New directions in grazing ecology research - a synthesis

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Introduction

The aim of this paper is to give a personal perspective on what direction research on grazing ecology should take in the future. Because we both come from an animal research background, we emphasise more the animal component than the plant or soil components of grazing ecology.

Advances from other branches of science
An oft-quoted paradigm of research is that understanding moves on a broad front with incremental advances occurring almost randomly as new insights come to light through advances in theory or from empirical findings, often spurred on by developments in adjacent or other branches of science. In the last two decades there is much evidence to suggest that this paradigm has applied to grazing ecology. Theory from the ecological and behavioural sciences has been applied specifically to grazing ecology and advances made. One of the major advances that has occurred in the past two decades has been the ability to apply an experimental approach, which has come from the agricultural field, to test theory developed in foraging ecology. For example, the use of hand-constructed sward boards, and the finding that animals can bite and chew at the same time, has led to a predictive understanding of the functional response in herbivores, something which was unimaginable 15 years ago. Also, the ability to make behavioural

measurements in the field through advances in electronics and instrumentation is an example of how experiment-based research has contributed to our understanding of how large herbivores graze. Similarly, improvements in our ability to measure intake and diet selection have enabled the study of grazing ecology to move forward. There is no reason to suggest that advances will not continue in the future through such approaches and it is part of our task to identify where the advances in theoretical and empirical research are likely to be and how they will be achieved. This is the first of the four issues that we will address in the core of the paper.

Interdisciplinary research

Grazing ecology research has been unique in that it has always brought together animal and plant scientists. Long before interdisciplinary became the current buzzword, animal and plant ecologists worked closely together. There have been many examples of such collaboration in the past twenty years because of the type of questions that required to be answered. This brings out an important concept - that the direction of research in the future depends on the questions that require to be answered. Currently, some of these key questions are about how ecosystems function where large herbivores are potentially major drivers and about how the scale, at which processes work, influences the functioning of these ecosystems. In the future, grazing ecologists will ask even broader questions about the way in which herbivores interact with, and impact upon, the ecosystems they inhabit and this is the second issue that we will address in the core of our paper. We will also argue that to answer these questions requires an even greater interdisciplinary approach in the future.

Role of society

Questions that science attempts to answer are not only posed by fellow scientists;they emanate, also, from a wider input from society, as reflected in the funding of research by government. For example, in the grazing ecology area, up until the 1980s, much of the impetus was in terms of increasing food production or improving the economic and biological efficiency of food production. However, since then, there has been a shift to developing sustainable grazing systems that view agricultural production within the broader context of maintaining the integrity of the ecosystem. Whilst increasing agricultural production will remain the emphasis for many developing countries, the questions asked by society in the developed world will relate more in the future to the biodiversity and ecosystem services provided by grazed ecosystems. For example, society will ask questions about what biodiversity should we conserve and how should we do it, although, unfortunately, not necessarily in that order, or how grazing could be managed to ensure the protection of a natural resource, such as the Great Barrier Reef, through reducing soil and nutrient loss from the terrestrial system. As a third issue in the core of our paper, we will explore what questions should be asked and how they could be explored in addressing the important issues of biodiversity and ecosystem functioning in grazed ecosystems.

Application of research

Many scientists, including the authors, have an interest in making research useful to policy makers and land managers. Grazing systems are complex and it is a considerable challenge to provide tools that are useful. In the past this was done by physically developing and demonstrating how new systems worked on the ground and by providing tools, like the HFRO sward stick to provide a more rigorous approach to management. This was a somewhat “black box” approach in that the outcomes were demonstrated without necessarily exposing the underlying complexity. To expose the issues surrounding the complexity of grazing systems, computer model-based decision support systems were developed so that a wide number of options could be explored and demonstrated. How best these can be used to deal with site-specific questions for the manager on the one hand and broad-brush answers for the policy maker on the other has not been resolved. How scientists and their clients can better exchange information will be addressed as the fourth issue in the paper.

