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Special Issue: Long-term ecological research

Environmental myopia: a diagnosis and a remedy

Jonathan Silvertown[1], Jerry Tallowin[2], Carly Stevens[1], Sally A. Power[3], Vicky Morgan[4], Bridget Emmett[5], Alison Hester[6], Philip J. Grime[7], Michael Morecroft[8], Robin Buxton[9], Paul Poulton[10], Richard Jinks[11] and Richard Bardgett[12]

[1] Department of Life Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA, UK
[2] North Wyke Research, Okehampton, Devon EX20 2SB, UK
[3] Division of Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY UK
[4] Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough, Cambridgeshire PE1 1JY, UK
[5] Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Rd, Bangor, Gwynedd LL57 2UW, UK
[6] Macaulay Land Use Research Institute, Macaulay Drive, Craigiebuckler, Aberdeen AB15 8QH, UK
[7] Unit of Comparative Plant Ecology, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
[8] Natural England, John Dower House, Crescent Place, Cheltenham GL50 3RA, UK
[9] Northmoor Trust, Little Wittenham, Oxfordshire OX14 4QZ, UK
[10] Rothamsted Research, Rothamsted, Harpenden, Hertfordshire AL5 2JQ, UK
[11] Forest Research, Centre for Forest Resources and Management, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK
[12] Soil and Ecosystem Ecology Laboratory, Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

Long-term ecological observation affords a picture of the past that uniquely informs our understanding of present and future ecological communities and processes. Without a long-term perspective, our vision is prone to environmental myopia. Long-term experiments (LTEs) in particular can reveal the mechanisms that underlie change in communities and ecosystem functioning in a way that cannot be understood by long-term monitoring alone. Despite the urgent need to know more about how climate change will affect ecosystems and their functioning, the continued existence of LTEs is extremely precarious and we believe that dedicated funds are needed to support them. A new non-profit organization called the Ecological Continuity Trust seeks to provide a solution to this problem by establishing an endowment that will be specifically earmarked to sustain LTEs as a scientific tool for the benefit of future generations.

The problem

Ecological science must contend with history as well as mechanism. The state of every environment and the organisms in it are contingent upon previous conditions, often to an unknown degree. This is true at every temporal scale from decades to millennia, and it is becoming increasingly important that we understand environmental history as the human impact upon the planet grows. This is especially the case because there is an inherent tendency to erroneously regard the impoverished environments that are familiar to us now as 'natural' and 'normal'. Few, for example, look at any landscape in North America or Europe and puzzle to themselves: "Where is the megafauna?" Yet, before humans arrived there were giant ground sloths, giant beaver, camels and horses in North America and woolly mammoth, rhinos and giant deer in Eurasia [1]. The circumstantial evidence that the arrival of humans was, directly or indirectly, responsible for the disappearance of the megafauna on every continent outside Africa, whence we came, is increasingly difficult to ignore [2,3]. These events, of around 10–50 thousand years ago, were only the beginning, and in the last two centuries the marine megafauna have begun to face the same fate [4,5].

The fate of the terrestrial megafauna was sealed so long ago that it might be regarded as an episode of pre-history with little contemporary relevance, but the recent and ongoing collapse of marine fisheries offers at least two lessons about the need for long-term data that we should heed [6]. Lesson one is that there is a need for an accurate baseline; otherwise, the extent of human impact will probably be underestimated. The over-exploitation of marine species and habitats began before systematic scientific records were kept and as a result, each successive generation of fishers has only been able to judge any perceived decline against their own recent experience [7]. This is the problem of 'shifting baselines' [8] that still bedevils a proper assessment of the condition and normal functioning of coral reefs [9]. A terrestrial example of the same problem is furnished by The Park Grass Experiment, established in 1856, making it the oldest ecological experiment in the world. Plant species richness in the Park Grass meadow is influenced mainly by nutrients and soil pH, both of which vary among plots. However, using contemporary variation in species richness among plots to measure the effect of nutrients and pH in the Park Grass Experiment significantly underestimates the known losses of species caused by fertilization and acidification over the 150-year history

Corresponding author: Silvertown, J. (j.silvertown@open.ac.uk).

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of the experiment [10]. The reason for the underestimate is that even control plots have lost species over the last 150 years, and so using their modern species richness in any comparison today constitutes the use of a shifting baseline.

