (climate constraint); spatially variable	Comparative approach within regions
Nutrient loading	Not only N and P, but these attract most attention; aerial (climate-influenced) and hydrological dynamics; point (cloud) sources (e.g. industrial, feedlot, dairies) with directional flow resulting in gradients	Gradient in relation to sources; geostatistical considerations
Rare events	Diverse in spatial scale, frequency of occurrence and degree of impact (cyclones, black frosts, floods, droughts, earthquakes, tsunamis, toxic spills, tanker wrecks, disease outbreak, pest outbreak)	Individual approach; time series; widespread recording increases probability of encountering event
Soil erosion	Variable across land uses, within land uses, and across environmental gradients. Strong biophysical constraints	Prediction using models
Geomorphological change	Localized, high energy fluvial or wind systems (coastal dunes, desert dunes, estuaries, rocky shores, (formerly) rocky rivers, wetlands, sodic soils, soil piping)	Fluvial–catchment scale; aeolian–local to regional; remote-sensing and site
System configuration	Reduced spatial scale; countrywide; repeated units across landscape; underpins degradation; management variation (grazing: system, animal type, fire regime; cropping: fertilization, irrigation, tillage)	Regional (consistency of land use) on a countrywide basis
Alien plants and animals	Widespread but with highly variable intensity. Predominates in wetter areas or moist habitats.	Geographic, habitat-specific
Pollution/poisons	Diverse with individual impacts; widespread with spatially variable intensity	Widespread; type-specific; gradient in relation to sources

affect availability of habitat and barriers to range adjustment.³⁶ Nutrient loading, rare events, system organization and alien plants and animals can impact at a regional or local level. Change in the abiotic template of a system or site will have a direct effect on supported diversity, and can arise from both geomorphological change and soil erosion.³⁷ Responses will be species-specific, depending on mobility and niche breadth. Biophysical influences and land use constitute critical barriers.³⁸ All these factors can compound, resulting in local extirpation becoming commonplace. Detection of species-level range changes therefore demands a geographic, spatially explicit, taxon-specific sampling approach conducted at the spatial scale relevant to the particular species.³⁹ The agricultural area of the country will be the key matrix over which most range expansion and contraction takes place. The grain of an observational approach should vary according to the attributes (mobility, habitat breadth, cryptic nature, ease of identification) of the species concerned and on the environmental gradients influencing distribution. Only an extensive observation network suffices to detect this.

Representative observation of change in used landscapes

Agricultural areas support much of South Africa's biodiversity and are the most important for carbon and nutrient fluxes, soils and sediments, and primary and secondary productivity simply on account of their size. These should, therefore, be the focus of any observation system. Crop production, on 14% of arable land, results in depletion of soil carbon and nitrogen stocks,⁴⁰ and loss of topsoil. Furthermore, disturbance regimes, especially fire and grazing, are components of management for all areas of natural assets under agriculture, such that agriculture defines the extant disturbance regime of what remains of most biomes.⁴¹ Patterns of fragmentation and the nature of land use are further indirect constraints on landscape-level behaviour of disturbance regimes.⁴²

Agricultural landscapes offer SAEON a potentially high sampling intensity that is well distributed in space and have relatively high temporal resolution (e.g. collected annually). For example, the strength of the answer to a simple question at the core of SAEON—how significant is the effect of global change on

primary productivity?—lies in its potential to extrapolate across the multitude of plant environments in South Africa. Records of crop or timber yield coupled to detailed study based on sophisticated growth models will yield more rapid insight than any amount of expense incurred in studying natural systems. Although existing agricultural data sets provide a foundation for future monitoring, they have some limitations such as absence of meta-databases and variation in analytical techniques, census methods and changes in the boundaries (provincial, regional and farm) defining their collection. In some cases confidentiality issues limit access to data held by forestry companies and research agencies.⁴³

Agricultural sectors, such as maize, wheat, beef, dairy and forestry, have accumulated databases on annual productivity and, frequently, other related variables collected from several hundred sites across large parts of South Africa.^{44,45} These data, which often span several decades or more, could conceivably be used to track past changes in ecosystem productivity and, importantly, could be used as a foundation for an observation database.

The forestry industry is illustrative of possibilities focusing on the effects of climate change, increases in atmospheric CO₂ and nutrient deposition on primary productivity—which are further influenced by site-specific environmental conditions. Tree growth, for instance, offers an integrated response to all these agents, the relative effect of which can only be disentangled empirically with analysis of a database covering variation in agents of change. The industry offers such a database. Its concern over sustainability has engendered a comprehensive proposal for monitoring⁴⁶ based mainly on permanent sample plots (PSPs), in which measurement of production from successive rotations is the key measure.⁴⁷ The forestry industry also has a network of research trials in which soil properties and foliar nutrient composition are measured on a regular basis. The density of PSPs (0.1–0.4 ha) is typically 1:500 ha and that of research trials is typically 1:5000 ha. A combined database of PSPs and research trial data could consequently be used to detect changes in soil chemistry properties, foliar nutrient uptake and produc-

tivity that have occurred in the high-rainfall regions of South Africa. The Modelling and Mensuration Research Consortium within the Institute for Commercial Forestry Research (ICFR) has already gone some way towards assembling such a database.^{46,47} Maplanka⁴⁸ has assessed some of its potential. For example, productivity has been measured over four rotations in the Usutu forests of Swaziland.⁴⁹