Core issues

We have identified 4 questions that we will now address. These are

1. What theoretical and empirical research needs to be carried out into foraging behaviour?

2. What type of research is required to answer questions about ecosystem functioning?

3. How can we best answer questions about what we need to know about biodiversity to assist the management of grazed ecosystems?

4. Can we resolve the paradox of making knowledge transparent and accessible and yet at the same time provide context-specific forecasts?

What theoretical and empirical research needs to be carried out into foraging behaviour?

Theoretical research

Because of the complexity of the foraging behaviour of large herbivores, through their interactions principally with vegetation, climate and topographical features, the use of theory in developing an understanding of their foraging behaviour and impacts has been limited. In general foraging theory, maximization of the long-term average rate of intake is taken as the equivalent of fitness maximisation. It is a frustrating theory as it appears impossible to totally refute, because of the difficulty of linking lifetime nutrient maximisation to lifetime reproductive success. However, despite the fact that some studies have purported to demonstrate that herbivores maximise short term or instantaneous intake, none have been able to scale up to daily, never mind lifetime energy intake maximisation. For example, using the Ideal Free Distribution Theory, which is a subset of Optimal Foraging Theory, we had to modify considerably the parameters of the equations, linking instantaneous intake rate to the distribution of intake across vegetation communities, to fit observed behaviour in the foraging sub-model of the decision-support tools that we were involved in developing in the 1990s. This lack of usefulness of current theory has led to the development of hypotheses about what works in more particular circumstances. This may not lead to the development of generalisable theory but it does allow us to provide useful insights and tools for land managers and policy makers.

Empirical research

As we gain more understanding of the determinants of intake and diet selection of herbivores in more complex situations, intake rate maximisation is too simple a concept. Large herbivores make trade-offs between multiple behavioural and nutritional goals whilst foraging. For example they balance nutrients, sample vegetation, learn about their environment, dilute toxins, avoid parasites and indulge in social behaviour. What is clear is that the scientist has a dilemma in taking forward the testing of the hypotheses about what determines what animals eat, how much they eat and where they eat. Making yet more descriptive measurements of foraging in uncontrolled ecosystems is unlikely to be productive. It is virtually impossible to undertake experiments to answer these questions because the full range of variation in the environment in time and space cannot be achieved or measured in such experiments. However, as has been amply demonstrated, it is only through controlled experiments that the functional and mechanistic basis of foraging behaviour can be tested. How can one resolve this dilemma?

One approach, that we favour in dealing with these predominately space-related issues, is to use simulation models, which include spatial vegetation, topography and animal population descriptors, to explore what hypotheses or combinations of hypotheses would deliver as outcomes in a range of modelled scenarios and use the outputs to design experiments which will advance our understanding at these scales. Such an approach is being adopted at the Macaulay Institute in relation to scaling up social behaviour of large herbivores to the landscape.

Whilst spatial issues are currently being explored actively, some of the temporal issues are not the subject of such active research. How animals integrate decisions over different time-scales is a challenging issue and a possible explanation of why current foraging theory is inadequate. Most systems show temporal variation in resource availability and distribution and we believe that previous experience has an important bearing on current foraging behaviour. This relates to learned responses both as an adult and as a juvenile, in learning from maternal behaviour. A new area of research that we believe will become important in the future, is the extent that some of the learning could take place *in utero* through information being received from the mother via the foetal fluids or indirectly through the extent to which individual variation in foraging behaviour of the mother will influence foetal growth at critical stages of development, and hence the ability of the foetus, as an adult, to respond to foraging decision options. Work in other species suggests that this is an area worth exploring and it could also lead to advances in our understanding of nature and nurture concepts. Furthermore, because of the impacts that herbivores have on the landscape, in effect they lay down a hoof-print of their previous foraging behaviour in the landscape, which may be learned by following generations through cultural transmission. The removal of flocks from hill areas following the Foot and Mouth Disease epidemic in the UK gave a great opportunity to test how much of this cultural transmission is fed through from mother to offspring as opposed to passed down in the landscape itself. This is behind some current work that we are undertaking in collaboration with the SAC.

