Meetings

Global environmental change and the uncertain fate of biodiversity

Global Environmental Change and Biodiversity – a DIVERSITAS/Tyndall Centre/TERACC/QUEST-sponsored workshop, Dourdan, France, May 2005

If any environmental problem is challenging the science of ecology for answers, fast, it is global environmental change, and climate change in particular. At the same time, a rapidly growing appreciation for the benefits of biodiversity, and concern over intensifying human-induced stresses on this poorly understood resource, have focused attention on what may be its greatest threat projected for this century. We use 'may be' because there is a wide range of views on how much climate and land use change really threatens biodiversity, for several reasons – lack of data on biodiversity and its trends in many regions of the world seems high on the list, but really lying at the nub of the problem is a poor understanding of biodiversity itself, and how it is controlled by environment (climate, resource, land use) and how it may respond to changes in these factors. The recent workshop on Global Environmental Change and Biodiversity (http://www.diversitas-international.org/home_article3.html), held in Dourdan in May 2005, was a direct response from the organizers (DIVERSITAS, Tyndall Centre, TERACC and QUEST; see Box 1) to start actively addressing this important issue. The workshop brought together a cross section of practitioners in an attempt to search for synergies and potential new methods and insights in addressing this complex issue. The stated objective of the workshop was 'to develop a research agenda that contributes to exchanges of ideas between fields of research, tests of hypotheses underlying models, and reflections on the use of observational and experimental studies'.

> *'The elegance of DGVMs, derived from their extreme abstraction of key processes from a complex world, underscores their power and position as the tool of choice in understanding ecosystem functional and structural responses from a mechanistic perspective.'*

Questions and emerging views

Three types of questions need answering to increase understanding of how global change is impacting on biodiversity. The first type concerns the role of climate in controlling the success of species in ecosystems. How are species ranges controlled by climate? What factors (biotic and abiotic) modify or even override climate in controlling species ranges? How rapidly can species respond to climate change either by shifting range or by behavioral/genetic changes? What climatic (or other) factors and their past changes resulted in such an uneven distribution of biodiversity across the globe? The second type of question concerns the control by climatic (or other) factors on the structure and function of ecosystems, and asks what ecosystem structure and function arises, given a minimum set of external limitations, such as climate, CO_2 and biophysical resources (e.g. soil nutrient availability or physical characteristics). Finally, the third type of question asks how biodiversity contributes to ecosystem functioning; for example, does increasing species richness increase indices of ecosystem function, such as nutrient cycling or resilience to drought? The Dourdan workshop brought together scientists working actively in one or more of these fields, several of them meeting here for the first time!

Box 1 Organizers of the 'Global Environmental Change and Biodiversity' workshop

DIVERSITAS	An international programme of biodiversity science	http://www.diversitas-international.org/
Tyndall Centre	Tyndall Centre for Climate Change Research	http://www.tyndall.ac.uk/welcome.html
TERACC	Terrestrial Ecosystem Responses to Atmospheric and Climatic Change	http://gcte-focus1.org/teracc.html
QUEST	Quantifying and Understanding the Earth System	http://quest.bris.ac.uk/index.html

There are emerging views on all three types of questions mentioned above. Firstly, it seems from paleo-historical information that past climate change induced species to respond individualistically to climate change, and species migrated (shifted geographic range) to track climate change, and/or showed some genetic adaptations, or suffered extinction. Recent analyses of ongoing changes suggest that species may already be starting to shift range (Parmesan & Yohe, 2003). Secondly, exploration of the second question through mechanistic modeling and some experimentation has shown that ecosystem composition and functioning may take decades at least to come into equilibrium with changing climatic and atmospheric CO_2 conditions (Woodward & Lomas, 2004), and that disturbance by fire is a key element in understanding ecosystem structure at the global scale (Bond *et al.*, 2005). Thirdly, a concerted effort to understand the third type of question has taught us that increasing species richness probably contributes to a greater efficiency of ecosystem function, and greater functional stability under conditions of stress (Loreau *et al.*, 2001). Scientists active in these three main fields are therefore ‘triangulating’ independently towards an answer to the question of how biodiversity will respond to anthropogenic climate change, each using imperfect tools with a range of assumptions, most of which have unquantified effects on uncertainty inherent in their projections.