Additionally, there are sampling issues to consider, one of which is the effect of plantations on soil properties.⁴¹ Changes in soil properties due to other anthropogenic activities would also need to be separated from such background trends. The value of the soil data from utilized landscapes would thus be increased by including some control sites in protected areas, and analysis would have to accommodate the effect on productivity of new tree cultivars, and of changes in management. A general trend of increased productivity per unit area of plantation would consequently be expected. Given that soil properties are routinely analysed and changes in cultivar type are recorded, this challenge could be met. For the purposes of detecting effects of CO₂ changes on growth, each plantation compartment effectively represents a separate experiment. Even if only several hundred of the several thousand forestry compartments were included in a countrywide analysis of changes in growth rates through time, the statistical power of such an analysis would be immense, complemented by more-intensive study of selected long-term sites in which ecosystem processes and eco-physiological behaviour are investigated. An appropriate statistical approach for this type of analysis is quantile regression,⁵⁰ which demarcates boundary lines around clouds of data, thereby highlighting the range of a particular environmental factor over which the expression of a biotic variable may vary from minimal to maximal.

Replication and coverage in existing research and observation network designs

Attempts at comparing land-use effects in a replicated way across environmental gradients in long-term research and observation vary. However, both NEON and BIOTA have paired observations on control (protected) sites, with matched observations on adjacent areas selected for land-use contrasts. Replication and gradient effects have been captured by using multiple sets of control and use sites (or nested designs) distributed across environmental gradients.

The establishment of monitoring and research infrastructure is expensive and this poses a logistical constraint for replication, particularly in a developing country such as South Africa. SAEON could overcome this constraint by serving as a coordinator of long-term data collected by other state agencies (such as the departments of Agriculture, Transport, and Water Affairs), parastatals (for instance, the South African National Biodiversity Institute), or private enterprise. This role matches the stated objectives of SAEON, namely, to coordinate collection of long-term data on environmental variables of importance to the wellbeing of the nation, to archive and disseminate data and to build capacity.⁵ Collection, integration, interpretation of data, and delivery of information to decision makers, is generally poor in SADC countries.⁵¹ By serving this useful function, SAEON would achieve broad geographical coverage without greatly increasing expenditure on infrastructure or staff.

Conclusion

Long-term research and observation are complementary, but distinct, endeavours and need to be planned for as such. The TKRC experience highlights the problems of pseudo-replication,

need for funding security, investment in field infrastructure and in data management, committed staff, and capacity building for succession planning, as well as the value of collaborative research.

Observation of most of the identified agents of change requires a geographically extensive sampling design of high sampling intensity and sampling approaches designed specifically for each agent of change and response variable to optimize the detection and prediction of impacts. Agricultural areas should constitute the mainstay of the observation network because of the land-use pattern in South Africa. The simplified nature of agricultural and forestry systems enhances focus on the agents of change, and pre-existing knowledge and databases should be used for more rigorous examination of scientific output.

Observation and ecological research are synergistic. Empirical data sets are required for evaluation of predictions from research efforts and research can identify variables or agents of change for observation. Observation could also be used to track the effects of an intervention replicated across a wide range of sites. In practice, observation and research grade into one another and for this reason a forum or single institution needs to take responsibility for integration of data, interpretation of integrated data, and feedback among agencies as well as to decision makers and other users.

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1. Strayer D., Glitzenstein J.S., Jones C.G., Kolasa J., Likens G.E., McDonnell M.J., Parker G.G. and Pickett S.T.A. (1986). *Long-term Ecological Studies: An Illustrated Account of their Design, Operation, and Importance to Ecology*. Institute of Ecosystem Studies, The New York Botanical Garden, Occasional Publication 2, New York.
2. Huntley B.J. (1994). Ten years of cooperative ecological research in South Africa. *S. Afr. J. Sci.* **83**, 72–79.
3. Krug C.B., Esler K.J., Hoffman M.T., Henschel J., Schmiedel U. and Jürgens N. (2006). North–South cooperation through BIOTA: an interdisciplinary monitoring programme in arid and semi-arid southern Africa. *S. Afr. J. Sci.* **102**, 187–190.
4. Van Jaarsveld A.S. and Biggs H.C. (2000). Broad participation enhances initial steps towards a South African ecosystem observatory system (LTER). *S. Afr. J. Sci.* **96**, 63–66.
5. Schimel D. (2007). National Ecological Observatory Network, NEON. Research design basis for the NEON relocatable systems. Online: www.neoninc.org/documents/NEONDESIGN-001vA.
6. Scholes R.J. (in press). International earth observation programmes. *S. Afr. J. Sci.*
7. Ellis G.F.R. (ed.) (1994). *Science Research Policy in South Africa: A discussion document*. Royal Society of South Africa, University of Cape Town.
8. Whitford W. (2002). *Ecology of Desert Systems*. Academic Press, San Diego.
9. Cowling R.M. (1986). A description of the Karoo Biome Project. *S. Afr. Natl Sci. Progr. Rep.* **122**, 1–43.
10. Cowling R.M., Roux P.W. and Pieterse A.J.H. (eds) (1986). The Karoo biome: a preliminary synthesis. Part 1 – physical environment. *S. Afr. Natl Sci. Progr. Rep.* **124**.
11. Cowling R.M. and P.W. Roux (eds) (1987). *S. Afr. Natl Sci. Progr. Rep.* **142**, 50–69.
12. Acocks J.P.H. (1953). Veld types of South Africa. *Mem. Bot. Surv. S. Afr.* **28**, 1–192.
13. Tidmarsh C.E. (1951). Veld management studies 1934–1950. Pasture Research in South Africa, Unpublished Progress Report III. Department of Agriculture, Pretoria.
14. Roux P.W. (1966). Die uitwerking van seisoenreënval en beweiding op gemengde karooveld. *Proc. Grassl. Soc. Sth. Afr.* **1**, 103–110.
15. Roux P.W. and Vorster M. (1983). Development of veld management research in the Karoo Region. *Proc. Grassl. Soc. Sth. Afr.* **18**, 30–34.
16. Hoffman M.T. (1988). The rationale for Karoo grazing systems: criticisms and research implications. *S. Afr. J. Sci.* **84**, 556–559.
17. Van der Heyden F. and Stock W.D. (1995). Non-structural carbohydrate allocation following different frequencies of simulated browsing in three semi-arid shrubs. *Oecologia* **102**, 238–245.
18. Milton S.J. (1995). Spatial and temporal patterns in the emergence and survival