Having said this, it is worth speculating that the heritability of foraging behaviour is probably quite high and that genetic markers for specific foraging traits could be found to speed up the process of selection. It might be possible to select for large herbivores that have the ability to be shrub selectors or indeed that avoid woody species for those interested in woodland regeneration. Since domestic large herbivores, in the future, will be required to provide conservation benefits as well as productive outputs, it will not matter if there are negative correlations between foraging and production traits though this is unlikely if you believe the relationships between general foraging theory and fitness maximisation.

What type of research is required to answer questions about ecosystem functioning?

The impact that large herbivores have on ecosystems where they are often considered a major driver or agent of disturbance is only partially understood. There are a plethora of concepts about the relationship between biodiversity and ecosystem function and these are not very well developed in grazed ecosystems. Empirical studies are in their infancy in terms of their size and the time-scale required for their study to provide useful tests of theory. Originally theory favoured a positive relationship between biodiversity and simple measures of ecosystem function, such as stability or resilience. This was followed in the 1970s by the development of the opposite view whereby the more complex the system the less stable the system was, because of the greater connectivity of such systems. In model food webs it was also suggested that resilience could also be reduced by greater complexity. Stability, however, has other components than resilience, such as resistance, robustness, variability and persistence, and evidence on these components has not necessarily fitted well with the view that simple systems are more stable. In the last 10 years, concepts have moved on through exploring the relationship between diversity and the functioning of ecosystems and the interplay between community-level dynamic processes and ecosystem processes. These new approaches have generally emphasised the potential stabilising influence of diversity on ecosystem properties. The concept of redundancy is being replaced by the concept of temporal complementarity. The variability of ecosystem processes associated with external environmental influences at higher levels of diversity is also considered to be lower. Much of the empirical research that has influenced the development of this theory was done on a small scale on grassland plots without the use of grazing large herbivores. In an ecosystem context it is now recognised that the local deterministic processes, such as niche differentiation, may also be strongly influenced by local and, so-called, regional stochastic processes. The extent to which both may be important under changing disturbance or other environmental conditions is not yet well understood.

There are great opportunities to do fundamental research linking how ecosystems change when subject to different patterns of disturbance through a combination of long-term field studies and more detailed short-term and smaller-scale experiments to allow feedback mechanisms to be understood. This requires a multidisciplinary and interdisciplinary approach which needs large groups of scientists, animal and plant ecologists, population biologists, plant and soil scientists committed to a long-term, say 10-year project. At the Macaulay Institute the PROBECO project, which is studying the extent to which chemical differences between trees influence how pine woodland ecosystems function, is an example of the scale of approach needed. However it has only being in place for a few years and has not attempted to manipulate disturbance. A similar project, perhaps growing from the current MOORCO project at the Macaulay Institute, on grassland/heathland ecosystems would be a valuable complement to the PROBECO project. Such projects are in the context of the role of biodiversity in the functioning of ecosystems, but there are other ecosystem services, such as carbon sequestration and nutrient cycling that are equally challenging issues which require an understanding of ecosystem functioning. There is also a need to develop international approaches to obtain the maximum from such large-scale projects. There are important opportunities for the proposed Aberdeen Centre for Environmental Sustainability to progress this area of research.

How can we best answer questions about what we need to know about biodiversity to assist the management of grazed ecosystems?