The second lesson, derived mainly from fisheries research, is that the longer a time-series of data has continued, the more valuable it becomes and the more reason there is to continue it even further. In 1988 a decision was taken by its then UK funding agency to cease the operation of the Continuous Plankton Recorder (CPR) that had been running since the 1930 s [11]. As luck would have it, this decision was made in the very year that a radical change in ocean ecosystems was taking place in the North Sea and the North Atlantic [12], although it was not until some years afterwards that this event was apparent from the long-term data. When monitoring of plankton using the CPR began, colder-water communities dominated the North Atlantic, but by the late 1980 s changes in ocean currents and temperature caused a regime shift to warmer-water communities that have persisted ever since [13]. A regime shift is an abrupt change in community composition that affects several trophic levels simultaneously and results in a switch between alternative stable states of an ecosystem [14]. It is now known that the regime shift that took place in the North Sea and the North Atlantic around 1988 was triggered when ocean temperatures crossed a critical thermal threshold of 9–10 °C [15].

A diagnosis

Sustaining ecological observations just because something like a regime shift might occur goes completely against conventional research funding requirements that favour novelty above continuity and demand specific and often short-term targets and milestones. The argument that a project should be extended merely because a lot of resources have already been invested into it is such an anathema that it can usually be dismissed by referring to it as an example of 'the Concorde fallacy' (after a notoriously expensive Anglo–French project to build the Concorde supersonic airliner in the 1960 s) [16]. To counter this argument, we propose a new term: 'environmental myopia'. Environmental myopia is the equivalent of a person with short-sight believing that nothing of interest or importance could possibly lie beyond the range of his or her own, limited vision. Environmental myopia is dangerous for the same reasons as its ocular namesake: the environment is neither featureless nor linear.

The concept of regime shift was first developed to describe abrupt changes seen in ocean and lake ecosystems, but many terrestrial examples are also known [17–19]. For example, in savannas a particular combination of fire, grazing and interspecific competition between trees and grasses can switch the ecosystem between alternate states that either have or do not have trees [20]. Also, in the Sahel region of Africa, overgrazing with its resultant soil erosion, compaction, reduced infiltration and increased water runoff, has been shown to trigger catastrophic shifts from a highly productive vegetated state to a severely degraded state [21,22]. In the Park Grass Experiment, there was a catastrophic loss of plant species in those plots where soil pH dropped below a value of 4.5 [23]. This threshold is determined by the solubility of Al^{3+} ions that come into solution at that pH and are toxic to many plants. Thresholds in environmental systems are usually much more difficult to predict than this, unless the dynamics are well understood and values of key parameters are known. Except in the case of epidemic diseases, where thresholds for spread can be calculated for well-characterized systems [24], phenomena like the regime shift in the North Atlantic are usually identified only after the event, using long-term monitoring data [25,26]. Not all evolutionary change is slow, but it too requires long-term observation and has been detected, for example, in the Park Grass Experiment [27].

It is likely that even when the dynamics of regime shifts are better understood, long-term data will still be essential for predicting when a particular system is approaching a threshold and could switch to an alternate state [28]. Long-term data are needed to tell us how resilient ecosystems are to change. The experiment at the Buxton Climate Change Impacts Laboratory (BCCIL) in northern England has been running for 17 years with winter warming, summer drought and additional summer rainfall treatments (Figure 1). It is now the second-longest-running climate change experiment on semi-natural vegetation in the world, although it was nearly a casualty of environmental myopia when its funding was cut only a few years after it was established. A sister experiment in the South of England was lost, but BCCIL was kept running for several years by the principal investigator at his own personal expense until alternative funding was found. Long-term experimentation at BCCIL has revealed the resistance of this plant community to climate change with initial changes remaining stable over 11 years [29]. Not only has this ecosystem remained surprisingly resistant to climate manipulation, but early shifts in the abundance of some species have subsequently become moderated.

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Figure 1. The climate change experiment at Buxton Climate Change Impacts Laboratory situated in calcareous grassland in Derbyshire, UK, is in its 17th year of continuous climate manipulation, including simulated summer drought imposed with the automated rain shelters seen here. Photo by J. Fridley.

