SEVENTH FRAMEWORK PROGRAMME

"Ideas" Specific Programme

European Research Council

Grant agreement for Consolidator Grant

Annex I - "Description of Work"

Project acronym: *PALEOGENIE*

Project full title: Past links in the Evolution of
Ocean's Global Environment and Ecology

Grant agreement no.: *617313*

Duration: 60 months

Date of preparation of Annex I (latest version): 25th November 2013

Date of revision of Annex I: 13th October 2014

Principal Investigator: Prof Andy Ridgwell
Host Institution: University of Bristol

Section 1b: Curriculum Vitae

Address : School of Geographical Sciences, Date of birth : 01/02/1969
University of Bristol, Nationality : British
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Website : www.seao2.org

EDUCATION

Dates From	To	University	Qualifications [award date]
10/1987	06/1990	Clare College, Cambridge University UK	BA in Natural Sciences (2:2) [June 1990]
10/1996	09/1997	University of Nottingham, Nottingham UK	MSc in Environmental Science (Distinction) [October 1997]
10/1997	09/2000	University of East Anglia, Norwich UK	PhD; "Glacial-interglacial perturbations in the global carbon cycle" [**11th July 2001**]

EMPLOYMENT HISTORY

Dates From	To	Firm/Organization	Status and description of work
11/2006	Present	University of Bristol	Royal Society University Research Fellow; Prof. in Earth System Modeling
04/2004	11/2006	UBC, Vancouver	Canada Research Chair in Global Process Modeling (Assistant Professor)
10/2002	03/2004	UC Riverside	Researcher; modeling analysis of Precambrian carbon cycling
05/2001	09/2002	University of East Anglia	Senior Research Associate – construction of an ocean carbon cycle model
10/2000	04/2001	University of East Anglia	Senior Research Associate – modeling ocean iron and carbon cycles
07/1993 10/1991	09/1996 03/1992	n/a	Variously: (i) contract instrumentation physicist; (ii) 'self-employed' – developing environmental software for schools and universities; environmental campaigning
04/1992	06/1993	ATI-Unicam Ltd.	Physicist/instrumentation scientist
09/1990	09/1991	University of Cambridge	Research assistant – infrared and optical spectroscopy of crystalline materials

CURRENT GRANTS

Value of PI grants given (in UKP).

Granting Body	Title	Duration	PI/Co-I
NERC	Assessing the role of millennial-scale variability in glacial-interglacial climate change	2012-15	Co-I
NERC	Molybdenum in the Oceans ('MOO') (~£350,000)	2013-15	PI
Royal Society	'Mechanistic Understanding of the Dynamics of Sedimentary proxies'	2011-14	(fellowship extension)
EPSERC	'Integrated Assessment of Geoengineering Proposals.	2011-14	Co-I
NERC	'CO$_2$-CarbonCycle-Climate-Interactions' (£220,528)	2010-13	PI
NERC	'Evolution of Carbon Cycle Dynamics (*e*CCD)'	2010-13	PI

	(£274,226)		
Bristol Alumni	'Historical impacts of ocean acidification on polar organisms'	2010-13	Co-I
EU – FP7	'Past4Future'	2010-14	Co-I

There is and there will be no funding overlap with the ERC grant requested and any other source of funding for the same activities and costs that are foreseen in this project.

GRADUATE STUDENT SUPERVISION

Currently, I am primary supervisor for three students:

- Nancy Jones – a PhD student studying tropical coral ecosystem dynamics and funded through a proposal submitted to the highly competitive EU-wide 'AXA Insurance' scheme.
- Sally Wood – supported by a UK NERC studentship and working on assessing the controls on coral reef 'connectivity' using ocean tracer-transport models.
- Sarah Jones – studying carbon cycle geoengineering as part of a UK-wide EPRSC funded geoengineering consortium project.

In addition, I am second supervisor for:

- Jamie Wilson – a PhD candidate in Cardiff studying ocean carbon cycle dynamics and controls.
- Suzanne Jennions – a Bristol PhD student studying historical records of Antarctic Ocean acidification.

Completed students include:

- Dr. Peter Irvine, whom I lead-supervised in a study of solar radiation management geoengineering impacts using fully coupled climate models.
- Elena Couce, whom I second-supervised, recently finished and viva-ed and studying the environmental controls on tropical coral reef habitat suitability.

I have also first-supervised a completed Masters student at UBC (Vancouver) and second-supervised one at SFU (Vancouver), plus informally acted as an additional supervisor to two completed PhD students at Penn State (US) whose research used the GENIE Earth system model.

Section 1c: Early achievements track-Record

SELECTED PUBLICATIONS

Since the start of my PhD (1997) I have received over 2100 citations in total (source: Thomson Reuters 'Web of Knowledge' (all databases): accessed 08/02/2013), averaging 144 per year, with 419 in the last full year (2012). I have an 'H' factor of 26. Google Scholar gives >2900 citations and an H-index of 29. Citations below excluding self are <u>**underlined in bold**</u> (including self: **bold only**). Publications <u>not</u> co-authored by PhD supervisor marked with *.

'Representative' publications

* Hönisch, B., **A. Ridgwell**, *et al.*, The Geological Record of Ocean Acidification, *Science* **335**, 1058-1063 (2012). **[<u>14</u> / 14]**

* **Ridgwell, A**., and D. N. Schmidt, Past constraints on the vulnerability of marine calcifiers to massive CO_2 release, *Nature Goescience*, doi:10.1038/ngeo755, 2010. **[<u>28</u> / 33]**

* **Ridgwell, A.**, J. S. Singarayer, A. M. Hetherington, and P. Valdes, Tackling regional climate change by leaf albedo bio-geoengineering, *Current Biology* **19**, doi:10.1016/j.cub.2008.12.025 (2009). **[<u>23</u> / 25]**

* **Ridgwell, A.**, Schmidt, D. N., Turley, C., Brownlee, C., Maldonado, M. T., Tortell, P., and Young, J. R., From laboratory manipulations to Earth system models: scaling calcification impacts of ocean acidification, *Biogeosciences* **6**, 2611-2623 (2009). **[<u>34</u> / 35]**

* Panchuk, K., **A. Ridgwell**, and L. R. Kump, Sedimentary response to Paleocene Eocene Thermal Maximum carbon release: A model-data comparison, *Geology* **36**, 315-318 (2008). **[<u>53</u> / 63]**

* **Ridgwell, A.**, and R. E. Zeebe, The role of the global carbonate cycle in the regulation and evolution of the Earth system, EPSL 234, 299-315, 2005. **[<u>89</u> / 94]**

* Jickells, T. D., *et al.*, **A. J. Ridgwell**, I. Tegen, and R. Torres, Global Iron Connections Between Desert Dust, Ocean Biogeochemistry and Climate, *Science* **308**, 67, 2005. **[<u>~617</u> / 618]**

* **Ridgwell, A. J.**, M. J. Kennedy, and K. Caldeira, Carbonate deposition, climate stability, and Neoproterozoic ice ages, *Science* **302**, 859-682, 2003. **[<u>71</u> / 73]**

Ridgwell, A. J., A. J. Watson, M. A. Maslin, and J. O. Kaplan, Implications of coral reef buildup for the controls on atmospheric CO_2 since the Last Glacial Maximum, *Paleoceanography* **18**, doi:10.1029/2003PA000893, 2003. **[37]**

Watson, A. J., D. C. E. Bakker, **A. Ridgwell**, P. W. Boyd, and C. S. Law, Effect of iron supply on Southern Ocean CO_2 uptake and implications for glacial atmospheric CO_2, *Nature* **407**, 730-733, 2000. **[261]**

Publications in the last <u>4</u> full years

* Holden, P. B., N. R. Edwards, S. A. Muller, K. I. C. Oliver, R. M. De'ath, and **A. Ridgwell**, Controls on the spatial distribution of oceanic $\delta^{13}C_{DIC}$, *Biogeosciences* (in press).

* Zirkfeld, K., *et al.*, **A. Ridgwell**, *et al.*, Long-term Climate Change Commitment and Reversibility: An EMIC Intercomparison, *Journal of Climate* (in press).

* Monteiro, F. M., R. D. Pancost, **A. Ridgwell**, and Y. Donnadieu, Nutrients as the dominant control on the extent of anoxia and euxinia across the Cenomanian-Turonian oceanic anoxic event (OAE2): Model-data comparison, *Paleoceanography*, DOI: 10.1029/2012PA002351 (2012). **[<u>0</u> / 0]**

* Wilson, J. D., S. Barker, and **A. Ridgwell**, Assessment of the spatial variability in particulate organic matter and mineral sinking uxes in the ocean interior: implications for the ballast hypothesis, *GBC* **26**, doi:10.1029/2012GB004398 (2012). **[<u>0</u> / 0]**

* Williams, R. G., P. Goodwin, **A. Ridgwell**, and P. L. Woodworth, Steric sea level rise from cumulative carbon emissions, *GRL* **39**, L19715 http://dx.doi.org/10.1029/2012GL052771 (2012). **[<u>0</u> / 0]**

* Palike, H., M. W. Lyle, H. Nishi, I. Raffi, **A. Ridgwell**, *et al.*, A Cenozoic record of the equatorial Pacific carbonate compensation depth, *Nature* **488**, 609–614 (2012). **[<u>1</u> / 1]**

* Wadham, J. M., S. Arndt, S. Tulaczyk, M. Stibal, M. Tranter, J. Telling, G. P. Lis, E. Lawson, **A. Ridgwell**, et al., Potential methane reservoirs beneath Antarctica, *Nature* **488**, 633–637 (2012). **[<u>1</u> / 1]**