The answer to this question, in terms of what components of ecosystems need to be conserved, whether they are enzyme systems, species or taxa, must await the outcome of the studies proposed to answer the question on ecosystem functioning outlined above. However, we have argued that this will take up to 10 years and there are important issues that need to be addressed by policy makers before then. This requires that we have to continue to address species diversity at the meso- to landscape scale through empirical studies. It is our contention that knowledge is insufficient yet to attempt to parameterise models involving the presence of insects and birds that will be valuable to conservation biologists and policy makers. They often want answers to questions of how to manage specific species in specific circumstances, whilst scientists are still seeking generalities.

One of our hobby-horses is that herbivore grazing pressure is a multifaceted process, involving the intensity of grazing, its timing and its distribution. Grazing has much subtlety to offer. Too many studies of the impacts of grazing on biodiversity test differences between grazing and exclosure of grazing. These studies are of limited value in providing information for land managers and policy makers interested in managing land for conservation and biodiversity. At the Macaulay Institute, the GRUB project, where the impact of grazing on food webs in relation to meadow pipit populations is being studied, is a good example of the type of approach that needs to be taken.

Whilst livestock numbers can be manipulated relatively easily, this is not the case for large wildlife herbivores, such as deer or kangaroo species, and there is a strong case for combining research on impacts with research on population biology. This leads to the need for large scale and expensive experimentation, albeit targeted to tackle the most important biodiversity issues. In Scotland we would contend that one of the key questions is - what is the population density of large herbivores that will result in predictable changes in plant, insect and bird diversity in particular landscapes? This needs a combination of modelling, and large- and small-scale empirical approaches similar to those advocated for ecosystem functioning above.

Can we resolve the paradox of making knowledge transparent and accessible and yet at the same time provide context-specific forecasts?

Our answer to this question is that computer-based decision-support tools can achieve this but not in the way that they have been used in the past. Because of the complex nature of grazed ecosystems, it is impossible to capture all the complexity of such systems in decision support tools, particularly when multiple questions are being asked, so that they can be used by practitioners and policy makers on their laptop or desktop computers. Local differences in topography, subtle changes in soil types, variation in the heterogeneity of vegetation, all of which have not been mapped and cannot be represented easily in current models, are likely to mean that the simple predictions generated are less than useful. Including stochasticity in some of the model environmental inputs is one way of generating a probability that the solution will lie in certain bounds but this does not ultimately help the precision of the prediction.

The way forward is not to throw the computer-based decision support tools in the waste-bin because they do capture much of our understanding in a known and consistent manner and allow many computations to be done rapidly. Moreover, with multiple outputs from grazing systems becoming more important, there is a greater need than ever for the use of computing power in scenario generation. To overcome difficulties of their implementation at the local scale, due to the difficulty of capturing small but potentially important differences in input information, the approach that we would favour is that the tool is used only by an expert who understands how the model works and who can provide additional interpretation and expertise over and above that provided by the model. This will require scientists to become familiar with conversing with land managers and policy makers, who may not have a science background. Scientists will also have to persuade the land manager and policy maker of the value of models in the synthesis of scientific knowledge.

Unless considerable awareness-raising among policy-makers and land managers is undertaken, such decision support tools will be of limited value. Experience with HillPlan, a decision support tool that we were involved in developing, suggests that policy makers do not have the time to become experienced in their use and that policy implementers have an insufficient skill base to use them effectively and hence react negatively to them. Their use by an expert consultant scientist has the benefit of direct interaction with the client so that the client can always feel in control of the situation. The use of internet allows the consultant working with the client to have direct access to the tool and more importantly to the range of input data sets that will become a more important part of the consultant's package in the future.

However, there are a number of tools in the knowledge transfer box that can be used and a well-produced paper-based publication can still make an important impact in communication of the results of research.

Conclusions

As a final word, both domestic and wild herbivores are part of our landscape and will continue to be so. Grazing ecology has made major advances in the past 30 years. We believe that there are a number of exciting challenges in grazing ecology that can and will be solved through a combination of theoretical and empirical approaches, and that their resolution will not only add to the broad front of increased scientific knowledge but also to its application for the benefit of all.