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FORUM

Identification of 100 fundamental ecological questions

William J. Sutherland[1], Robert P. Freckleton[2], H. Charles J. Godfray[3], Steven R. Beissinger[4], Tim Benton[5], Duncan D. Cameron[2], Yohay Carmel[6], David A. Coomes[7], Tim Coulson[8], Mark C. Emmerson[9], Rosemary S. Hails[10], Graeme C. Hays[11], Dave J. Hodgson[12], Michael J. Hutchings[13], David Johnson[14], Julia P. G. Jones[15], Matt J. Keeling[16], Hanna Kokko[17], William E. Kunin[18], Xavier Lambin[14], Owen T. Lewis[3], Yadvinder Malhi[19], Nova Mieszkowska[20], E. J. Milner-Gulland[21], Ken Norris[22], Albert B. Phillimore[23], Drew W. Purves[24], Jane M. Reid[14], Daniel C. Reuman[21,25], Ken Thompson[2], Justin M. J. Travis[14], Lindsay A. Turnbull[26], David A. Wardle[27] and Thorsten Wiegand[28]

[1]Department of Zoology, Conservation Science Group, Cambridge University, Downing Street, Cambridge, CB2 3EJ, UK; [2]Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK; [3]Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK; [4]Department of Environmental Science, Policy & Management, 137 Mulford Hall #3114, University of California, Berkeley, CA, 94710-3114, USA; [5]Global Food Security Programme, University of Leeds, c/o IICB, Leeds, LS2 9JT, UK; [6]Faculty of Civil and Environmental Engineering, Techion-Israel Institute of Technology, Haifa, Israel; [7]Forest Conservation and Ecology Group, Dept of Plant Sciences, University of Cambridge, Downing Street, Cambridge, CB1 3EA, UK; [8]Department of Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY, UK; [9]School of Biological Sciences, Queen's University Belfast, 97 Lisburn Road, Belfast, BT9 7BL, Northern Ireland, UK; [10]CEH Wallingford, Maclean Building, Crowmarsh Gifford, Wallingford, Oxon, OX10 8BB, UK; [11]Department of Biosciences, College of Science, Swansea University, Singleton Park, Swansea, SA1 8PP, UK; [12]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn, Cornwall, TR10 9EZ, UK; [13]School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex, BN1 9QG, UK; [14]Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, AB14 3UU, UK; [15]School of Environment, Natural Resources & Geography, Thoday Building, Bangor University, Bangor, LL57 2UW, UK; [16]School of Life Sciences & Maths Institute University of Warwick, Gibbet Hill Road, Coventry, CV4 7AL, UK; [17]Division of Ecology, Evolution and Genetics, Research School of Biology, Australian National University, Canberra, ACT 0100, Australia; [18]School of Biology, University of Leeds, Leeds, LS1 9JT, UK; [19]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, OX1 3QY, UK; [20]Marine Biological Association of the UK, Citadel Hill, Plymouth, PL1 2PB, UK; [21]Department of Ecology and Evolution, Silwood Park Campus, Imperial College London, Buckhurst Road, Ascot, Berks, SL5 7PY, UK; [22]Centre for Agri-Environmental Research, University of Reading, Reading, PO Box 137, RG6 6AR, UK; [23]Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, EH9 3JT, UK; [24]Computational Ecology and Environmental Science group, Microsoft Research, 7 JJ Thomson Ave, Cambridge, CB3 0FP, UK; [25]Rockefeller University, 1130 York Ave, New York, NY, 10065, USA; [26]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland; [27]Department of Forest Ecology and Management, Faculty of Forestry, Swedish University of Agricultural Sciences, S901-83 Umeå, Sweden; and [28]Department of Ecological Modelling, UFZ Helmholtz Centre for Environmental Research-UFZ, Permoserstr 15, 04318, Leipzig, Germany

Summary

1. Fundamental ecological research is both intrinsically interesting and provides the basic knowledge required to answer applied questions of importance to the management of the natural world. The 100th anniversary of the British Ecological Society in 2013 is an opportune moment to reflect on the current status of ecology as a science and look forward to high-light priorities for future work.

Correspondence author. E-mail: w.sutherland@zoo.cam.ac.uk

2. To do this, we identified 100 important questions of fundamental importance in pure ecology. We elicited questions from ecologists working across a wide range of systems and disciplines. The 754 questions submitted (listed in the online appendix) from 388 participants were narrowed down to the final 100 through a process of discussion, rewording and repeated rounds of voting. This was done during a two-day workshop and thereafter.

3. The questions reflect many of the important current conceptual and technical pre-occupations of ecology. For example, many questions concerned the dynamics of environmental change and complex ecosystem interactions, as well as the interaction between ecology and evolution.