Long-term studies are the only way that cumulative or slow-acting impacts can be detected. For example, long-term experimentation at Hubbard Brook Experimental Forest, New Hampshire, USA, revealed that short-term data on acidification were a misleading indicator of long-term trends. It took 18 years before acidification of waters showed a statistically significant trend in this experiment [30]. Unforeseen discoveries are also more likely to result from long-term investigations than from short-term ones. In the UK, long-term monitoring of water quality in the Acid Waters Monitoring Network [31] revealed unexpected increases in dissolved organic carbon across the whole country with important implications for water quality as well as indicating a climate change effect. Further investigation of these trends has indicated that they might be due to a reduction in acid deposition [32]. This program has recently been scaled-down considerably due to funding cuts and this represents the loss of an important long-term resource.

Towards a remedy

The examples given above show the importance of long-term data for detecting environmental and, indeed, evolutionary changes that might be unpredictable, episodic, cumulative, slow-acting, non-linear, subject to thresholds and underestimated due to a shifting baseline. However, detecting such changes is only the first step to understanding their causes and, for this, long-term experiments (LTEs) such as Park Grass, Hubbard Brook and the Buxton climate change experiment are needed. Long-term experiments provide a complement to the correlative evidence from monitoring studies, helping us reach a deeper level of understanding than can be obtained by ecological monitoring alone. They allow us to attribute change to specific causes and to identify mechanisms through manipulation of drivers and measurement of the consequences. This level of understanding is essential for the prediction of future change. Experiments also permit manipulation of conditions beyond currently prevailing limits. Through such manipulations, the resistance of ecosystems to change and resilience to extreme events can be measured.

Long-term experiments

The first long-term field experiments were on agricultural crops. In 1843, John Lawes and Henry Gilbert established the first of a series of long-term experiments at Rothamsted, England. These experiments, including Park Grass already mentioned, examined the effects of manure and inorganic fertilizers on individual crops and, to a lesser extent, on crop rotations. Although the experiments were not designed to be long-term, Lawes and Gilbert came to realize that the full impact of the applied treatments might not be apparent for decades; thus, the experiments were continued. They were supported initially by income from Lawes' business, the sale of which was later used to establish a Trust fund. Some funding also came from public subscription and other sources [33]; now, most funding comes from the UK Biotechnology and Biological Sciences Research Council.

Throughout the World, the value of long-term field experiments in agriculture was slowly recognized. The Sanborn Rotation Field was established in Missouri in 1888. In the first half of the 20th century agricultural, agroforestry and forestry experiments were established in Rutherglen and other sites in Australia (1913 onwards), in Eastern Europe from 1923 and in Uganda and other tropical countries from 1937. After WWII, long-term experiments were fairly fashionable in agriculture and forestry, but also with observations relevant to nature conservation. However, many of these experiments lasted at most for 30 years as local leadership or national policy interest declined.

The Long-Term Ecological Research program (LTER) [34] in the USA represents the first example of a research programme explicitly intended to conduct long-term research and was established by the National Science Foundation in 1976. About 26 major field sites are currently involved, including some that participated in the International Biological Programme (IBP) launched by UNESCO in the early 1960 s. Although funding applications are reviewed on a six-yearly rotation to set new targets, there is a high probability of continuation. Most sites include long-term experiments, the forest sites dating back to the 1930 s, but with most experiments initiated in the 1970 s and 1980 s. The LTER program is a model for successful, sustained long-term ecological research, but one that has failed to be replicated to the same extent outside the USA, although it has inspired and supported the establishment of the International Long-term Ecological Research network. The new National Ecological Observatory Network (NEON), also in the USA, will provide infrastructure for large-scale, and potentially long-term, continent-scale ecological monitoring. Experiments, which may or may not be long-term, are also planned [35].

In the remainder of this article we focus on the situation in the UK because this is where we have the most direct experience. Firstly, with respect to monitoring, the UK has a number of examples of long-term monitoring programs, including the Environmental Change Network (ECN), which brings together the monitoring of a wide range of different ecological variables at a series of major research sites [36] and Countryside Survey (CS) which is an audit of soils, headwaters, vegetation and land use throughout Great Britain (www.countrysidesurvey.org.uk). The first survey took place in 1978 and was repeated in 1990, 1998 and 2007. A robust statistical design is employed to ensure results can be scaled up to indicate national trends. A database of all long-term environmental observation activities in the UK has recently been developed (http://www.ukeof.org.uk/). No initiative has the security of long-term funding, but all have the support of a broad section of a range of funders and stakeholders which have to date ensured long-term, integrated monitoring data is available for the UK. By contrast, new long-term experiments have been established and maintained on a much more *ad hoc* basis, without the benefit of secure funding from a single source. A rare success is a network of long-term nitrogen deposition experiments (UKREATE) [37] that has been sustained from multiple funding sources for the last 10–15 years.