* **Ridgwell, A.**, M. Maslin, and J. O. Kaplan, Flooding of the continental shelves as a contributor to deglacial CH_4 rise, *Journal of Quaternary Science*, DOI: 10.1002/jqs.2568 (2012). **[<u>0</u> / 0]**

* Couce, E., **A. Ridgwell**, and E. J. Hendy, Environmental controls on the global distribution of shallow-water coral reefs, *Journal of Biogeography* **39**, 1508–1523 (2012). **[<u>0</u> / 0]**

* Irvine, P. J., **A. Ridgwell**, and D. J. Lunt, Climatic Impacts of Surface Albedo Geoengineering, *JGR* **116**, D24112, doi:10.1029/2011JD016281 (2011). **[<u>1</u> / 1]**

* Lunt, D. J., **A. Ridgwell**, A. Sluijs, and J. Zachos, A model for orbital pacing of methane hydrate destabilization during the Palaeogene, *Nature Geoscience*, doi:10.1038/ngeo1266 (2011). **[<u>2</u> / 2]**

* **Ridgwell, A.**, T. J. Rodengen, and K. E. Kohfeld, Geographical variations in the effectiveness and side effects of deep ocean carbon sequestration, *GRL* **38**, L17610, doi:10.1029/2011GL048423 (2011). **[1 / 1]**

* Cui, Y., L. R. Kump, **A. J. Ridgwell**, *et al.*, Slow release of fossil carbon during the Paleocene-Eocene Thermal Maximum, *Nature Geoscience*, DOI: 10.1038/NGEO1179 (2011). **[12 / 14]**

* Haywood, A. M., **A. Ridgwell**, D. J. Lunt, *et al.*, Are there pre-Quaternary geological analogues for a future greenhouse warming?, *Phil. Trans. R. Soc. A* **369**, 933-956 (2011). **[14 / 14]**

* Irvine, P. J., **A. Ridgwell**, and D. J. Lunt, Assessing the Regional Disparities in Geoengineering Impacts, *GRL* **37**, L18702, doi:10.1029/2010GL044447 (2010). **[7 / 8]**

* Lunt, D. J., P. J. Valdes, T. Dunkley-Jones, **A. Ridgwell**, *et al.*, CO_2 driven ocean circulation changes as an amplifier of PETM hydrate destabilization, *Geology* **38**, 875-878 (2010). **[9 / 11]**

* Matsumoto, K., K. Tokos, and **A. Ridgwell**, Characterizing postindustrial changes in the natural ocean carbon cycle in an Earth system model, *Tellus* **62B**, 296–313 (2010). **[3 / 3]**

* Maslin, M., M. Owen, R. Betts, S. Day, T. Dunkley Jones, and **A. Ridgwell**, Gas hydrates: past and future geohazard?, *Phil. Trans. R. Soc. A* **368**, 2369-2393, doi:10.1098/rsta.2010.0065 (2010). **[23 / 25]**

* Dunkley Jones, T., **A. Ridgwell**, *et al.*, A Palaeogene perspective on climate sensitivity and methane hydrate instability, *Phil. Trans. R. Soc. A* **368**, 2395-2415, doi:10.1098/rsta.2010.0053 (2010). **[3 / 6]**

* Goodwin, P., and **A. Ridgwell**, Ocean-atmosphere partitioning of anthropogenic carbon dioxide on multi-millennial timescales, *Global Biogeochemical Cycles* **24**, GB2014, doi:10.1029/2008GB003449, 2010. **[3 / 5]**

* Kump, L. R., T. J. Bralower, and A. **Ridgwell**, Ocean Acidification in Deep Time, *Oceanography* **22**, 94-107, 2009. **[26 / 28]**

* Singarayer, J. S., **A. Ridgwell**, and P. Irvine, Assessing the benefits of crop albedo bio-geoengineering, *Environ. Res. Lett.* **4**, doi:10.1088/1748-9326/4/4/045110 (2009). **[4 / 5]**

* Irvine, P. J., D. J. Lunt, E. J. Stone, and **A. Ridgwell**, Fate of the Greenland Ice Sheet in a geoengineered, high CO_2 world, *Environ. Res. Lett.* **4**, doi:10.1088/1748-9326/4/4/045109 (2009). **[4 / 6]**

* Archer, D., M. Eby, V. Brovkin, **A. Ridgwell**, *et al.*, Atmospheric lifetime of fossil-fuel carbon dioxide, *Annual Reviews of Earth and Planetary Sciences* **37**, 117-134 (2009). **[55 / 59]**

* Goodwin, P., R. G. Williams, **A. Ridgwell**, and M. J. Follows, Climate sensitivity to the carbon cycle modulated by past and future changes in ocean chemistry, *Nature Geoscience* doi:10.1038/ngeo416 (2009). **[10 / 14]**

* Cao, L., M. Eby, **A. Ridgwell**, *et al.*, The importance of ocean transport in the fate of anthropogenic CO_2, *Biogeosciences* **6**, 375-390 (2009). **[10 / 16]**

* Meyer, K. M., L. R. Kump, and **A. Ridgwell**, Biogeochemical controls on photic-zone euxinia during the end-Permian mass extinction, *Geology* **36**, 747-750 (2008). **[35 / 35]**

* Chikamoto, M. O., K. Matsumoto, and **A. Ridgwell**, Response of deep-sea $CaCO_3$ sedimentation to Atlantic meridional overturning circulation shutdown, *JGR* **113**, G03017, doi:10.1029/2007JG000669 (2008). **[8 / 8]**

* Singaraye, J. S., D. A. Richards, **A. Ridgwell**, P. J. Valdes, W. E. N. Austin, and J. W. Beck, An oceanic origin for the increase of atmospheric radiocarbon during the Younger Dryas, *GRL* **35**, L14707, doi:10.1029/2008GL034074 (2008). **[15 / 17]**

* Lunt, D. J., **A. Ridgwell**, P. J. Valdes, and A. Seale, Sunshade World.: a fully coupled GCM evaluation of the climatic impacts of geoengineering, *GRL* **35**, L12710, doi:10.1029/2008GL033674 (2008). **[28 / 32]**

INVITED PRESENTATIONS (excluding public lectures and university seminars)

Conference –- keynote: Gordon Conference on Hydrates (2012, Ventura, US), SCOR 50th Anniversary Symposium (2008, Woods Hole), 2008 Darwin Day (2008, Netherlands), Goldschmidt (2006, Melbourne), EGS-AGU-EUG (2003, Nice), AGU-CGU (2004, Montreal). (Also: 2 to be given at Goldschmidt 2013)

Conferences –- invited: Goldschmidt (2012, Montreal), Royal Society URF conference (2012, London), ASLO (2011, Portland), EGU (2010, Vienna), IPC3 (2010, London), ICP10 (2010, San Diego), AGU Fall (2009, San Francisco), AGU Fall (2008, San Francisco), Oceans in High CO_2 Worlds (2008, Monte Carlo), EGU (2007, Vienna), Gordon Conference (2002, Oxford).

Summer-schools: ACDC (2011, Seattle), USSP (2012, 2011, 2010, Italy), SOLAS (2009, 2007, Corsica).

PRIZES & AWARDS

1989 Clare College Scholarship (1st in Part I exams, Cambridge)
1997 Campbell Scientific Prize (best Masters Dissertation in Environmental Science, Nottingham)
2000 Norman Heaps Prize for Best Student Presentation (2000 Challenger Society Conference, UEA)
2006 Royal Society University Research Fellowship

Section 2a: 'State-of-the-art' and objectives

Background

Projected future global pressures on the marine environment, such as surface warming, stratification, deoxygenation, and acidification, may have significant impacts on organisms and ecosystems [*Turley et al.*, 2010]. To-date, much of our understanding of the possible biotic reactions to environmental change has been based on laboratory and mesocosm studies [*Riebesell et al.*, 2000, 2008] augmented by field observations [*Fabricius et al.*, 2011, *Hall-Spencer et al.*, 2008]. Although additional insights from year-long laboratory studies are starting to emerge regarding the capacity of plankton to adapt and even evolve [*Lohbeck et al.*, 2012], environmental manipulation experiments have generally been restricted to time scales that are too short to reveal the longer-term potential for species to cope with changing environmental conditions. Furthermore, because experiments have typically been limited to focusing on a relatively few species or isolated strains, up-scaling to make projections at the ecosystem-level effects is difficult. This has spurned renewed interest in the additional information that the geological record may hold [*Hönisch et al.*, 2012].

The geological record reveals (albeit incompletely) the ecosystem responses and sensitivities to a variety of natural perturbations in global carbon cycling, climate, and associated environmental changes. For instance, the Paleocene-Eocene Thermal Maximum (PETM, 56 Ma, Figure 1) was associated with pronounced warming and ocean acidification [*Zachos et al.*, 2005] and hence potentially somewhat akin to the current experiment of rapid fossil fuel burning [*Hönisch et al.*, 2012]. Importantly, good micropaleontological evidence exists for how planktic ecosystems responded to this event [*Gibbs et al.*, 2006a, 2012; *Kelly*, 2002; *Sluijs et al.*, 2007]. Catastrophic events such as at the end Cretaceous (65 Ma) were characterized by geologically instantaneous and potentially more extreme global environmental change, driving elevated rates of extinction amongst most groups of life on Earth including planktic calcifiers [*Bown et al.*, 2004; *D'Hondt et al.*, 1994]. We would like to know what the driver(s) of these ecological changes were and whether thresholds of environmental change (e.g. *Gibbs et al.* [2012]) exist at which significant extinction takes place. Deducing this is however confounded by the multitude of co-varying environmental parameters that often occur [*Hönisch et al.*, 2012; *Ridgwell and Schmidt*, 2010]. Furthermore, in the aftermath of major extinctions such as at the end Cretaceous [*D'Hondt et al.*, 1998] the disruption of marine ecosystems and carbon cycling lasted for up to several million years before recovering (Figure 2). What does this mean for the stability of ecosystems and global biogeochemical cycles and the mechanisms of recovery from disruption?