- of seedlings in arid Karoo shrubland. *J. Appl. Ecol.* **32**, 145–156.
19. Kerley G.I.H. (1991). Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. *J. Arid Environ.* **20**, 63–69.
 20. Dean W.R.J. and Yeaton R.I. (1993). The influence of harvester ant *Messor capensis* nest-mounds on the productivity and distribution of some plant species in the southern Karoo, South Africa. *Vegetatio* **106**, 21–35.
 21. Yeaton R.I. and Esler K.J. (1990). The dynamics of a succulent Karoo vegetation a study of species association and recruitment. *Vegetatio* **88**, 103–113.
 22. Milton S.J. and Dean W.R.J. (1992). An underground index of rangeland degradation: cicadas in arid Karoo shrublands, southern Africa. *Oecologia* **92**, 288–291.
 23. Milton S.J. and Wiegand T. (2001). How grazing turns rare seedling recruitment events to non-events in arid environments. In *Sustainable Land-Use in Deserts*, eds S-W. Breckle, M. Veste and W. Wucherer, pp. 197–207. Springer-Verlag, Heidelberg.
 24. Dean W.R.J. (2004). *Nomadic Desert Birds*. Adaptations of Desert Organisms series. Springer-Verlag, Berlin.
 25. Wiegand T., Milton S.J., Esler K.J. and Midgley G. (2000). Live fast, die young: estimating size-age relations and mortality pattern of shrub species in the semi-arid Karoo, South Africa. *Plant Ecol.* **150**, 115–131.
 26. Dean W.R.J. and Milton S.J. (2001). The density and stability of birds in shrubland and drainage line woodland in the southern Karoo, South Africa. *Ostrich* **72**, 185–192.
 27. Wiegand T., Milton S.J. and Wissel C. (1995). A simulation model for a shrub-ecosystem in the semi-arid Karoo, South Africa. *Ecology* **76**, 2205–2221.
 28. Wiegand T. and Milton S.J. (1996). Vegetation change in semiarid Karoo rangelands: simulating probabilities and time scales. *Vegetatio* **125**, 169–183.
 29. Dean W.R.J. and Milton S.J. (eds) (1999). *The Karoo, Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
 30. Milton, S.J. and Dean W.R.J. (1996). *Karoo Veld: Ecology and Management*. Range and Forage Institute, Agricultural Research Council, Pretoria.
 31. Esler K.J.E., Milton S.J. and Dean W.R.J. (2006). *Karoo Veld: Ecology and Management*. Briza Press, Pretoria.
 32. Seastedt T.R., Hayden B.P., Owensby C.E. and Knapp A.K. (1998). Climate change, elevated CO₂, and predictive modeling: past and future climate change scenarios for the tallgrass prairie. In *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*, eds A.K. Knapp, J.M. Briggs, D.C. Hartnett and S.C. Collins, pp. 283–300. Oxford University Press, New York.
 33. Rutherford M.C., Powrie L.W. and Schulze R.E. (1999). Climate change in conservation areas in South Africa and its potential impact on floristic composition: a first assessment. *Divers. Distrib.* **5**, 253–262.
 34. Carpenter S.R. and Kitchell J.F. (1988). Consumer control of lake productivity. *BioScience* **38**, 764–769.
 35. Brown J.H., Whitham T.G., Ernest S.K.M. and Gehring C.A. (2001). Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science* **293**, 643–650.
 36. O'Connor T.G. (2005). Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the southern Drakensberg, South Africa. *J. Appl. Ecol.* **42**, 975–988.
 37. Pickup G. (1985). The erosion cell – a geomorphic approach to landscape classification in range assessment. *Austr. Range J.* **7**, 114–121.
 38. McIntyre S. and Martin T.G. (2001). Biophysical and human influences on plant species richness in grasslands: comparing variegated landscapes in subtropical and temperate regions. *Austral Ecol.* **26**, 233–245.
 39. Penry H. (1994). *Bird Atlas of Botswana*. University of Natal Press, Pietermaritzburg.
 40. Mills A.J. and Fey M.V. (2003). Declining soil quality in South Africa: effects of land use on soil organic matter and surface crusting. *S. Afr. J. Sci.* **99**, 429–436.
 41. Tainton N.M. (ed.) (1999). *Veld Management in South Africa*. University of Natal Press, Pietermaritzburg.
 42. Forman R.T.T. and Godron M. (1986). *Landscape Ecology*. John Wiley, New York.
 43. Scotney D.M. (1988). The agricultural area of South Africa. In *Long-term data series relating to southern Africa's renewable natural resources*. *S. Afr. Natl Sci. Progr. Rep.* **157**, eds I.A.W. Macdonald and R.J.M. Crawford, pp. 316–336.
 44. Institute for Commercial Forestry Research (1996). *Annual Report*. Pietermaritzburg.
 45. Louw W.J.A. (2004). General history of the South African forest industry: 1991 to 2002. *Sthn Afr. For. J.* **201**, 65–76.
 46. Smith C., Littler K., Rolanda C. and du Toit B. (2005). A framework for monitoring and measuring the sustainability of intensively managed southern African forest plantations. *ICFR Bulletin* 8/2005, Pietermaritzburg.
 47. Morris A.R. and Smith C.W. (2002). Growth and yield as an indication of sustainable forest management in industrial plantations. *Sthn Afr. For. J.* **195**, 47–56.
 48. Maplanka N. (2005). *Investigating the soil and foliar analysis as indicators of productivity in short rotation plantations in South Africa*. M.Sc. thesis, University of the Witwatersrand, Johannesburg.
 49. Evans J. (2006). Growth rates over four rotations of pine in Swaziland. *Int. For. Rev.* **7**, 305–310.
 50. Cade B.S. and Noon B.R. (2003). A gentle introduction to quantile regression for ecologists. *Front. Ecol. Environ.* **1**, 412–420.
 51. Scholes R.J., van der Merwe M.R. and van Tienhoven A.M. (2001). A survey of environmental information systems in southern Africa. In *Global Terrestrial Observing System (GTOS). Regional implementation plan for southern Africa*, ed. R.J. Scholes, pp. 20–96. GTOS 21.