A recognition of the need for the need for long-term data is now being promoted by the UK Natural Environment

Table 1. A selection of long-term ecological experiments from a survey of examples in the UK

Vegetation type & site	Ref.	Date begun	Treatments					
			Warming (W)	Precipitation (P)	Nutrients (N)	Grazing / cutting (G)	Other (O)	Interactions
Calcareous grassland								
Wytham	[40]	1982	–	–	–	Y	Insecticide	
Buxton BCCIL	[29]	1990	Y	Y	–	Y		W × P
Neutral grassland								
Park Grass	[10]	1856	–	–	Y	Y	Lime	N & N × P/K × pH
Raisbeck and Pentwyn	[41]	1999	–	–	Y		Lime	N × lime
Craddocks Farm	[42]	2007	–	–	–	Y	Seed added	
Acid grassland								
Sourhope	[43]	1999	–	–	Y		Lime, biocide	N × lime × biocide
Pwllpeiran	[44]	1995	–	–	Y	Y		Grazing treatments not replicated
Wardlow	[45]	1995	–	–	Y	–	–	N × P
Upland heath								
Clocaenog	[46]	1999	Y	Y	–	–	–	P × W
Lowland heath								
Thursley Common	[47]	1998	–	–	Y	Y	Burning	N × G
Bog								
Whim	[48]	2003	–	–	Y	–		N × PK

Research Council employing the concept of 'National Capability' to provide more proactive support of a wide range of long-term initiatives including the ECN and CS and various long-term experiments, including three belonging to UKREATE. This is in line with initiatives by the European Union and the United Nations Economic Commission for Europe in establishing or linking monitoring programs and developing networks of experimental facilities including greater security of funding and encouragement of their greater exploitation by the broader community. Recent examples include a series of six long-term climate change experiments (www.increase-infrastructure.eu), recent calls for funding for ecosystem, and hydrological observatories, and a 'roadmap' for more ambitious activities through the European Strategy Forum on Research Infrastructures or ESFRI (http://ec.europa.eu/research/infrastructures/index_en.cfm?pg=esfri).

To identify the legacy of LTEs in the UK, and to gauge the success of these new initiatives in securing their future and to determine how representative surviving LTEs are of different habitats, we conducted a survey of the status and fate of LTEs in the UK (Table 1). Of the 49 experiments surveyed, only six (12%) were 15 years or older (See Box 1). The survey showed that long-term experiments in the UK are few and that they very rarely include treatments such as warming and altered precipitation that we know will be dominant drivers of long-term change in vegetation, soils and ecosystem processes. The new initiatives have secured the future of several LTEs for at least the medium term, but these do not represent the range of habitats in the UK or all the main drivers of change. There is a particular absence of experiments that contain interactions between different drivers (Box 2). On this basis, we conclude that UK ecologists of the future will still lack the long-term

Box 1. A survey of long-term ecological experiments in the UK

By consulting experts and the literature we identified 49 ecological experiments in herbaceous, heathland, fen, bog and montane vegetation that had long-term goals, as defined by the authors. Only six (12%) of the 49 experiments were more than 15 years old and 22 (45%) of the 49 were considered to be at risk of termination at the time of our analysis in May 2008.

The quality of the experiments was assessed using 14 criteria to identify the experiments most valuable for future long-term research in the UK. The criteria were: novelty, expansion potential, security of tenure, continuity of treatment, plot size, statistical design, number of drivers investigated, variety of data collected, association with and links to other databases, data availability, existence of a sample archive, national and international links, longevity and accessibility to collaborators. Experiments varied greatly in their quality. Out of a maximum total score of 36, 14 sites scored 30 and above, including Park Grass and the Buxton Climate Change Experiment (Figure 1).