Global ocean carbon cycle and circulation models – our primary tools for quantitatively interpreting the marine geological record of the past and directly testing hypotheses – are typically: (a) based on a 'functional type' representation of pelagic ecosystems (e.g. *Moore et al.* [2002], *Le Quéré et al.* [2005]), (b) treat plankton biomass as a single state variable, or (c) simply do not explicitly consider plankton at all (e.g. *Ridgwell et al.* [2007]). The functional type model approach, which is able to represent a degree of biodiversity and has proved successful in reproducing many important features of the modern ocean [*Le Quéré et al.*, 2005], considers a number (typically 2-10) of distinct 'types' of phytoplankton in addition to one or two size classes of grazers (zooplankton) plus parameterization of the bacterial recycling of carbon and nutrients [*Anderson*, 2005]. The types of phytoplankton are chosen so that as many of the apparent key 'functions' of an ecosystem are represented, such as nitrogen fixation, carbonate production, and ability to create intense blooms (such as by diatoms). The physiological details of each species encoded in the model are thentaken directly from laboratory culture experiments of isolated strains [*Le Quéré et al.*, 2005]. Because of this, one must question whether these models, inherently tightly encoded with our understanding of modern species characteristics and their roles, are also applicable to past climates and oceans? In fairness – such models were never designed or intended for this purpose, but which is also the problem here – Earth system models have not yet been designed that can explore the potential for adaptation (selection between genetically differing sub-populations of a 'species') as well as the role of evolution in response to past climate perturbations and recovery from extinction events.

Recently, a new approach has been devised to provide an alternative and more synthetic ('*in silico*') view onto marine ecology and relationship to the ocean environment [*Bruggeman et al.*, 2007; *Follows et al.*, 2007; *Follows and Dutkiewicz*, 2011]. This approach involves the creation of a large number (as high as $n \sim$ 100) of differing hypothetical phytoplankton species. Rather than prescribe characteristics for each species individually and explicitly from laboratory culture experiments, 'trade-offs' between different physiological characteristics ('traits') [*Litchman et al.*, 2007] such as large cell size vs. high affinity for nutrient uptake, temperature ranges and optima, are instead defined [*Bruggeman et al.*, 2007; *Dutkiewicz et al.*, 2009]. Each

modeled species is initialized with randomized properties according to these rules (the trade-offs). Ecosystems then 'self assemble' and plankton biogeography becomes an emergent rather than effectively prescribed property [*Follows and Dutkiewicz*, 2011]. That plankton species are characterized according to (albeit often inferred) physiologically-rooted trade-offs gives the potential for such models to be applicable to past environments. However, this approach also has its own specific limitations and even at $n = 100$, simulated ecosystems end up being comprised of relatively few fit plankton. Yet without a considerably greater diversity throughout the global ocean, the potential for adaptation again cannot be addressed and the response ecosystems and biogeochemical cycles to past perturbations and extinctions may be biased. Recently, ways of parameterizing the effect of adaptation [*Merico et al.*, 2009] or acclimation [*Smith et al.*, 2009] in individual functional type (species) have started to be developed, and could provide a complementary approach to the conceptually simpler starting point for exploring past ecosystems that PALEOGEN*i*E will take.

It is also important not to forget that marine organisms and ecosystems do not exist passively in the ocean, but through the uptake and redistribution of carbon and nutrients (the 'biological pump' [*Ridgwell*, 2011]) and the precipitation and sedimentation of mineral hard parts (carbonate and opal), influence ocean nutrient inventories and via climate, circulation. This can be side-stepped in models of the modern ocean because circulation and nutrient fields and hence the geochemical environment that the ecosystem experiences, can be tightly calibrated against observations [*Wunsch and Heimbach*, 2006]. But it is critical for the past when the geochemical state of the marine environment is rarely well constrained. The two-way interaction between ecology and environment creates the potential for feedback [*Lopez-Urrutia et al.*, 2006]
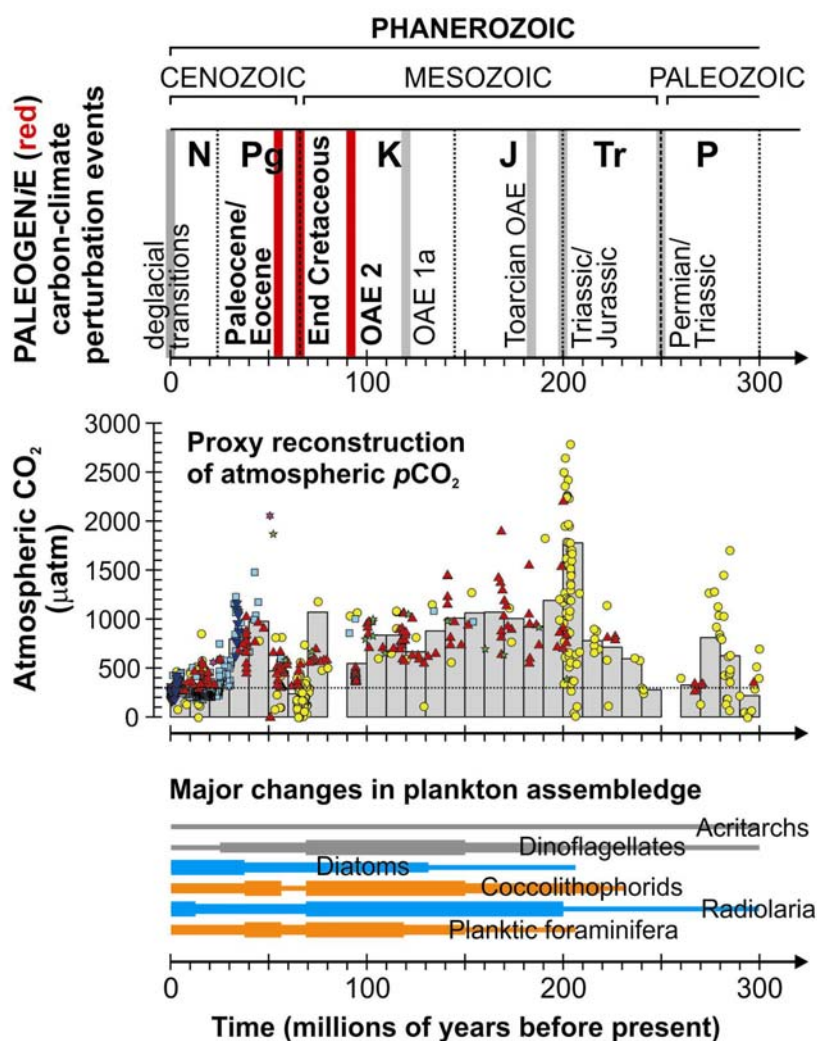

and dynamic behavior on the time-scales of ocean nutrient and carbon regulation (10 to >100 kyr) and species origination (and evolution). Coupled systems such as this have the potential for multiple stable states to exist and which may be highly relevant to understanding a number of enigmatic ecological transitions observed in the geological record. For instance, following the end Cretaceous impact, the marine carbon cycle transitioned into an apparently radically different 'mode', characterized by reduced export production and/or shallower recycling of carbon and nutrients, and hence a weaker and/or less efficient biological pump (Figure 2). This state persisted for over 1 Ma before recovery was achieved [*Coxall et al.*, 2006]. On the longer-term, correlations exist between plankton size and the ocean environment [*Schmidt et al.*, 2004] such as in the case of diatoms and Cenozoic cooling [*Cermeño et al.*, 2008]. Yet, as with shorter-term events, multiple physical and biogeochemical changes co-vary and it is not possible from the data alone to deduce what the driving factor(s) might be.

Finally, new analytical techniques for quantifying changes

Figure 1. Paleo-environmental and marine ecological context of the PALEOGEN*i*E events. Adapted from: *Hönisch et al.* [2012] and *Martin* [1995].

in the characteristics of e.g. the size, morphology, and shell thickness of fossils [*Beaufort et al.*, 2011; *Schmidt et al.*, 2004] and species composition of assemblages [*Gibbs et al.*, 2006a] are providing unprecedented insights into the nature of the ancient ocean and how species and ecosystems change on a wide spectrum of time-scales. For instance, palaeobiological database compilations have provided us with a first order understanding of the history of Phanerozoic biotic evolution (Figure 1) and its interruption by the huge diversity losses known as mass extinctions [*Sepkoski*, 1984; *Alroy et al.*, 2008]. However, attempts to resolve the records of lower-level biotic disruption, such as the spectrum of biotic events that have accompanied the carbon perturbations of the last ca. 250 Ma have often been hampered by the sensitivity of fossil diversity data to sampling biases, temporal resolution, preservation quality, and taxonomic coherence. Assessing biotic disruption beyond this level of response requires a different approach. In particular, population/assemblage variability analysis can provide geographically resolved data over long durations that are sensitive to a wide range of rates and amplitudes of environmental change (Figure 3) [*Gibbs et al.*, 2012.]. Crucially, abundance variability metrics are also independent of taxonomic composition and so enable direct comparison of event- and background-level change over long time periods of time and across biological groups of quite different taxonomic composition. What is still lacking, however, is a mechanistic framework suitable for more critically assessing such metrics as well as creating a link between past observed changes and potential future response.