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Milton S.J., Dean W.R.J., O'Connor T.G. and Mills A.J. (2007). Scaling up from site-based research to a national research and monitoring network: lessons from Tierberg Karoo Research Centre and other design considerations. *S. Afr. J. Sci.* **103**, 311–317.

Publications of the Tierberg Karoo Research Centre

- Armstrong A.J. and Siegfried W.R. (1990). Selective use of *heuweltjie* earth mounds by sheep in the Karoo. *S. Afr. J. Ecol.* **1**(2), 77–80.
- Bond W.J., Stock W.D. and Hoffman M.T. (1994). Has the Karoo spread? A test for desertification using carbon isotopes from soils. *S. Afr. J. Sci.* **90**, 391–397.
- Brain P. (1989). Genetic races in a ring species, *Acacia karroo*. *S. Afr. J. Sci.* **85**, 181–185.
- Brooke R.K. and Dean W.R.J. (1990). On the biology and taxonomic position of *Drymoica substriata* Smith, the so-called Namaqua prinia. *Ostrich* **61**, 50–55.
- Bruyns P. (1990). New taxa from the arid regions of southern Africa. *S. Afr. J. Bot.* **56**, 125–132.
- Dean W.R.J. and Milton S.J. (eds) (1999). *The Karoo, Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
- Dean W.R. and Milton S.J. (1993). The use of *Galium tomentosum* (Rubiaceae) as nest material by birds in the southern Karoo. *Ostrich* **64**(4), 187–189.
- Dean W.R.J. and Griffin E. (1993). Seasonal activity patterns and habitats in Solifugae (Arachnida) in the southern Karoo, South Africa. *S. Afr. J. Zool.* **28**, 91–94.
- Dean W.R.J. and Milton S.J. (1991). Emergence and oviposition of *Quintillia cf. conspersa* Karsch (Homoptera, Cicadidae) in the southern Karoo, South Africa. *J. Ent. Soc. Sthn Afr.* **54**(2), 111–119.
- Dean W.R.J. and Milton S.J. (1991). Disturbances in semi-arid shrubland and arid grasslands in the Karoo, South Africa mammal diggings as germination sites. *Afr. J. Ecol.* **29**, 11–16.
- Dean W.R.J. and Milton S.J. (1991). *Galium tomentosum* – a yarn for the birds. *Veld & Flora* **77**, 82–83.
- Dean W.R.J. and Milton S.J. (1991). Prey capture by *Solpuga chelicornis* (Solifugae, Solpugidae). *J. Ent. Soc. Sthn Afr.* **54**, 266–267.
- Dean W.R.J. and Milton S.J. (1992). Emergence and density of *Quintillia cf. vitripennis* Karsch (Homoptera, Cicadidae) in the southern Karoo, South Africa. *J. Ent. Soc. Sthn Afr.* **55**, 71–75.
- Dean W.R.J. and Milton S.J. (1993). Soils and seed harvesting ants in the Karoo. *Veld & Flora* **79**(1), 22–23.
- Dean W.R.J. and Milton S.J. (1994). The use of *Galium tomentosum* (Rubiaceae) as nest material by birds in the southern Karoo. *Ostrich* **64**, 187–189.
- Dean W.R.J. and Milton S.J. (1995). Plant and invertebrate assemblages on old fields in the arid southern Karoo, South Africa. *Afr. J. Ecol.* **33**(1), 1–13.
- Dean W.R.J. and Milton S.J. (1999). Animal foraging and food. In *The Karoo, Ecological Patterns and Processes*, eds W.R.J. Dean and S.J. Milton, pp. 164–177. Cambridge University Press, Cambridge.
- Dean W.R.J. and Milton S.J. (2001). Responses of granivorous birds to rainfall and seed abundance in the southern Karoo, South Africa. *J. Arid Environ.* **47**, 101–121.
- Dean W.R.J. and Milton S.J. (2001). Responses of granivorous birds to rainfall and seed abundance in the southern Karoo, South Africa. *J. Arid Environ.* **47**, 101–121.
- Dean W.R.J. and Milton S.J. (2001). The density and stability of birds in shrubland and drainage line woodland in the southern Karoo, South Africa. *Ostrich* **72**, 185–192.
- Dean W.R.J. and Siegfried W.R. (1990). The use of wool as nest material by birds in the Karoo, South Africa, bane or bonus? *S. Afr. J. Ecol.* **1**(1), 31–32.
- Dean W.R.J. and Siegfried W.R. (1997). The protection of endemic and nomadic avian diversity in the Karoo, South Africa. *S. Afr. J. Wildl. Res.* **27**, 11–21.
- Dean W.R.J. and Turner J.S. (1991). Ants nesting under stones in the semi-arid Karoo, predator avoidance or temperature benefits? *J. Arid Environ.* **21**, 59–69.