An analysis of habitat types revealed that there was a strong bias towards certain broad habitat types. The most well represented habitats were grasslands (26 experiments out of 49) the majority of which were in neutral grassland (14 experiments) reflecting a past focus on agricultural production. Lowland heathland and upland heathland were also relatively well represented (six experiments in upland heathland and eight in lowland heathland). Broad habitat types with no, or very poor representation (few in number or experiments that did not score well in the assessment above) were: coastal habitats, montane, fen meadow, and boundary features. Bogs were also poorly represented although the one long-term bog experiment scored highly on quality criteria.

The treatments applied to experiments also showed a strong bias. The most commonly applied treatments were nutrient manipulation (29 experiments) and grazing (22), with cutting (15), biotic manipulation (12), and liming (7) relatively well represented. None of the experiments manipulated UVB and very few manipulated CO_2, water table, temperature or soil disturbance. There were only seven experiments that attempted to measure interactive effects of different treatments, although many applied more than one driver.

We separately surveyed a database of 521 forestry trials and long-term experiments managed by The UK Forestry Commission and found that the majority were concerned with genetics and silviculture rather than ecology. About 2% of the 521 studies were classed under ecosystem research, but these were all concerned with monitoring [38]. Two other long-term experiments in woodland were scored by the quality criteria used above: Henfaes FACE (Free Air Carbon dioxide Enrichment) experiment in Bangor that manipulated CO_2 in plantation woodland and which has since been terminated, and an experiment investigating the impact of cattle on invertebrate populations in upland woodland [39].

Box 2. Designing experiments for an unknown future

When the Park Grass Experiment was started at Rothamsted in 1856, neither Darwin nor Mendel had yet published their revolutionary work, biostatistics had not been invented and Justus von Liebig, the doyen of 19th century agricultural chemistry, had convinced the scientific world erroneously that all plants obtained their nitrogen from the atmosphere. Yet, Lawes and Gilbert were still able to design experiments that have gone on being useful to science for more than 150 years [10,33]. If they could do it then, we most certainly can now, given the benefit of 150 years of scientific progress. The aim for any such experiment should be to provide a platform for future research, rather than to try to anticipate exactly what the scientific questions of the future will be. We know what the principal drivers of vegetation change are (partly thanks to Lawes and Gilbert) and we highlight the importance of three of these:

1. Climate is a highly important driver with very few existing long-term field experiments dedicated to it (there are currently four experiments manipulating temperature in the UK). Model predictions for temperature consistently predict an increase, with discrepancies between models mostly concerning the rate of change. Manipulations of both temperature and rainfall are desirable climate treatments since their effects interact.
2. Land management shapes many ecosystems. A major management tool for semi-natural vegetation is grazing and has been used for many hundreds of years. Although some ecosystem responses to grazing are rapid, many changes are only seen over long timescales. Simulated 'grazing' management, such as cutting, does not replicate the selectivity of grazers, the physical effects on soils (e.g. poaching and compaction) and nutrient returns of grazing through feces, which collectively can modify the response of communities and ecosystem processes to climate change. Grazing is therefore a desirable experimental manipulation.
3. Nutrient manipulation provides the opportunity to contrast low and high productivity systems within the same habitat. In the case of nitrogen, manipulation also allows an evaluation of ecosystem response to elevated atmospheric deposition of this element, a key global change phenomenon and one with considerable ecological implications.

It would be desirable for new experiments to include interactions between the major drivers; with a few notable exceptions (e.g. Figure 1), these are lacking from existing experiments (Box 1). The importance of a sound experimental design is clearly paramount, with potential for nesting additional treatments within the three major treatments listed above. We also stress the need for building in spare capacity to respond experimentally to future ecological questions which have not yet been envisaged. Incorporating such flexibility would substantially increase the long-term value of such experiments. Archiving of data as well as materials is also essential. Indeed, plant and soil samples from the Park Grass experiment that have been archived since the 19th century are an invaluable resource.

experimental data they will need to understand the legacy of environmental change they will inherit from us. This is especially ironic given the long-term experiments at Rothamsted that our Victorian forebears bequeathed to us. Valuable though these still are, they were not designed to address the scientific agenda of the 21st century and beyond. For that, we need permanent, field-scale experiments that enable the testing of multiple global-change drivers on community and ecosystem-level properties.