Objectives

The overarching objective of the PALEOGEN*i*E project is to develop a completely new modeling approach to past marine ecosystems and biogeochemical cycles, collect new and collate existing data sufficient to offer some critical constraints on the model, and develop new methodologies for linking models and data and in doing so explore the reasons for a series of enigmatic geological observations. The five specific objectives of PALEOGEN*i*E are then to:

1. First and foremost, and because it underpins all the model-based analysis of past events: develop and test a global model capable of explicitly addressing questions of paleo-ecology and improve our abilities to interpret the rich pelagic ecological record of the Mesozoic and Cenozoic. Specifically: PALEOGEN*i*E will create a uniquely high diversity plankton ecosystem model which will be embedded in an Earth system model.
2. Collect new nannofossil data across the end Cretaceous and compile available micropaleontological observations spanning this as well as the PETM and OAE2.
3. Test a series of hypotheses for the specific environmental change(s) that best explain the observed response of plankton biogeography to past perturbations of carbon cycling and climate. Using emerging results from experimental evolution studies, PALEOGEN*i*E will also test hypotheses for observed changes in the rates of origination and disappearance of open ocean phytoplankton associated with events such as the PETM.
4. Assess the potential for feedback between marine ecology and global biogeochemical cycles (and climate), explicitly testing for the first time whether multiple steady states exist in the marine biosphere and whether transitions between them can be (and in fact were) induced through mass extinction events. And informed by modern experimental evolution studies, test how the assumed rate of evolutionary change affects the projected time-scale of ecological recovery and whether this is consistent with observations of the aftermath of the end Cretaceous.
5. Finally: create novel inter-disciplinary collaborations and stimulate new and innovative thinking regarding the function and evolution of the Earth system, and train the next generation of Earth system modelers in sought-after techniques and skills, exposing them to a variety of topical questions of both past and future global change.

Novel interdisciplinary dimensions

Above all else, PALEOGEN*i*E will excel in generating novel collaborations and in creating a bridge between geologists, paleoceanographers, and micropaleontologists, global environmental and climate modelers, as well as with modern ecological modelers and experimental evolutionary biologists.

Specifically: the project will firstly engage directly with micropaleontologists, who provide the cornerstone of the data constraints and past evolutionary understanding and context. In return, the modeling and methodological tools generated through PALEOGEN*i*E will provide the micropaleontology community with new means of exploring and interpreting data and hypothesis testing. Dr. Daniela Schmidt (Bristol), Prof. Paul Bown (UCL), and Dr. Sam Gibbs (NOCS, Southampton) are central in this respect. Secondly, the
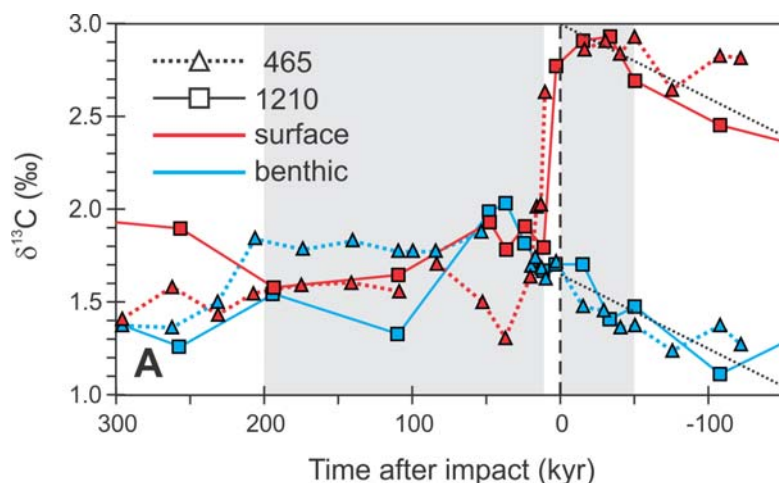
Figure 2. Disruption of ecosystems and global biogeochemical cycles in the earliest Paleocene.

Planktic (bulk carbonate) and benthic records from Sites 1210 (squares) and 465 (triangles) from a pair of sites in the Pacific, both plotted on orbitally tuned age scales and relative to an assumed impact age of 65.6 Ma (vertical dashed line). An apparent 'collapse' in the biological pump is reflected in the disappearance of a substantive offset between surface and deep ocean ('benthic') carbon isotopes ($\delta^{13}C$). Notable is how long-lasting the apparent reorganization of global biogeochemical cycles is. *Why?* What prevents rapid recovery of the system once the initial perturbation has subsided, or does it simply reflect the time-scale for the re-evolution of important traits and/or reestablishment of specific ecological structures? (Adapted from *Ridgwell et al.* [in prep].)

PALEOGEN*i*E project will directly engage with modern marine ecological modellers – specifically Dr. Mick Follows and Dr. Stephanie Dutkiewicz (MIT). In return, the fast modeling framework developed in PALEOGEN*i*E will enable a variety of new strategies for e.g. more efficiently filling trait space [*Follows and Dutkiewicz*, 2011] to be tested and hence potentially guide future Darwin model development. Thirdly, in asking questions regarding the rate(s) and characteristics of evolutionary change in plankton, PALEOGEN*i*E will engage directly with Dr. Sinead Collins (Edinburgh) whose research can provide constraints on the modeling in terms of the rate of evolution under environmental stress. In return, PALEOGEN*i*E provides a model tool of potential use in aiding the interpretation of e.g. long-term mesocosm experiments.

Through the establishment of novel models of past environments, development of new data interpretation methodologies, and furthering of understanding of past marine ecological sensitivities to global change, the PALEOGEN*i*E project embodies the greatest possible dimension of interdisciplinarity. Lessons learned here (both positive and negative) also have the potential to help inform the next (or next-but-one) generation of marine ecosystem models needed to make improved projections of future global change impacts on ocean ecosystems, and hence engaging a broad range of global change scientists and ultimately, policy makers.

Section 2b: Methodology

Overall description of the work

The proposed plan of research (summarized in Table 1) requires that innovative numerical model development be brought close together with paleo-ecological data collection and analysis. This coming together of previously rather separate approaches and disciplines directly enables the probing of a series of hypotheses, formulated in the context of major past perturbations of the global carbon cycle and climate. Three highlighted geological 'case studies' (Figure 1) provide a focus for the data collection and model-data analysis and have been chosen carefully to differ in magnitude, duration, and rates of biotic and environmental change, but while all being linked by evidence of climate and carbon cycle perturbation, and biotic disruption, and so as to provide a common thread through PALEOGEN*i*E. These events (and associated hypotheses) are:

- **Paleocene-Eocene Thermal Maximum (PETM):** During the hyperthermals of the Paleogene (65.5-23 Ma), isotopically light carbon was rapidly released into the ocean-atmosphere system leading to global warming and deep-sea carbonate dissolution [*Zachos et al.*, 2005]. The most prominent of these, the Paleocene-Eocene Thermal Maximum (~55.5Ma) is cited as one of the best analogs for the future [*Hönisch, et al.*, 2012] although such events are likely to represent only minimum estimates of future biotic and ecosystem changes due to the lower rates of change [*Ridgwell and Schmidt*, 2010]. The release of carbon during the PETM led to geologically rapid (<10kyrs) global warming with a temperature increase of the surface ocean as large as 9-10°C and 4-5°C in the deep sea [*McInerney and Wing*, 2011]. The carbon input lowered ocean pH and carbonate ion concentrations and resulted in a rapid shoaling of the calcite compensation depth [*Zachos et al.*, 2005]. PETM sediments record the largest extinction amongst deep-sea benthic foraminifers of the last 75 My [*Thomas*, 2007], and a major change in trace fossils indicates a disruption of the macrobenthic community [*Rodríguez-Tovar et al.*, 2011]. However, the co-variation of ocean acidification, warming and corresponding oxygen depletion precludes the attribution of this extinction to a single cause [*Thomas*, 2007; *Ridgwell and Schmidt*, 2010] based on data alone. In marginal marine settings, coccolithophore [*Gibbs et al.*, 2006b] and dinoflagellate cyst [*Sluijs and Brinkhuis*, 2009] assemblages display changes in species composition but these are interpreted to reflect sensitivity to temperature, salinity stratification and/or nutrient availability [*Sluijs and Brinkhuis*, 2009; *Sluijs et al.*, 2009]. (Again – teasing apart the driving factor(s) is a challenge.) Finally, in the open ocean, the occurrence of deformities in some species of calcareous nannoplankton has been described [*Raffi and De Bernardi*, 2008], but despite a strong change in assemblages, there is no bias in extinction or diversification in favor of or against less or more calcified planktic species [*Gibbs et al.*, 2006a].
  PALEOGEN*i*E will test whether: *(1) The combination of warming and nutrient restriction due to stratification together, in giving rise to novel environmental conditions (and niches) rather than either on its own, is important in driving increased rates of origination and extinction*, and *(2) The rate of onset of the event was sufficiently slow so as to enable range shifts to occur rather than mass extinction, in contrast to the K/Pg.*

- **End Cretaceous (K/Pg):** The well-known mass extinction at 66 Ma is generally accepted to have been triggered by a large asteroid impact [*Schulte et al.*, 2010]. Although planktic calcifiers exhibited elevated rates of extinction and reduced production [*Bown et al.*, 2004; *D'Hondt et al.*, 1994], benthic foraminifers were not affected in either shallow or deep waters [*Thomas*, 2007]. Because multiple environmental changes co-varied, unambiguous attribution of the planktic extinctions to any one environmental driver has not been possible. Furthermore, following the end Cretaceous impact, the marine carbon cycle transitioned into an apparently radically different 'mode', characterized by reduced export production and/or shallower recycling of carbon and nutrients, and hence a weaker and/or less efficient biological pump (Figure 2). This state persisted for over 1 Ma before recovery was achieved [*Coxall et al.*, 2006] and may have been characterized by a diachronous pattern of nannoplankton recovery [*Hull et al.*, 2011; *Jiang et al.*, 2010].
  The end Cretaceous is the linchpin event for the PALEOGEN*i*E project and provides the context for attempts to understand how ecosystems respond to catastrophic disruption particularly in terms of the recovery of larger sizes in the newly evolving taxa but also diversity recovery, with the progressive emergence of ecologically distinct groups. The relatively large numbers of coincidental global environmental changes including the potential occurrence of acidification of the surface ocean [*Hönisch et al.*, 2012] also provides a challenging test of the use of models (in conjunction with data) to attempt to identify or at least constrain, the likely primary environmental drivers of ecological disruption.
  PALEOGEN*i*E will test whether: *(3) The extreme rate of surface ocean climatic change, in exceeding the potential for range shift, was the largest single causal factor in planktic extinction*, and *(4) Feedback between ecosystem composition and ocean biogeochemical cycles stabilized the post impact planktic system at a low small mean cell size.*