- Dean W.R.J. and Williams J.B. (1999). Sunning behaviour and its possible influence on digestion in the Whitebacked Mousebird *Colius colius*. *Ostrich* **70**(3&4), 239–241 (R.K. Brooke memorial issue).
- Dean W.R.J. and Yeaton R.I. (1992). The importance of harvester ant *Messor capensis* nest-mounds as germination sites in the southern Karoo, South Africa. *Afr. J. Ecol.* **30**, 335–345.
- Dean W.R.J. and Yeaton R.I. (1993). The effects of harvester ant *Messor capensis* nest-mounds on the physical and chemical properties of soils in the southern Karoo, South Africa. *J. Arid Environ.* **25**, 249–260.
- Dean W.R.J. and Yeaton R.I. (1993). The influence of harvester ant *Messor capensis* nest-mounds on the productivity and distribution of some plant species in the southern Karoo, South Africa. *Vegetatio* **106**, 21–35.
- Dean W.R.J. (1988). Seeds, ants and students, the FitzPatrick Institute's research in the Karoo. *UCT News Mag.* **15**, 9–11.
- Dean W.R.J. (1988). Spider predation on termites. *J. Ent. Soc. Sthn Afr.* **51**, 147–148.
- Dean W.R.J. (1989). Foraging and forager-recruitment in *Ophthalmopone hottentota* Emery (Hymenoptera Formicidae). *Psyche* **96**, 123–130.
- Dean W.R.J. (1992). Effects of animal activity on the absorption rate of soils in the southern Karoo, South Africa. *J. Grassl. Soc. Sthn Afr.* **9**, 178–180.
- Dean W.R.J. (1992). Temperatures determining activity patterns of some ant species in the southern Karoo, South Africa. *J. Ent. Soc. Sthn Afr.* **55**, 149–156.
- Dean W.R.J. (1993). Alpine swifts opportunistically feeding on cicadas. *Ostrich* **64**, 42–43.
- Dean W.R.J. (1993). Unpredictable foraging behaviour in *Microhodotermes viator*, an antipredator tactic? *J. Afr. Zool.* **107**, 281–285.
- Dean W.R.J. (1995). Die invloed van die neshope van die graanvretende mier *Messor capensis* op Karoo-plantegroei. *Suid-Afrikaanse Tydskrif vir Natuurwetenskap en Tegnologie* **14**(1), 17–23.
- Dean W.R.J. (1997). The distribution and biology of nomadic birds in the Karoo, South Africa. *J. Biogeog.* **24**, 769–779.
- Dean W.R.J. (2004). *Nomadic Desert Birds*. Adaptations of Desert Organisms series. Springer-Verlag, Berlin.
- Dean W.R.J., Hoffman M.T., Meadows M.E. and Milton S.J. (1995). Desertification in the semi-arid Karoo, South Africa, review and reassessment. *J. Arid Environ.* **30**, 247–264.
- Dean W.R.J., Midgley J.J. and Stock W.D. (1995). The distribution of mistletoes in South Africa, patterns of species richness and host choice. *J. Biogeog.* **21**, 503–510.
- Dean W.R.J., Milton S.J. and Du Plessis M.A. (1995). Where, why and to what extent have rangelands in the Karoo, South Africa, desertified? *Environ. Monitor. Assess.* **37**, 103–110.
- Dean W.R.J., Milton S.J. and Siegfried W.R. (1990). Dispersal of seeds as nest material by birds in semi-arid Karoo shrubland. *Ecology* **71**, 1299–1306.
- Dean W.R.J., Williams J.B. and Milton S.J. (1993). Breeding of the whitebacked mousebird *Colius colius* in relation to rainfall and the phenology of fruiting plants in the southern Karoo, South Africa. *J. Afr. Zool.* **107**, 105–111.
- Du Plessis A. and Kerley G.I.H. (1991). Refuge strategies and habitat segregation in two sympatric rodents, *Otomys unisulcatus* and *Parotomys brantsii*. *J. Zool. (Lond.)* **224**, 1–10.
- Du Plessis A., Kerley G.I.H. and Winter P.E.D. (1992). Refuge microclimates of rodents, a surface nesting *Otomys unisulcatus* and a burrowing *Parotomys brantsii*. *Acta Theriologica* **37**(4), 351–358.
- Eccard J.A., Walther R.B. and Milton S.J. (2000). How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. *J. Arid Environ.* **46**(2), 103–106.
- Esler K.J. and Cowling R.M. (1993). Edaphic factors and competition as determinants of pattern in South African Karoo vegetation. *S. Afr. J. Bot.* **59**(3), 287–295.