Park Grass and the other long-term research at Rothamsted survived thanks to the protection of the Lawes Agricultural Trust that owns the land on which the experiments are situated and that is charged with supporting them. When the future of the CPR was threatened by the withdrawal of government funding, the project was rescued by the foundation of a charitable trust, the Sir Alastair Hardy Foundation for Ocean Science, which has successfully run surveys with the CPR ever since. Inspired by these examples, in 2008 the authors of this paper and other supporters started a charity called the Ecological Continuity Trust that is specifically dedicated to fostering long-term experimental research in ecology and ultimately to raising an endowment that will be used to support this aim (www.ecologicalcontinuitytrust.org). Our vision is that this will provide an underlying stability for long-term experiments, allowing running costs to be met and long-term planning decisions to be made. Government funding is of course still necessary for targeted research projects based around such experiments and also for major capital investments that require a large, short-term outlay. This model will, however, provide better value and greater long-term security than either a purely public or entirely private initiative. It is commonplace nowadays to project what the state of ecosystems and climate may be in 2050 or 2100. It is time we also thought about what scientists of the future will require, and to prepare long-term experimental platforms for the benefit of future generations.

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References

1 Koch, P.L. and Barnosky, A.D. (2006) Late quaternary extinctions: State of the debate. *Annu. Rev. Ecol. Evol. S.* 37, 215–250
2 Turney, C.S.M. *et al.* (2008) Late-surviving megafauna in Tasmania, Australia, implicate human involvement in their extinction. *Proc. Natl. Acad. Sci. U. S. A.* 105, 12150–12153
3 Burney, D.A. and Flannery, T.F. (2005) Fifty millennia of catastrophic extinctions after human contact. *Trends Ecol. Evol.* 20, 395–401
4 Roberts, C. (2007) *The Unnatural History of the Sea*, Gaia
5 Estes, J.A. *et al.* (2009) Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective. *Philos. T. Roy. Soc. B.* 364, 1647–1658
6 Jackson, J.B.C. *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638
7 Bunce, M. *et al.* (2008) Shifting baselines in fishers' perceptions of island reef fishery degradation. *Ocean Coast. Manage.* 51, 285–302
8 Pauly, D. (1995) Anecdotes and the shifting base-line syndrome of fisheries. *Trends Ecol. Evol.* 10, 430
9 Knowlton, N. and Jackson, J.B.C. (2008) Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biol.* 6, 215–220
10 Silvertown, J. *et al.* (2006) The Park Grass Experiment 1856-2006: Its contribution to ecology. *J. Ecol.* 94, 801–814
11 Reid, P.C. *et al.* (2003) The Continuous Plankton Recorder: concepts and history, from Plankton Indicator to undulating recorders. *Prog. Oceanogr.* 58, 117–173
12 Weijerman, M. *et al.* (2005) Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Mar. Ecol.- Prog. Ser.* 298, 21–39
13 Beaugrand, G. *et al.* (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296, 1692–1694
14 Scheffer, M. *et al.* (2001) Catastrophic shifts in ecosystems. *Nature* 413, 591–596
15 Beaugrand, G. *et al.* (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol. Lett.* 11, 1157–1168