- **Mid-Cretaceous Oceanic Anoxic Event 2 (OAE2):** The Mesozoic OAEs (in particular OAE 2 ~93 Ma, OAE1a ~120 Ma, and Toarcian OAE ~183 Ma) were intervals during which the ocean's oxygen minimum and deep anoxic zones expanded markedly [*Jenkyns*, 2010]. The onsets of these OAEs have been linked to the emplacement of large igneous provinces, degassing large amounts of CO_2, and associated environmental consequences of warming, lower oxygen solubility, and possibly ocean acidification [*Jenkyns*, 2010]. Some of the Cretaceous OAEs were associated with turnover in

plankton communities [*Leckie et al.*, 2002]. Deformities and some minor size reduction in coccoliths, as well as a massive decrease in the abundance of heavily calcified nannoconids have been observed [*Erba and Tremolada*, 2004; *Erba et al.*, 2010].

PALEOGEN*i*E will test whether: *(5) Warming in combination with increased phosphate supply to the open ocean surface, rather warming together with decreased phosphate supply, explains the differential ecological response of OAE2 as compared to the PETM.*

How these events will be interrogated and the hypotheses tested are delineated through a series of specific activities and methodologies.

Specific activities and methodologies

The work proposed in the 5-year PALEOGEN*i*E project is broken down into a number of linked activities as summarized in Table 1.

Activity I: Including marine communities in global models of past environments: The Paleo Assemblage Model ('PAM')

The initial work required in creating the Paleo Assemblage Model ('PAM') will be to carry out in-depth review of marine plankton traits and assess the potential physiological trade-offs (cf. *Litchman et al.* [2007]). For this, we will build directly on knowledge gained by the MIT Darwin project of which a close project collaborator, Dr. Fanny Monteiro (Bristol) was a part of during her PhD. An important advance in PAM for addressing past events and distinction from the Darwin model will firstly be in making optimal use of array space. In the Darwin model [*Dutkiewicz et al.*, 2009; *Follows et al.*, 2007] – of the 78 initial potential plankton only ca. 10-20 are ever ecologically 'important'. This is because values are assigned randomly throughout the n-dimensional 'trait space', yet only a small fraction of this space will represent a 'species' with the potential to be well adapted (or close to being well adapted) to some environment existing in the ocean [*Follows and Dutkiewicz.*, 2011]. The approach in PAM, whilst initially seeding trait space randomly following *Dutkiewicz et al.* [2009], will be to identify plankton species that can be considered extinct (i.e. are effectively completely unfit everywhere in the ocean) and re-initialize them as a finite deviation in trait values from an existing, and hence by definition, reasonably adapted plankton species. At what numerical concentration plankton can be considered to be extinct and hence how evenly species are distributed within an ecosystem will be investigated. Secondly, we envisage a large number ($n \sim 1000$ or more) of resolved species, or equivalently a rather small number of 'species' but the existence of a range of genetic variability within each species, and hence the ability to start addressing questions surrounding adaptation. Emerging ideas regarding the importance of e.g. cellular stoichiometry [*Göthlich and Oschlies*, 2012] and grazer feeding strategies [*Prowe et al.*, 2012] in creating niches and hence enhancing diversity will also be encoded and tested in the model.

In the simple and relatively abstracted trait-based approach of PAM, simulating 'real' evolution is not possible. Instead, we will assume that all the main evolutionary innovations have occurred by the Mesozoic and hence the respective traits (e.g., N fixation, calcification, ability to make an opaline frustule, etc.) already exist and can be assigned a scaling value (even if zero). Mutation will be crudely simulated by creating new plankton 'species', characterized by one (or more) changes in trait value compared to an existing species, but still governed by the same underlying trade-offs [*Litchman et al.*, 2007] (to prevent the rise of a super-organism that may be implausible from a resource allocation view point [*Dutkiewicz et al.*, 2009]). Uncertainties to be explored and tested against micropaleontological data as well as being informed by the results of experimental evolution studies (e.g. [*Lohbeck et al.*, 2012]), will encompass: (i) how many traits to vary simultaneously, (ii) how large a 'step size' to take in trait space, and (iii) how frequently to generate new potential plankton.

Seasonal changes in the depth of the mixed layer in the ocean and of water column turbulence are thought to be critical controls on plankton ecology [*Cermeño et al.*, 2008, 2010] with long-term changes in e.g. water column stratification potentially playing an important role during the Cenozoic [*Finkel et al.*, 2005; *Schmidt et al.*, 2004]. In conjunction with Activity V we will therefore improve the physics and vertical resolution (e.g., following *Muller et al.* [2005]) of the cGENIE Earth system model whilst retaining some of its low horizontal resolution essential to performing extended (>>10 kyr) geologically-relevant experiments. A mixed layer scheme [*Kraus and Turner*, 1967] already exists as part of the *c*GENIE model framework – we will make use of this, and calibrate and evaluate a new configuration of the model. We will also include a parameterization for stratification-dependent mixing that has been used previously [*Annan and Hargreaves*,

2010; *Oliver and Edwards*, 2008]. As part of the development of PAM, we will test parameterizations linking water column stability with plankton nutrient supply by increasing the half-saturation constant under more stratified conditions and disproportionately for larger cells. This will allow us to explore the idea that turbulence is critical to the transport of nutrients across the boundary lager of larger (diatom) cells [*Finkel et al.*, 2005]. This will be particularly relevant for the first PhD project (Activity IV).

The coupled *c*GENIE-PAM model will be configured initially for the modern ocean and PAM provisioned with a limited number of species and a comparable set of trade-offs to the existing MIT Darwin model [*Dutkiewicz et al.*, 2009; *Follows et al.*, 2007; *Monteiro et al.*, 2010]. Comparing directly between models will highlight important ways in which the low resolution ocean circulation represented in *c*GENIE differs from the MIT model ocean circulation [*Wunsch and Heimbach*, 2006] and affects ecosystem structure. Facets of simulated ecology identified as 'poor' will either be re-parameterized or avoided in paleo interpretation. The projected patterns of organic matter export plus ocean distributions of nutrients, oxygen, etc. projected by *c*GENIE-PAM will also be contrasted with observations (e.g. *Garcia et al.* [2010]). The model will then be reconfigured with a full (*n* ~1000) complement of plankton analogues and the evaluation against the MIT Darwin model and observations repeated. Given that the relatively coarse resolution of the *c*GENIE Earth system model is essential to extended simulations (>10 kyr) and the intended geological (not necessarily future) applicability of the model, reproducing only the large-scale patterns of plankton biogeography as well as of nutrients in the ocean may be sufficient but will be something that will be tested carefully as well as in the context of paleo data.

Activity II: New observations and syntheses of past marine ecological responses to global environmental perturbation

The goal of this activity is to quantify the biotic disruption associated with the chosen events. Calcareous nannoplankton will be used as the primary representatives of the plankton ecosystem communities of the past, as they have an abundant, global, and continuous fossil record back to the Triassic (Figure 1). Nannoplankton lie at the base of the oceanic food web and so represent a proxy of marine ecosystem function. A wealth of high-quality published nannofossil data will be utilized, supplemented by new records from critical sections. For instance: 60 archived records have already been identified by collaborators Prof. Paul Bown and Dr. Sam Gibbs from sites spanning all ocean basins and providing quantitative assemblage and stratigraphic range data for the focal nannofossil groups. Because much of this data is event focused, a number of key records will be expanded in order to develop unbroken, long-time-series biotic records that will incorporate intervening intervals of supposed background level state. These will include the Paleogene of Shatsky Rise (Site 1209, equatorial Pacific, building on, e.g., *Gibbs et al.* [2006a]; *Petrizzo* [2007]), the mid-Cretaceous and Paleogene of Tanzania (building on, e.g., *Bown and Pearson* [2009]), and the mid-Cretaceous OAE succession of the Vocontian Basin (France, building on, e.g., *Herrle* [2002]; *Friedrich et al.* [2005]). In particular, new observations will be made on samples obtained from the Walvis Ridge across the K/Pg, where excellent nannofossil preservation and a high resolution age model will enable new analyses of lith and cell size evolution, and in particular documentation of the recovery of larger cell sizes, as well as the recovery of species and ecological diversity.