- Esler K.J. and Cowling R.M. (1995). The comparison of selected life-history characteristics of Mesembryanthema species occurring on and off Mima-like mounds (heuweltjies) in semi-arid southern Africa. *Vegetatio* **116**, 41–50.
- Esler K.J. and Phillips N. (1994). Experimental effects of water stress on semi-arid Karoo seedlings, implications for field seedling survivorship. *J. Arid Environ.* **26**, 325–337.
- Esler K.J. (1999). Plant reproductive ecology. In *The Karoo, Ecological Patterns and Processes*, eds W.R.J. Dean and S.J. Milton, pp. 123–144. Cambridge University Press, Cambridge.
- Esler K.J., Cowling R.M. and Ivey P. (1992). Seed biology of three species of *Mesembryanthema* in the southern Succulent Karoo. *S. Afr. J. Bot.* **58**, 343–348.
- Esler K.J.E., Milton S.J. and Dean W.R.J. (2006). *Karoo Veld, Ecology and Management*. Briza Press, Pretoria. ISBN 1 875093 52 4 (English).
- Esler K.J., Milton S.J. and Dean W.R.J. (2006). *Karoo Veld – Ekologie en Bestuur*. Briza Press, Pretoria. ISBN 1 875093 55 9 (Afrikaans).
- Gess F.W. and Gess S.K. (1988). A contribution to the knowledge of the ethology of the genera *Parachilus* Giordani Soika and *Paravespa* Radoszkowski (Hymenoptera: Eumenidae) in southern Africa. *Annal. Cape Prov. Mus. (Nat. Hist.)* **18**, 57–81.
- Gess F.W. and Gess S.K. (1988). A further contribution to the knowledge of the ethology of the genus *Ceramius* Latreille (Hymenoptera Masaridae) in the southern and western Cape Province of South Africa. *Annal. Cape Prov. Mus. (Nat. Hist.)* **18**, 1–30.
- Gess F.W. and Gess S.K. (1989). Solitary wasps. *Afr. Wildl.* **43**, 24–29.
- Gess S.K. and Gess F.W. (1989). Flower visiting by masarid wasps in southern Africa. *Annal. Cape Prov. Mus. (Nat. Hist.)* **18**, 95–134.
- Hoffman M.T., Bond W.J. and Stock W.D. (1995). Desertification of the eastern Karoo, South Africa. Conflicting paleoecological, historical, and soil isotopic evidence. *Environ. Monitor. Assess.* **37**, 159–177.
- Kerley G.I.H. and Erasmus T. (1992). Small mammals in the semi-arid Karoo, South Africa, biomass and energy requirements. *J. Arid Environ.* **22**, 251–260.
- Kerley G.I.H. (1988). On bossies, boere and mice. *Karoo Region Newsl.* **2**, 7–8.
- Kerley G.I.H. (1989). Diet of small mammals from the Karoo, South Africa. *S. Afr. J. Wildl. Res.* **19**, 67–72.
- Kerley G.I.H. (1990). Browsing by *Lepus capensis* in the Karoo. *S. Afr. J. Zool.* **25**(3), 199–200.
- Kerley G.I.H. (1991). Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. *J. Arid Environ.* **20**, 63–69.
- Khöhler G., Samietz J. and Wagner G. (2001). Field observations on the bush locust *Phymateus leprosus* (Fabricius, 1993) in the Great Karoo, South Africa. *Opuscula Zoologica Fluminensia* **191**, 1–15.
- Köhler G., Wagner G., Roth S., Samietz J., Opitz S. and Green S.U. (2001). Auf Excursion im südlichen Afrika, 1. Kurzfühlerschrecken (Caelifera) in der sud Afrikanischen Kapregion. *Veröffentlichungen Naturkunde Museum Erfurt* **20**, 129–150.
- McKechnie A.E. and Lovegrove B.G. (2001). Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* **74**, 238–249.
- McKechnie A.E., Körtner G. and Lovegrove B.G. (2004). Rest-phase thermoregulation in free-ranging white-backed mousebirds. *Condor* **106**, 144–150.
- Milton S.J. and Dean W.R.J. (1993). The leopard tortoise in the Karoo. *Afr. Wildl.* **47**(1), 212–213.
- Milton S.J. and Collins H. (1989). Hail in the southern Karoo. *Veld & Flora* **75**(3), 69–73.
- Milton S.J. and Dean W.R.J. (1988). Flower and fruit production of *Rhigozum obovatum* (Bignoniaceae) in road reserves and grazing land. *S. Afr. J. Sci.* **84**, 798–799.
- Milton S.J. and Dean W.R.J. (1990). Mima-like mounds in the south-western Cape are the origins so mysterious? *S. Afr. J. Sci.* **86**, 207–208.
- Milton S.J. and Dean W.R.J. (1990). Seed production in rangelands of the southern Karoo. *S. Afr. J. Sci.* **86**, 231–233.
- Milton S.J. and Dean W.R.J. (1992). An underground index of rangeland degradation, cicadas in arid Karoo shrublands, southern Africa. *Oecologia* **92**(2), 288–291.
- Milton S.J. and Dean W.R.J. (1993). Selection of seeds by harvester ants (*Messor capensis*), in relation to condition of arid rangeland. *J. Arid Environ.* **24**, 63–74.
- Milton S.J. and Dean W.R.J. (1995). Factors influencing the recruitment of forage plants in arid Karoo shrublands, South Africa. In *Proc. Wildland Shrub and Arid Land Restoration Symposium*. October 19–21, Las Vegas, compilers B.A. Roundy, E. McArthur, J.S. Haley and D.K. Mann, pp. 216–222. *General Technical Report INT-GTR-315*. Forest Service, Intermountain Research Station, U.S. Dept of Agriculture.
- Milton S.J. and Dean W.R.J. (1996). *Karoo Veld, Ecology and Management*. Range and Forage Institute, Agricultural Research Council, Pretoria.