16 Dawkins, R. and Brockmann, H.J. (1980) Do digger wasps commit the Concorde fallacy? *Anim. Behav.* 28, 892–896
17 Folke, C. *et al.* (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. S.* 35, 557–581
18 Wilson, J.B. and Agnew, A.D.Q. (1992) Positive-feedback switches in plant communities. *Adv. Ecol. Res.* 23, 263–336
19 vandeKoppel, J. *et al.* (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends Ecol. Evol.* 12, 352–356
20 Bond, W.J. (2008) What limits trees in C4 grasslands and savannas? *Annu. Rev. Ecol. Evol. S.* 39, 641–659
21 Rietkerk, M. and vandeKoppel, J. (1997) Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* 79, 69–76
22 Rietkerk, M. *et al.* (1997) Site-specific properties and irreversible vegetation changes in semi-arid grazing systems. *Oikos* 80, 241–252
23 Silvertown, J.W. (1980) The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *J. Appl. Ecol.* 17, 491–504
24 Anderson, R.M. and May, R.M. (1991) *Infectious Diseases of Humans: Dynamics and Control*, Oxford University Press
25 Walker, B. and Meyers, J.A. (2004) Thresholds in ecological and social-ecological systems: a developing database. *Ecol. Soc.* 9, 7
26 Andersen, T. *et al.* (2009) Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol. Evol.* 24, 49–57
27 Freeland, J. *et al.* (2010) Selection pressures have caused genome-wide population differentiation of *Anthoxanthum odoratum* despite the potential for high gene flow. *J Evol Biol* 4, 776–782
28 Contamin, R. and Ellison, A.M. (2009) Indicators of regime shifts in ecological systems: What do we need to know and when do we need to know it? *Ecol. Appl.* 19, 799–816
29 Grime, J.P. *et al.* (2008) Long-term resistance to simulated climate change in an infertile grassland. *Proc. Natl. Acad. Sci. U. S. A.* 105, 10028–10032
30 Likens, G.E. and Bormann, F.H. (1995) *Biogeochemistry of a Forested Ecosystem*, Springer-Verlag
31 Monteith, D.T. and Evans, C.D. (2005) The United Kingdom Acid Waters Monitoring Network: a review of the first 15 years and introduction to the special issue. *Environ. Pollut.* 137, 3–13
32 Monteith, D.T. *et al.* (2007) Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* 450, U537–U539
33 Johnston, A.E. (1994) The Rothamsted classical experiments. In *Long-Term Experiments in Agricultural and Ecological Sciences* (Leigh, R.A. and Johnston, A.E., eds), pp. 9–37, CaB International
34 Hobbie, J.E. *et al.* (2003) The US Long Term Ecological Research Program. *Bioscience* 53, 21–32
35 Schimel, D. *et al.* (2009) *The NEON Strategy. Enabling Continental Scale Ecological Forecasting*, (2 edn), NEON
36 Morecroft, M.D. *et al.* (2009) The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biol. Conserv.* 142, 2814–2832
37 UKREATE (2008) Terrestrial umbrella – Effects of eutrophication and acidification on terrestrial ecosystems Annual Report 2008 by UKREATE. In *CEH Contract Report C03425. Defra Contract No. AQ0802.*, Centre for Ecology and Hydrology
38 Mason, W.L. *et al.* (2008) An overview of long-term forest experiments in Great Britain managed by Forest Research. In *Long-Term Field Experiments in Forest Research* (Karlsson, K., ed.), pp. 13–20, Finnish Forest Research Institute
39 Vanbergen, A.J. *et al.* (2006) Consequences for host-parasitoid interactions of grazing-dependent habitat heterogeneity. *J. Anim. Ecol.* 75, 789–801
40 Gibson, C.W.D. *et al.* (1987) Spring grazing by sheep: effects on seasonal changes during early old field succession. *Vegetatio* 70, 33–43
41 Kirkham, F.W. *et al.* (2008) The impact of organic and inorganic fertilizers and lime on the species-richness and plant functional characteristics of hay meadow communities. *Biol. Conserv.* 141, 1411–1427
42 Griffith, B.A. and Tallowin, J.R.B. (2007) Agronomic value of biodiverse grasslands. High value grassland. *BGS/BES/BSAS*, 225–228
43 Usher, M.B. *et al.* (2006) Understanding biological diversity in soil: The UK's Soil Biodiversity Research Programme. *Appl. Soil Ecol.* 33, 101–113
44 Emmet, B.A. *et al.* (2001) *Grazing/Nitrogen Interactions in Upland Acid Grassland.* Report of Contract COO311-NERC-DETR Terrestrial Umbrella, Centre for Ecology and Hydrology (CEH), Institute of Terrestrial Ecology Bangor Research Station
45 Horswill, P. *et al.* (2008) Base cation depletion, eutrophication and acidification of species-rich grasslands in response to long-term simulated nitrogen deposition. *Environ. Pollut.* 155, 336–349
46 Sowerby, A. *et al.* (2005) Microbial community changes in heathland soil communities along a geographical gradient: interaction with climate change manipulations. *Soil Biol. Biochem.* 37, 1805–1813
47 Barker, C.G. *et al.* (2004) Effects of habitat management on heathland response to atmospheric nitrogen deposition. *Biol. Conserv.* 120, 41–52
48 Sheppard, L. *et al.* (2004) An automated wet deposition system to compare the effects of reduced and oxidised N on ombrotrophic bog species: Practical considerations. *Water Air Soil Poll.* 4, 197–205