The new and collated data will be analyzed using an ensemble of techniques, including: (1) simple and Shannon diversity (e.g. *Hayek and Buzas* [1997]); (2) simple evolutionary rate metrics (e.g., *Gibbs et al.* [2006a]); (3) per capita method evolutionary rates [*Foote*, 2000]; (4) summed standard deviation analysis as a metric for assemblage variability (Figure 3) [*Gibbs et al.*, 2012]; and (5) lith and cell size biometrics [*Gibbs et al.*, 2013]. By using nannofossil abundance data grouped at the generic level, the effects of differing taxonomic concepts will be minimized, and in any case this is the most efficient method of collecting data of this kind [*Gibbs et al.*, 2012]. The evolutionary trends within groups that have strong palaeoecological preferences or distinct morphological characters and that may provide further evidence of environmental forcing factors will also be examined through the different chosen events, e.g., warm- and cool-water-favouring taxa, opportunistic and specialist taxa, and heavily calcified and small, delicate taxa. The distribution of these paleoecologically distinct groups following the K-Pg mass extinction will furthermore provide a measure of the recovery within the phytoplankton ecosystem. Biotic data will be compared with palaeoenvironmental proxies (temperature, carbon flux/perturbation and nutrient availability) initially through literature data compilation but later explored more widely through the global environmental modeling (Activity III). Lith and coccosphere size analysis will provide a quantitative record of cell size evolution in the first several million years following the K-Pg mass extinction, an interval characterized by

newly evolved, but minute coccolithophores, which incrementally gave rise to diversifying lineages in which cell size increased, eventually reaching sizes, comparable to pre-extinction levels [*Bown et al.*, 2004].

Activity III: Can models help interpret the geological record of marine ecological change?

Micropaleontological data has never before been explicitly contrasted with global models of past climates and ecosystems. To a degree, the optimal methodology for making model-data comparison and the most
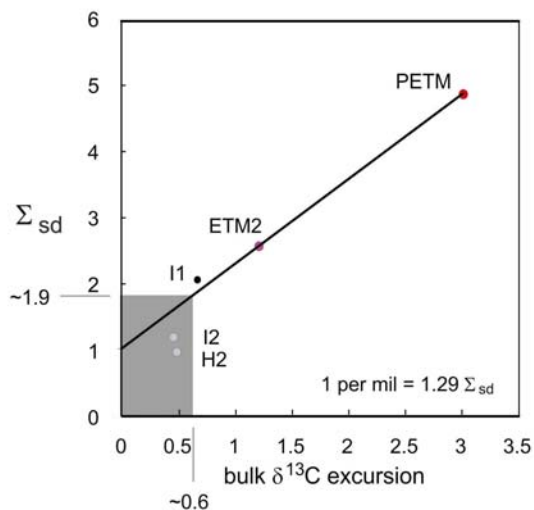

Figure 3. Example estimation of biotic thresholds using fossil assemblages.

Scatter plot of ODP Site 1209 (Shatsky Rise) summed standard deviation of nannoplankton abundance (Σsd – a measure of biotic disturbance) against maximum magnitude of δ^{13}C excursion (bulk carbonate δ^{13}C from Walvis Ridge) for the early Eocene interval that includes several carbon cycle perturbation events ('hyperthermals' denoted PETM, ETM2, I1, I2, H2). The grey area represents 'background' values between the hyperthermals. The magnitude of this biotic change scales to that of the δ^{13}C excursion. Excursions smaller than event I1 show no statistically significant assemblage variability, pointing to a critical threshold level of environmental perturbation. Adapted from *Gibbs et al.* [2012.].

efficient use of mechanistic models in isolating and exploring the role of individual environmental parameters remains to be determined. In other words: given the uniqueness of this undertaking, a complete and mature methodology for confronting paleo ecological models with the micropaleontological record does not exist yet and will be an emergent outcome of the PALEOGEN*i*E project. However, we will start by applying the same statistical analyses to the synthetic, model assemblages as are used for observations, particularly measures of diversity, size distributions, and evolutionary rate. Indeed, an equivalent commonality between widely used 'real world' ecological indices and the MIT Darwin model has already been tested and has provided new insights in respect to the modern marine environment and ecosystems [*Barton et al.*, 2010].

   As the project progresses we envisage that as a direct benefit of combining the two disciplines, new and more creative approaches will emerge. For instance – PAM is a perfect vehicle for quantifying preservation biases and the 'complete' (in model world) projections of past assemblages can be sub-sampled in different ways and the impact of differential preservation and incompleteness on established micropaleontological methodologies, explored. In doing so, it is likely that more robust and improved data (only) methodologies will emerge. The ecological model can also make projections regarding organic-walled and/or species with poor (or no) preservation potential in the geological record and hence the degree to which nannofossils may or may not be representative of the wider phytoplankton community in the first place.

   Equipped with a common set of statistical assemblage analysis tools together with the advantage of being able to sub-sample the model population to test for preservation artifacts, direct model-data comparisons will be carried out and the hypotheses (*1-5*) associated with the three events explored. In practice, this will invariably involve starting by changing the assumptions about the size and rate at which the species in the model evolve, how and which traits and trade-offs are represented, and the size and nature of the global

environmental perturbation induced in the Earth system model, re-running the model and repeating the model-data analysis. Hypotheses can then be refined (or proposed) and the entire modeling-side of the process repeated. For the actual model-data comparison, rather than plotting ecological metrics vs. indicators of environmental change (Figure 3), one could for instance plot the same metric of observed vs. model ecology with data points taken from across a range of (Paleogene hyperthermal) events sizes or as a function of time. Further and more involved statistical techniques can also be employed to relate the equivalent of model and data ecological metrics as a function of time (across events) and/or in space (comparisons of modeled and reconstructed biogeographical patterns).

Activity IV: Graduate student training

Two graduate studentships are planned in PALEOGEN*i*E, providing exposure to a broad range of facets of the working of the Earth system, both past and present, in-depth training in a variety of cutting edge modeling techniques, and hence helping prepare the next generation of modelers and Earth scientists. Both students will start at the same time and initially share a common modeling environment consisting of the PAM model but embedded into a 1D water column physical (transport and light) and biogeochemical virtual environment. Both will develop and test variants of the plankton ecosystem model against experimental and oceanographic observations within this framework, before exploring global-scale geological questions with the same plankton assemblage model but now embedded in the *c*GENIE Earth system model.

'Evolution in diatom assemblages' – Diatoms are silicifying phytoplankton, responsible for about 40% of total primary production in oceans [*Nelson et al.*, 1995]. However, despite being the most successful group of eukaryotic phytoplankton in the modern ocean [*Bowler et al.*, 2010], they are also relatively 'new' (Figure 1). The first major evolutionary change in modern plankton happened during the mid Eocene, a time interval characterized by substantial changes in the global climate, e.g. the beginning of major Antarctic glaciations at 42 Ma [*Ehrmann and Mackensen*, 1992]. During this time, the frequency of both diatom speciation and extinction events intensified in the Southern ocean region and the silica use of radiolarians started its Cenozoic downward trend (Lazarus et al. 2009), possibly directly linked to the rise of diatoms. The reasons for these observations are not simple and the underlying environmental factors may be exerting conflicting pressures – for instance, atmospheric pCO$_2$ is generally accepted to have followed a broadly declining trend over much of the Cenozoic (Figure 1) and which would be expected to create a pressure for reduced diatom growth rate [*Hopkinson, et al.*, 2011; *Riebesell and Tortell*, 2011]. At the same time; lower ocean temperatures and a deeper mixed layer would reduce light stress on diatoms [*Gao et al.*, 2012] and increase turbulence that is suspected to be critical to the transport of nutrients across the boundary layer of larger (diatom) cells [*Finkel et al.*, 2005]. What is needed to mechanistically tease apart how different environmental pressures as well as how competition with e.g. non silicifying phytoplankton and interactions with grazers all play out, is an ecological model to test ideas and explore hypotheses.

The research of the 1st studentship will involve the formulation of a diverse ecology of diatoms in the PAM modeling framework. Providing constraints on how diatoms evolve in response to environmental pressure, not only on their own, but within the ecosystem, is critical to go beyond purely abstracted modeling. The student will therefore be co-supervised by Dr. Sinead Collins at the University of Edinburgh and work closely with a PDRA there studying evolution in diatom communities in marine mesocosms (work initiated as part of the BIOACID program). Single-strain laboratory experiments are also planned by Dr. Collins which will help directly parameterize the individual potential species in the model in terms of the rate and magnitude of change in specific trait values. The student with also be co-supervised by Dr. Fanny Monteiro at Bristol who has extensive previous experience using and developing the emergent ecosystem models (e.g. *Monteiro et al.* [2010, 2011]).

In specifics: the student will start by parameterizing a diversity of diatom analogues in the common 1D physical and biogeochemical environment (see above), initially collapsed to a homogeneous representation of a chemostat and a single initial strain and hence directly testable against observed rates of evolutionary change in the laboratory. The framework will be reconfigured to represent a mesocosm with climatological boundary conditions directly from observations with the aim of providing a mechanistic link between single-strain laboratory and whole-ecosystem mesocosm results and hence offer an additional (theoretical) means of gaining insights into the role of competition in evolution. Finally, while the question of the Cenozoic evolutionary history of diatoms is beyond the scope of the studentship (and in any case no new micropaleontological data collection is planned here), how marine ecosystems might have responded and diatoms evolve in response to a progressive cooling of climate and pCO$_2$ drawdown will be explored and will add to the excitement and inherent training of this novel research project. In this, *c*GENIE will utilize

the same representation of marine silica cycling (plus sedimentary burial) as described in *Ridgwell et al.* [2002] and *Ridgwell* [2007].

'*Modelling diversity of foraminifera in the global ocean*' – Models are essential to filling the gap in ocean observations and for exploring the global influence of climate on the marine ecosystem. Foraminifera are important organisms in the marine environment, both ecologically and as major carbonate producers [*Schmidt et al.*, 2006], but typically are not represented in ocean models. A few recent studies have started to include foraminifera in biogeochemical models, but they have a limited number of foraminifer types which do not necessarily represent the real ecosystem [*Fraile et al.*, 2009; *Lombard et al.*, 2009]. The PhD will include a representation of planktic foraminifera in PAM to explore the key ecological trade-offs of foraminifera in relation to calcification, temperature, food sources, and size [*Schmidt et al.*, 2004]. This work will allow the potential influence of ocean acidification, temperature and oxygen stressors on the distribution and diversity of foraminifera in the global ocean to be explored and provide a mechanistic link to micropaleontological records of past events.