- Milton S.J. and Dean W.R.J. (1996). Rates of wood and dung disintegration in arid South African rangelands. *Afr. J. Range Forage Sci.* **13**(3), 89–93.
- Milton S.J. and Dean W.R.J. (1999). Nesting thyme – the use of aromatic plants in Cape Sparrow nests. *Africa, Birds & Birding* (Feb/Mar 1999) **4**(1), 37–39.
- Milton S.J. and Dean W.R.J. (1999). The selective use of green aromatic plants in Karoo bird nests. *Ostrich* **70**(3&4), 243–245. (R.K. Brooke memorial issue).
- Milton S.J. and Dean W.R.J. (2001). Seeds dispersed in dung of insectivores and herbivores in arid southern Africa. *J. Arid Environ.* **47**, 465–483.
- Milton S.J. and Hoffman M.T. (1994). The application of state-and-transition models to rangeland research in arid succulent and semi-arid grassy Karoo, South Africa. *Afr. J. Range Forage Sci.* **11**(1), 18–26.
- Milton S.J. and Wiegand T. (2001). How grazing turns rare seedling recruitment events to non-events in arid environments. In *Sustainable Land-Use in Deserts*, eds S-W Breckle, M. Veste and W. Wucherer, pp. 197–207. Springer, Heidelberg.
- Milton S.J. (1988). Back to basics veld management research in the Karoo. *S. Afr. Inst. Ecol. Bull.* **7**(1), 22–28.
- Milton S.J. (1990). Above-ground biomass and plant cover in a succulent shrubland in the southern Karoo, South Africa. *S. Afr. J. Bot.* **56**, 587–589.
- Milton S.J. (1990). Life-styles of plants in four habitats in an arid Karoo shrubland. *S. Afr. J. Ecol.* **1**(2), 63–72.
- Milton S.J. (1991). Plant spinescence in arid southern Africa, does moisture mediate selection by mammals? *Oecologia* **87**, 279–287.
- Milton S.J. (1992). Effects of rainfall, competition and grazing on flowering of *Osteospermum sinuatum* in arid Karoo rangeland. *J. Grassl. Soc. Sthn Afr.* **9**(4), 158–164.
- Milton S.J. (1992). Plants eaten and dispersed by *Geochelone pardalis* (Reptilia, Chelonii) in the southern Karoo. *S. Afr. J. Zool.* **27**(2), 45–49.
- Milton S.J. (1993). Insects from the shrubs *Osteospermum sinuatum* and *Pteronia pallens* (Asteraceae) in the southern Karoo. *Afr. Entomol.* **1**(2), 257–261.
- Milton S.J. (1994). Growth, flowering and recruitment shrubs in grazed and in protected rangeland in the arid Karoo. *Vegetatio* **111**, 17–27.
- Milton S.J. (1994). Small scale re-seeding trials in Karoo rangeland, effects of rainfall, clearing and grazing on seedling survival. *Afr. J. Range Forage Sci.* **11**(2), 54–58.
- Milton S.J. (1995). Effects of rain, sheep and tephritid flies on seed production of two arid Karoo shrubs in South Africa. *J. Appl. Ecol.* **32**, 137–144.
- Milton S.J. (1995). Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *J. Appl. Ecol.* **32**, 145–156.
- Milton S.J., Davies R.A.G. and Kerley G.I.H. (1999). Population level dynamics. In *The Karoo, Ecological Patterns and Processes*, eds W.R.J. Dean and S.J. Milton, pp. 183–207. Cambridge University Press, Cambridge.
- Milton S.J., Dean W.R.J. and Kerley G.I.H. (1992). Tierberg Karoo Research Centre, history, physical environment, flora and fauna. *Trans. R. Soc. S. Afr.* **48**(1), 15–46.
- Milton S.J., Dean W.R.J. and Leuteritz T. (2005). Opportunistic and multiple breeding attempts in plants and vertebrates of semi-deserts with unpredictable rainfall events through the year. *Trans. R. Soc. S. Afr.* **59**(2), 37–47.
- Milton S.J., Dean W.R.J., du Plessis M.A. and Siegfried W.R. (1994). A conceptual model of arid rangeland degradation, the escalating cost of declining productivity. *BioScience* **44**(2), 70–76.
- Milton S.J., Gasser S., Bortenschlager S. and Dean W.R.J. (1999). Invertebrates and leaf damage on alien *Atriplex lindleyi* and indigenous *A. vestita* in the southern Karoo, South Africa. *Afr. Entomol.* **7**(2), 298–301.
- Milton S.J., Gourlay I.D. and Dean W.R.J. (1997). Shrub growth and demography in arid Karoo, South Africa, inference from wood rings. *J. Arid Environ.* **37**, 487–496.
- Milton S.J., Siegfried W.R. and Dean W.R.J. (1990). Seeds in fleeces a clue to the prehistoric distribution of mammals in the arid Karoo, South Africa. *J. Biogeog.* **17**, 25–34.
- Mucina L., Rutherford M.C., Palmer A.R., Milton S.J., Scott L., Lloyd J.W., van der Merwe B., Hoare D.B., Bezuidenhout H., Vlok J.H.J., Euston Brown D.I.W., Powrie L.W. and Dold A.P. (2006). Succulent Karoo biome. In *The Vegetation of South Africa, Lesotho and Swaziland*, eds L. Mucina and M.C. Rutherford. *Strelitzia* **19**, 325–347. South African National Biodiversity Institute, Pretoria.
- Riginos C., Milton S.J. and Wiegand T. (2005). Context-dependent negative and positive interactions between adult shrubs and seedlings in a semi-arid shrubland. *J. Vegetation Sci.* **16**, 331–340.