The Dourdan workshop set about exploring these views with a series of presentations covering experimental, modeling and observational studies that set the scene for discussion and debate. Topics explored included experimental overviews on elevated CO_2, nitrogen deposition and warming effects on community composition and function, and wide-ranging experiments investigating the the role of diversity controlling function. Modeling presentations focussed on ecosystem community dynamics, individual species ranges and global patterns of vegetation structure and function [dynamic global vegetation models (DGVMs)], complemented by observational studies on species responses to developing climate trends. In this report, we present and discuss a number of highlights from the workshop.

Ecosystem function, structure and composition – on all scales

Species distribution modelers were quick to admit that this approach is heavily constrained by assumptions of equilibrium between species geographic range and climate, assumptions of control of species range by climate and its inability to incorporate mechanistic understanding, for example of plant species’ responses to rising atmospheric CO_2. However, it is an approach that extracts information on potential climate limits from the ‘natural experiments’ that are represented by extant species’ geographic ranges, and does so for large numbers of species, so is therefore well suited to projections of biodiversity change over large areas (Thuiller *et al.*, 2005). Recent recognition of disparate projections using different valid statistical methods (Thuiller, 2004; Araújo *et al.*, 2005) has led to the development of the ‘consensus’ approach, which expresses uncertainty in projections of species range across different modeling methods. Clearly, there is a strong need to develop synergies between species distribution models and the extensive and careful observational studies such as those presented at the workshop – this is a logical and natural next step which seems to lack only the necessary coordination.

Modelers at ‘patch’ or watershed scale presented convincing implementations of their approach that gave useful insight into ecosystem function, structure and even species composition change at relatively limited spatial scales (Bugmann, 2001; Reynolds *et al.*, 2001). However, the elegance of DGVMs, derived from their extreme abstraction of key processes from a complex world, underscores their power and position as the tool of choice in understanding ecosystem functional and structural responses from a mechanistic perspective. Their potential in answering penetrating questions about what really matters in these responses was highlighted by William Bond (University of Cape Town, South Africa), who set the cat among the pigeons by pointing out that, for a substantial proportion of the world’s terrestrial surface (concentrated in the tropics and southern Hemisphere), ecosystem structure is far from its modeled ‘climate potential’ in the absence of disturbance by fire (Bond *et al.*, 2005). Many workshop attendees were aware of this pattern at the local scale, but unaware of its global extent. This work was particularly important in showing how modeling and experimental results at a global scale (from long-term fire exclusion in this study) are a compelling way of learning, in this case about a globally important class of ecosystems termed ‘open ecosystems’. These even contain a rich diversity of species dependent on the disturbance, and must therefore be of sufficient antiquity to have allowed their evolution and diversification.

Ecological context and spatial scale

From the presentations on experimental approaches, it became clear that the focus is strongly on northern Hemisphere ecosystems. Cursory analysis of the distribution of TERACC sites (http://gcte-focus1.org/activities/activity_11/task_112/NEWS/map.html), for example, reveals that the vast majority are situated in the northern Hemisphere, and are generally north of 35° N. Complex experimentation using meticulous factorial experiments of different combinations of species and functional types has revealed much about the importance of increasing species richness in enhancing ecosystem function (Penuelas *et al.*, 2004). However, it now seems necessary to look hard at the ecological context of these experiments, and their spatial scale limitations. Much work has been done in temperate herbaceous systems – unfortunately these are typically 'open ecosystems' that are maintained either by fire or herbivore disturbance (and often now by mechanical mowing!). The learning gained from nitrogen addition to such systems, for instance, which enhances the success of certain grass species, seems less useful given the changes in structure expected with the introduction of grazing mammals and/or fire. The results from complex factorial experiments at Jasper Ridge (CA, USA) (Shaw *et al.*, 2002), and field CO_2 experiments in short grass prairie (Morgan *et al.*, 2001) also challenge the usefulness of single-factor experiments, and raise concerns about the abrupt application of treatments, whose effects may take years to decades to cascade through an ecosystem. Again, these experiments have a strong bias towards herbaceous ecosystems of short stature, and almost none are to be found in the southern Hemisphere.

Reality check – validating the models

Three very useful plenary discussion sessions, primed by short introductory presentations, discussed issues designed to provide a reality check for modelers (who it seems will ultimately provide the answer to the central questions of the workshop). Can results from bioclimatic models be compared with observed changes in species ranges? Are diversity responses in experimental systems comparable to those of models? Do models of species range response account effectively for dispersal and migration limitations? From these, four major issues were identified which provided the basis for parallel discussion groups: developing tests of and improvements to species distribution modeling approaches; developing an understanding of 'open ecosystems'; designing experimental tests for determining range limits of species and functional types; and incorporating extreme events in experimental design.