In detail: the research of the 2nd studentship will surround creating a diversity of zooplankton in PAM, taking the same framework as for how phytoplankton are generated and adapt as a basis and involving an initial extensive literature review. The student will parameterize calcifying, siliceous, and organic walled zooplankton analogues in a range of sizes and with varying feeding strategies. Different configurations and parameterizations for what might give rise to believable diverse zooplankton ecology will be tested in *c*GENIE-PAM and potential trade-offs tested. Model environmental sensitivities will be tested against observations made by the Continuous Plankton Recorder survey and biogeographical model projections against core-top and last glacial reconstructions as well as making comparisons with the MIT-Darwin model [*Follows et al.*, 2007; *Ward et al.*, 2012]. Working closely with the project PDRAs, the student will explore the importance of changes in continental configuration and hence large-scale ocean circulation patterns, atmospheric pCO$_2$ (and hence ocean temperature and stratification), and phytoplankton ecology and marine biogeochemical cycles. In this, the student will aim to separate out influences of the physical environment and the biological environment and test hypotheses for long-term morphological trends observed in the geological record.

The student will be co-supervised by Dr. Daniela Schmidt (Earth Sciences, Bristol) who has internationally recognized expertise in the evolutionary history of foraminifera and Dr. Fanny Monteiro who holds a NERC Fellowship to implement the Darwin model in *c*GENIE.

Activity V: Technical support and dissemination

*c*GENIE is not parallelized at present. Whilst this lends itself to large ensembles (e.g. *Ridgwell et al.* [2011]) it becomes an increasing disadvantage as computer processing capacity progresses via increasing numbers of cores-per-die and processors-per-node, rather than increasing clock speeds. Rate-limiting steps in the run-time operation of *c*GENIE will be identified (already identified are: tracer transport and vertical particulate matter transformations/remineralization) and limited parallelization undertaken through the computing/programming support position. To address the sub day-scale characterizing plankton growth and competition, a shorter time-step than commonly employed in the ocean circulation model (~3 days) is required but rather than necessarily reduce the time-step of the entire model, different ways of sub time-stepping will be explored and rigorously tested to ensure numerical stability.

In addition to 'normal' results-orientated publications, the new models will be fully described and evaluated in the journal GMD and the model code made open source.

Activity VI: International training and collaboration

Members of the PALEOGEN*i*E project will undertake two major training/outreach activities: in Earth system modeling and in advances in the interpretation of the geological (micropaleontological) record, particularly as relevant to global computer modeling.

Firstly, a series of three Earth system modeling workshops based around the 'GENIE' workshops that the PI has been running annually for the past 6 years in Bristol (as well as overseas including the US, Netherlands, and Germany). These have proved highly successful with more than 150 people in total to date, from undergraduate project students through established researchers to senior faculty attending. The workshops will provide basic hands-on training in Earth system modeling followed by a series of case studies in climate dynamics and ocean carbon cycling (first 2 days). There will be a 3rd, more advanced day

that will be themed according to the stage of the project (i.e., an ecological modeling focus, a past global environmental perturbation and extinction focus).

Secondly: an international summer-school in past ecosystems and ecosystem modeling will be organized. The few summer schools that exist tend to be orientated towards a more general understanding the past (such as the annual Urbino Summer School in Paleoclimatology). A course that bridges ecosystems and rock cycles and combines micropaleontology with the latest advances in ecosystem modeling does not exist. The PALEOGEN*i*E summer-school will hence provide complementary training in key elements of understanding the geological record, including: tutorials in Earth history, micropaleontology, and Earth system modeling, and hence offer unique and hands-on training for PhD students and young Post Docs. Using the *c*GENIE-PAM to illustrate the theory, the summer school will cover: planktonic ecosystems and marine productivity, ocean biogeochemical cycles, deep-sea sediments, and the long-term regulation of atmospheric pCO$_2$. Also provided will be teaching in the fundamentals of Earth history, with lectures on the tectonic, climatic, biogeochemical, and evolutionary changes taking place through the Phanerozoic, and hands-on lab training in micropaleontology. The PI will provide the integrating teaching and computer modeling practical sessions, Dr. Fanny Monteiro (Geography, Bristol) will provide lectures on plankton ecology and its modeling, Dr. Sandr Arndt (Geography, Bristol) will provide lectures on marine sediments and feedbacks, and Dr. Daniela Schmidt (Earth Science, Bristol) will lead the micropaleontology laboratory sessions and lectures. UK and overseas experts will be entrained for specific aspects and will be encouraged to stay for the full week to fully interact with the students.

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Activity	2014	2015	2016	2017	2018
Ia. Research and define tradeoffs					
Ib. Encalsulate tradeoffs in phytoplankton model					
Ic. Explore basic zooplankton scheme & dynamics					
IIa. Collate existing data					
IIb. New new K-Pg data					
IIIa. Assessment vs. observations + Darwin model					
IIIb. Paleo event hypothesis testing					
IVa. PhD #1: Diatom adaptation and evolution					
IVb. PhD #2: Zooplankton diversity					
Va. Ocean physics development, parallelization					
Vb. Development of interface and teaching materials					
Vc. Release model as open source; documentation					
VIIa. Earth system modelling workshops					
VIIb. International Summer-school					
MANGEMENT: AR based in UoB					

Table 1. Time-line of program of research and allocation of human resources.

Here, the colors reflect the main activities – red is model-development and evaluation (mostly PDRA#1, some PDRA#2, and PI), blue is data collection (PDRA #2), grey are technical computing and model numerics developments (PI and computer support position), and green the PhD studentships.

In black towards the bottom ('MANAGEMENT: AR base at UoB') are the proposed intervals in which the PI will be based at UoB.

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Section 2c: Resources

Summary of costs

iii. Budget Table	Please enter duration in months[1] ==> :	60				
	Cost Category	month 1 to 18	month 19 to 36	month 37 to 54	month 55 to 60	**Total**
	Personnel:					
	P.I.[2]	152,113.00	110,170.00	122,003.00	43,786.00	**428,072.00**
	Senior Staff	-	-	-	-	**-**
	Post docs	91,038.00	162,994.00	215,294.00	74,992.00	**544,318.00**
	Students	19,539.00	60,808.00	53,318.00	10,962.00	**144,627.00**
	Other	52,965.00	61,869.00	69,610.00	24,495.00	**208,939.00**
Direct Costs:	**Total Personnel:**	**315,655.00**	**395,841.00**	**460,225.00**	**154,235.00**	**1,325,956.00**
	Other Direct Costs:					
	Equipment	-	-	-	-	**-**
	Consumables	66,212.00	56,328.00	4,127.00	981.00	**127,648.00**
	Travel	29,175.00	30,110.00	31,537.00	11,850.00	**102,672.00**
	Summer Schools / Workshops	10,000.00	11,000.00	12,000.00	3,000.00	**36,000.00**
	Publications	1,800.00	2,000.00	2,300.00	1,211.00	**7,311.00**
	Total Other Direct Costs:	**107,187.00**	**99,438.00**	**49,964.00**	**17,042.00**	**273,631.00**
	Total Direct Costs:	**422,842.00**	**495,279.00**	**510,189.00**	**171,277.00**	**1,599,587.00**
Indirect Costs (overheads):	20% of Direct Costs	84,568.40	99,055.80	102,037.80	34,255.00	**319,917.00**
Subcontracting Costs:	(No overheads)	-	3,500.00	3,650.00	3,818.00	**10,968.00**
Total Requested Grant:	**(by reporting period and total)**	**507,410.40**	**597,834.80**	**615,876.80**	**209,350.00**	**1,930,472.00**

[1] Adapt to actual project duration.
[2] Please take into account the percentage of your dedicated working time (minimum 50%) to run the ERC funded activity when calculating the salary

For the above cost table, please indicate the % of working time the PI dedicates to the project over the period of the Grant :					54.00%

Justification of costs

Personnel

PI: The PI requests 67% funding of his time up until June 30th 2015 and then 50% from July 1st 2015 until the project end. Time is hence still weighted more heavily during the initial stages of the project so as to ensure rapid initial progress as per the original proposal (as well as at the end, to ensure maximum outputs and publications are realized from the project). From July 1st 2015 the PI will be paid from the grant at the same rate as from May 1st through June 30th 2015, but working 50% rather than 67% FTE. The un-allocation PI salary will be instead used to support a higher grade or additional duration of computer programming and technical support post. This post will now take on additional responsibilities, such as managing (including re-structuring and converting to a common f90 format) the model code – tasks that were previously allocated to the PI.

Post docs: A 5-year PDRA position is requested to specialize in Earth system modeling. This person will be responsible for development and coupling (and technical support) of the paleo assemblage (ecological) model 'PAM'. As a post spanning the entire project, they will provide an important element of continuity. They will also work closely with the 2nd PDRA position on model-data analysis and testing hypotheses against the geological record, and will closely support the modeling research involving the 2 PhD students. The second PDRA position is 3 years in duration and the person hired will be responsible for new data collection as well as collation of existing data associated with the three geological events the project will focus on. They will work jointly with the 1st PDRA on model-data analysis and testing hypotheses.

Students: Two graduate studentships are required in the project, providing exposure to a broad range of facets of the working of the Earth system, both past and present, in-depth training in a variety of cutting edge modeling techniques, and hence helping to prepare the next generation of modelers and Earth scientists. The

purpose of the students on the project will be to develop and test variances of the plankton ecosystem model against experimental and oceanographic observations within this framework, before exploring global-scale geological questions additional to the work of the PDRAs.