Schurr F, Bossdorf O, Schumacher J. and Milton S.J. (2004). Spatial pattern formation in semi-arid shrubland, a priori predicted versus observed pattern characteristics. *Plant Ecol.* **173**, 271–282.

Settele J., Hoffmann I., Jahn R., Samietz J., Schafer C. and Vetterlein D. (eds) (1999). Rangeland management in the southern Karoo (South Africa), conflicts of landuse and environmental conservation. *UFZ Report 23/1999*. ISSN 0948-9452. Available from UFZ Centre for Environmental Research, Leipzig.

Van der Heyden F. and Stock W.D. (1995). Non-structural carbohydrate allocation following different frequencies of simulated browsing in three semi-arid shrubs. *Oecologia* **102**, 238–245.

Van der Heyden F. and Stock W.D. (1996). Regrowth of a semi-arid shrub following simulated browsing, the role of reserve carbon. *Func. Ecol.* **10**, 647–653.

Walton A. and Milton S. (2004). *A Very Busy World*. Grade 6 Read and Learn. Juta, Landsdowne, Western Cape.

Wiegand T., Milton S.J., Esler K.J. and Midgley G. (2000). Live fast, die young, estimating size-age relations and mortality pattern of shrub species in the semi-arid Karoo, South Africa. *Plant Ecol.* **150**, 115–131.

Wiegand T. and Milton S.J. (1995). A simulation model for shrubland ecosystem dynamics in arid Karoo, South Africa. pp. 135–142. In *Proc. Shrubland Ecosystem Dynamics in a Changing Environment*, May 23–25, Las Cruces, NM, compilers J.R. Barrow, E.D. McArthur, R.E. Sosebee and R.J. Tausch. *General Technical Report INT-GTR-388*. U.S. Dept of Agriculture, Forest Service, Intermountain Research Station.

Wiegand T. and Milton S.J. (1996). Vegetation change in semiarid Karoo rangelands, simulating probabilities and time scales. *Vegetatio* **125**, 169–183.

Wiegand T., Dean W.R.J. and Milton S.J. (1997). Simulated plant population responses to small scale disturbances in semiarid shrublands. *J. Vegetation Sci.* **8**(2), 163–176.

Wiegand T., Milton S.J. and Wissel C. (1995). A simulation model for a shrub-ecosystem in the semi-arid Karoo, South Africa. *Ecology* **76**(7), 2205–2221.

Wiegand T., Moloney K.A. and Milton S.J. (1998). Population dynamics, disturbance, and pattern evolution, identifying the fundamental scales of organization in model ecosystems. *Am. Nat.* **152**(3), 321–337.

Yeaton R.I. and Esler K.J. (1990). The dynamics of a succulent Karoo vegetation a study of species association and recruitment. *Vegetatio* **88**, 103–113.

Theses and unpublished reports

Du Plessis A. (1989). *Ecophysiology of the bush Karoo rat Otomys unisulcatus and the whistling rat Parotomys brantsii*. M.Sc. thesis, University of Port Elizabeth, South Africa.

Helme N. (1990). Disturbance and community dynamics on heuweltjies. Honours Project, Botany Department, University of Cape Town.

Kerley G.I.H. (1990). *Small mammals as granivores in the Karoo*. Ph.D. thesis, University of Port Elizabeth, South Africa.

Dean W.R.J. (1991). *Ecological effects of mound building by the harvester ant Messor capensis on Karoo plants*. M.Sc. thesis, University of Natal, Pietermaritzburg.

Milton S.J. (1992). *Studies on herbivory and vegetation change in Karoo shrublands*. Ph.D. thesis, University of Cape Town, South Africa.

Van der Heyden F. (1992). *Effects of defoliation on regrowth and carbon budgets of three semi-arid Karoo shrubs*. Ph.D. thesis, University of Cape Town, South Africa.

Esler K.J. (1993). *Vegetation pattern and plant reproductive processes in the succulent Karoo*. Ph.D. thesis, University of Cape Town, South Africa.

Dean W.R.J. (1995). *Where birds are rare or fill the air, the protection of the endemic and the nomadic avifaunas of the Karoo*. Ph.D. thesis, University of Cape Town, South Africa.

Witbooi B. (1998). *An assessment of the effects of soil fertility on the success of Atriplex lindleyi*. Honours Botany, University of the Western Cape, Bellville.

Eisinger D. (1998). *Density effects on the mortality and growth of young shrubs in the semi-arid Karoo*. M.Sc. thesis, University of Cape Town, South Africa.

Gasser S. (1999). *Factors determining the spatial distribution of Atriplex lindleyi*. Diplom Arbeit thesis, University of Innsbruck, Austria.

Milton S.J., Dean W.R.J., Siegfried W.R., Moll E.J., Cowling R.M. and Hockey P.A.R. (1989). *Seed-granivore systems in the Karoo*. Final report for Foundation for Research Development, Terrestrial Ecosystems Section of the National Programme for Environmental Sciences, CSIR, Pretoria.

Wagner G. (ed) (1995). *Südafrika, Capensis–Karoo–Kalahari – grossexkursion durch die Kapprovinz Südafrikas mit einen kurzen Abstecher nach Namibia*. Institut für Ökologie, Friedrich-Schiller Universität, Jena, Germany.

Leuteritz T. (2004). *Reproductive biology of Psammobates tentorium on the Tierberg Karoo Research Centre*. Unpublished postdoctoral research report, Chelonian Biology Unit, University of the Western Cape, Bellville.