Clearly, the focus on 'open ecosystems' as a topic of global importance now challenges the blanket acceptance that species will respond individualistically to climate change – in the often species-rich ecosystems governed by disturbance, a switch in disturbance regime induced either by climate change or by human interference will have major diversity ramifications that can be fairly well predicted from a simple understanding of which species respond positively, neutrally or negatively to the change in ecosystem structure and function. It now remains to identify where on the globe these transitions may occur, how fast they might happen and how they could be managed to minimize diversity loss. A better global spread of both experimental and modeling work is necessary to advance this issue, and DGVMs and mechanistic patch-scale models should contribute strongly to this effort in future.

The discussion on bioclimatic modeling agreed that the term 'species distribution modeling' would be a preferable description of their activities, but that they now need to focus strongly on validating the approach using experimental, observational and natural experiments (such as those derived from study of alien species invasions). Incorporation of mechanism in the models seems plausible in terms of modeling dispersal, migration and population growth, but capturing plant species' response to rising atmospheric CO_2 in this approach remains elusive. This activity seems also to be missing a clear opportunity in synthesizing a broader understanding of the environmental factors that appear to explain species' range limits in different parts of the globe – careful use of meta-analytic approaches involving many groups around the world (taking care to avoid geographic bias) may rapidly improve understanding in this regard.

Experimental approaches, it was argued, may need to increase in spatial scale and boldness, and especially need to focus on a broader range of ecosystem types and climatic conditions. It may be more useful, for example, to carry out less complex experiments, but do more of them across more extensive geographic gradients. Reciprocal transplant experiments to test range limits, especially for plants, are amenable to this kind of work, but are difficult and possibly even unethical for animal species that could become invasive, especially given the need to estimate R_o, the intrinsic rate of population growth at and beyond species' range margins. Experimental work on ecosystem function and diversity should focus more on more complete ecosystems, and incorporate disturbance regimes (i.e. include herbivory and fire).

Perspectives

The workshop closed on a wider perspective, with a useful presentation on conveying the message to policy makers and broader society. This sharp, salutary criticism of the way results are presented (and sometimes misrepresented) to policy makers was an important message from the world of '*realpolitik*', and is worth underscoring as an independent highlight. It confronted this audience of enthusiastic theoreticians with the ultimate usefulness of their work to society, and the problems of communicating results effectively. The bottom line seems to be that there is a common failure to indicate in a simple way why this work really matters. As a result, the message may be lost against a backdrop of more immediate problems, possibly owing to its complexity, competing counter claims by skeptical voices, and a dangerous sense of helplessness by the lay public exposed to poorly interpreted conclusions and 'headline hyperbole' (our term) in the media. Our personal assessment of the success of this workshop is based on how it contributed to supporting or refuting emerging views on biodiversity responses to global change, and whether it provided the opportunity to develop new insights, new collaborations and ways forward. On the whole, the workshop exceeded our expectations, especially because a receptive mood from all involved allowed frank and productive discussions on many key topics. We hope that several new insights that are surfacing will provide the topics for useful discussions in the future, and will improve integration between modelers and experimental scientists for the benefit of all.

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Letters

A reinterpretation of the earliest quantification of global plant productivity by von Liebig (1862)

Photosynthetic assimilation of atmospheric carbon dioxide (CO_2) is a fundamental process of the biosphere that is capable of affecting atmospheric composition and climate. According to an historical review by Lieth (1975), the first global-scale quantification of plant productivity was carried out in Germany in 1862 by Justus von Liebig, one of the founders of organic chemistry and agronomy. On p. 263 of his book '*Der chemische Process der Ernährung der Vegetabilien*', von Liebig (1862) stated that 'if the total surface of the earth were one coherent meadow from which annually 100 centner hay per ha could be gained [1 German centner = 50 kg], the meadow plant would reap within 21–22 yr all CO_2 from the atmosphere and all life on earth would end' (translation in Lieth, 1978). Lieth (1975) considered this statement to be one of the milestones in primary production research, similar to the first speculation by Aristotle and the worldwide survey by the International Biological Programme (IBP). von Liebig did not provide an absolute value for productivity, but Lieth (1975) calculated it to be 230–240 × 10^{12} kg CO_2 yr^{-1} (equivalent to 62.7–65.5 × 10^{12} kg C yr^{-1}). Despite the very simple assumptions, this value