Other: 2 ½ years of computer and programming support are requested. Necessary to fully achieve the aims of the proposal is an improved efficiency (esp. parallelization) of the Earth system model (*c*GENIE), the development of suitable and efficient coupling and transport schemes between PAM and *c*GENIE, support for the modeling-based research of the 2 PhD students, support for the model-led workshops and summer school, and help in bringing the combined model to an open source status.

Consumables

The research is based on computer modeling and involves the development and application, sometimes in massive ensembles of experiments, of an advanced Earth system model. However, this model is currently not parallelized and runs on a single core. A typical mode of operation is to run multiple sensitivity experiments (on occasion, order 1,000) for extended simulation time, from 10,000 years (~1 day real time) up to 1,000,000 years. Even with limited parallelization envisaged in the project, it would be running on ca. 4-6 cores, i.e. a single processor. University and national supercomputers are generally configured for massively parallel jobs (i.e. >100 cores for a single model experiment), short run-times (~1 day real time), and can have extensive queues of users. It is impractical to carry out the necessary model development and research on generic massively parallel supercomputer facilities. Hence, an essential component of the total budget is devoted to the creation of such a small bespoke cluster facility.

   The PI has previously built a series of small clusters. This is highly cost-effective, as it does not require professional installation and the clustering software is open source (free). Only components specifically suited to running the *c*GENIE model need be purchased. This exact route is proposed in PALEOGEN*i*E.

   The components composing the computing cluster required are:

(i)   Head node – High end rack-mount server e.g. with a spec: 2 x 8 core ~3 GHz processors, 64 GB RAM, high capacity fast (15,000 rpm) SCSI disks in RAID 6 configuration with a minimum 1 TB capacity. The head node is the core of the entire cluster and has to handle all disk-writes and data saving from model experiments run on the compute nodes and the speed and capacity (and fault redundancy) is critical.

(ii)   Compute nodes – 10 compute nodes are requested, with spec: 2 x 4 core ~3 GHz processors, 32 GB RAM, low capacity only hard-disk. The compute nodes are what in practice the model experiments actually run on and a large total number of cores are required so that ensembles up to order 1,000 can be run practically.

(iii)   Hardware – High throughput network switch, cabling, monitor, full height rack.

(iv)   UPS – Uninterruptible power-supply to prevent loss of model experiments (and ensure no hard-disk corruption) in the event of blackouts and brownouts. Capacity must be sufficient to serve both head node and all computer nodes, e.g. 5000 VA.

(v)   Backup – An HP 'Ultrium 5' format internal tape drive (plus e.g. 10-20 tapes) plus server for carrying out tape backup of model data.

The University of Bristol will provide the necessary floor space plus power supply and internet connection in a climate-controlled computing room.

   For office-based working of the research group, the project requires:

(vi)   Workstations – high end (multiple processor/ core systems with ~16 GB RAM, large capacity hard disks, and dual monitors) required for the necessary data processing and visualization, which can be computationally highly intensive for 3-D Earth system model fields, plus general MATLAB modeling and processing of large observational datasets. Funds sufficient to cover the needs of the PI, 2 PDRAs, and 2 PhD students, are requested.

(vii)   Laptop – A long battery lifetime (ca. 10 hours) laptop is essential to making full use of long haul flights, but needs to be sufficiently powerful to run and analyze models and create presentation-quality output. A Sony SSD disk based system has previously proved ideal. This will be a shared resource amongst the entire research group.

(viii) Licenses for data analysis and visualization, e.g. MATLAB or IDL Licenses for software production of publications and presentations, e.g. CorelDraw or Adobe Illustrator are required by the research group.

Publications

(i)   Publication pages charges and charges for color figures in a journal published by AGU or EGU, Nature, Science, or PNAS (all target journals) is requested, with 'free for 'life', i.e. fully open access.

Travel

(i)   In order to effectively communicate and present the results of the project and further the career development of the PDRAs (and PhD students), funds to cover a number of international (non EU) conferences such as AGU, GSA, and Goldschmidt, are requested. Assuming that one trip per year for each staff member (PI and PDRAs) and one trip total for each PhD student, equates to 15 trips in total.

(ii)   Similar justifications apply to EU meetings and conferences.

(iii) Funds are also requested for project members to attend UK meetings (Royal Society, Geological Society) and workshops.

(iv)   Funds are requested to ensure adequate interaction with collaborators on the nannofossil data collection and analysis –regular travel for PDRA #3 to NOCS (Southampton) and UCL (London) to work closely with Prof. Paul Bown and Dr. Sam Gibbs.

(v)   To further facilitate graduate student training and career opportunities, funds sufficient for 1 international summer-school (e.g. Urbino) for each of the 2 PhD students are requested. The Urbino Summer School provides a comprehensive and wide-ranging introduction and training in paleooceanography and paleoclimatology, from climate models and basics of the long-term carbon cycle, to stratigraphy and Earth history. Hence, it represents the most complete and relevant possible general training for the PhD students. Importantly, given that both PhD students will be working very extensively with a variety of paleo and nanofossil data, the Urbino Summer School provides an essential early career opportunity to make and develop key contacts with the leading researchers in the field.

Summer Schools / Workshops

(i)   Funds for an international graduate Summer-school on past marine ecosystems and modeling are requested. Assuming 25 participants and 5 overseas instructors with a duration of 7 days.

(ii)   Finally: funds are requested for 3 themed Earth system modeling workshops. Assuming 10 participants over 3 days.

External collaboration will be purely intellectual in nature and none of the collaborators will be receiving any of the ERC funding.

Subcontracting

Audit fees

Section 2d: Ethical Issues

Areas Excluded From Funding Under FP7 *(Art. 6)*

(i)   Research activity aiming at human cloning for reproductive purposes;

(ii)   Research activity intended to modify the genetic heritage of human beings which could make such changes heritable (Research relating to cancer treatment of the gonads can be financed);

(iii) Research activities intended to create human embryos solely for the purpose of research or for the purpose of stem cell procurement, including by means of somatic cell nuclear transfer;

All FP7 funded research shall comply with the relevant national, EU and international ethics-related rules and professional codes of conduct. Where necessary, the beneficiary(ies) shall provide the responsible Commission services with a written confirmation that it has received (a) favourable opinion(s) of the relevant ethics committee(s) and, if applicable, the regulatory approval(s) of the competent national or local authority(ies) in the country in which the research is to be carried out, before beginning any Commission approved research requiring such opinions or approvals. The copy of the official approval from the relevant national or local ethics committees must also be provided to the responsible Commission services.

Research on Human Embryo/ Foetus	YES	Page
Does the proposed research involve human Embryos?		
Does the proposed research involve human Foetal Tissues/ Cells?		
Does the proposed research involve human Embryonic Stem Cells (hESCs)?		
Does the proposed research on human Embryonic Stem Cells involve cells in culture?		
Does the proposed research on Human Embryonic Stem Cells involve the derivation of cells from Embryos?		
I CONFIRM THAT NONE OF THE ABOVE ISSUES APPLY TO MY PROPOSAL	**YES**	

Research on Humans	YES	Page
Does the proposed research involve children?		
Does the proposed research involve patients?		
Does the proposed research involve persons not able to give consent?		
Does the proposed research involve adult healthy volunteers?		
Does the proposed research involve Human genetic material?		
Does the proposed research involve Human biological samples?		
Does the proposed research involve Human data collection?		
I CONFIRM THAT NONE OF THE ABOVE ISSUES APPLY TO MY PROPOSAL	**YES**	

Privacy	YES	Page
Does the proposed research involve processing of genetic information or personal data (e.g. health, sexual lifestyle, ethnicity, political opinion, religious or philosophical conviction)?		

			YES	Page
	Does the proposed research involve tracking the location or observation of people?			
	I CONFIRM THAT NONE OF THE ABOVE ISSUES APPLY TO MY PROPOSAL		**YES**	

	Research on Animals[1]	**YES**	**Page**
	Does the proposed research involve research on animals?		
	Are those animals transgenic small laboratory animals?		
	Are those animals transgenic farm animals?		
	Are those animals non-human primates?		
	Are those animals cloned farm animals?		
	I CONFIRM THAT NONE OF THE ABOVE ISSUES APPLY TO MY PROPOSAL	**YES**	

	Research Involving non-EU Countries (ICPC Countries[2]) [3]	**YES**	**Page**
	Is the proposed research (or parts of it) going to take place in one or more of the ICPC Countries?		
	Is any material used in the research (e.g. personal data, animal and/or human tissue samples, genetic material, live animals, etc) : a) Collected in any of the ICPC countries?		
	b) Exported to any other country (including ICPC and EU Member States)?		
	I CONFIRM THAT NONE OF THE ABOVE ISSUES APPLY TO MY PROPOSAL	**YES**	

	Dual Use	**YES**	**Page**
	Research having direct military use		
	Research having the potential for terrorist abuse		
	I CONFIRM THAT NONE OF THE ABOVE ISSUES APPLY TO MY PROPOSAL	**YES**	

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[1] The type of animals involved in the research that fall under the scope of the Commission's Ethical Scrutiny procedures are defined in the Council Directive 86/609/EEC of 24 November 1986 on the approximation of laws, regulations and administrative provisions of the Member States regarding the protection of animals used for experimental and other scientific purposes Official Journal L 358 , 18/12/1986 p. 0001 - 0028

[2] In accordance with Article 12(1) of the Rules for Participation in FP7, 'International Cooperation Partner Country (ICPC) means a third country which the Commission classifies as a low-income (L), lower-middle-income (LM) or upper-middle-income (UM) country. Countries associated to the Seventh EC Framework Programme do not qualify as ICP Countries and therefore do not appear in this list.

[3] A guidance note on how to deal with ethical issues arising out of the involvement of non-EU countries is available at: ftp://ftp.cordis.europa.eu/pub/fp7/docs/developing-countries_en.pdf