4. The questions reveal a dynamic science with novel subfields emerging. For example, a group of questions was dedicated to disease and micro-organisms and another on human impacts and global change reflecting the emergence of new subdisciplines that would not have been foreseen a few decades ago.

5. The list also contained a number of questions that have perplexed ecologists for decades and are still seen as crucial to answer, such as the link between population dynamics and life-history evolution.

6. *Synthesis*. These 100 questions identified reflect the state of ecology today. Using them as an agenda for further research would lead to a substantial enhancement in understanding of the discipline, with practical relevance for the conservation of biodiversity and ecosystem function.

Key-words: community ecology, ecology, ecosystems, evolutionary ecology, population ecology, research priorities

Introduction

Ecologists seek to understand how organisms interact with each other and the abiotic environment, and also apply this knowledge to the management of populations, communities and ecosystems, and the services they provide. Ecologists today find it relatively straightforward to list the major applied challenges facing the field. Previous exercises in which applied ecologists or plant scientists have come together to draw up lists of the most important questions facing the field have revealed a diverse, complex and sometimes daunting set of challenges (Sutherland *et al.* 2006, 2009, 2010; Grierson *et al.* 2011). Similar exercises, providing a list of the major unanswered questions in basic ecology, have rarely been attempted (but see Thompson *et al.* 2001). This is not the first time that the British Ecological Society has used an anniversary as a prompt for an exercise of this type. For its 75th anniversary in 1988, Cherret (1989) identified the central existing concepts. The aim of the current exercise was to look forward to identify key issues.

Such an exercise may be used to evaluate the current state of the discipline and where its challenges lie. It also helps to identify areas of research that have the potential to advance the science of ecology significantly. Furthermore, it may be particularly valuable as a reference line for future evaluations of progress in ecology. The last two decades have seen debates on whether general laws in ecology could be identified (Moffat 1994; Lawton 1999; Ghilarov 2001; Dodds 2009; Colyvan & Ginzburg 2012) and the extent to which ecology is making progress (Abrahamson, Whitham & Price 1989; Belovsky *et al.* 2004; O'Connor 2000; Graham & Dayton 2002). The current exercise could add a concrete dimension to these debates by identifying key issues and providing an agenda against which progress can be assessed.

The fundamental aim of ecology is to increase understanding of how organisms interact with the biotic and abiotic environment rather than address a particular societal, conservation or economic problem. We sought to draw up a list of important questions facing ecology, with an emphasis on fundamental science. Participants were therefore asked to rank questions by how they would advance ecological science, rather than by the direct importance of the answer to the major problems facing society and humanity. Our aim is thus to set an agenda for means of improving our understanding of fundamental ecology. There was no attempt to build in consideration of possible application in the future: despite an increase in horizon-scanning activities (e.g. Sutherland *et al.* 2008, 2012), it is inherently difficult to predict what science will eventually be useful.*

Materials and methods

APPROACH

Our aim was to identify 100 important unanswered questions in basic ecology. We wanted to avoid very broad, general questions and instead sought those describing a challenge that could be tackled with the concerted effort of a small group of researchers or perhaps through a research programme supported by a limited number of research grants. As summarized in Table 1, we adopted a previously used methodology (e.g. Sutherland *et al.* 2011a) as described in detail

*Benjamin Franklin said that asking the worth of a new discovery was like saying "What is the use of an infant?". This is not an argument that all basic science is equally good, but it is an argument that the best basic science may have unimaginably important applications.

in Sutherland *et al.* (2011b), which places great emphasis on making the process to identify the most important questions rigorous, democratic and transparent.

Participants, which included an editor from each of the five BES journals, were selected by WJS, RPF and HCJG after broader consultation to cover a wide range of approaches to ecology. The attendees were invited based on their track records of publishing significant science in international journals, which we hoped demonstrated their knowledge of the cutting edge of their subjects. For logistical and financial reasons, the participants were predominately from the UK; each is an author of this paper. The attendees were encouraged to consult widely resulting in the active participation of 388 people (including those who attended preparatory workshops and discussions, or who responded to emails, but not those who were sent but did not respond to emails). The 754 questions submitted are listed in Appendix 1.

The questions were initially assigned to 12 broad themes reflecting areas of ecology defined by subject or methodological approach. Participants were asked to identify and vote for the 6–12 most important questions in those sections they felt competent to comment on and suggest rewording where appropriate. All participants were sent and asked to reflect on the results of the voting and the reworded questions before the meeting.

A two-day workshop was held at the British Ecological Society's headquarters at Charles Darwin House, London, in April 2012. Questions within each of the themes were considered by working groups (four consecutive rounds of three parallel sessions). Panel chairs identified duplicate questions (and ensured that duplication did not lead to dilution of votes for a particular topic), those that had already been answered, and those that could be improved by further rephrasing. Participants were also encouraged to support potentially important questions that had not attracted many votes if they considered them overlooked because of their subject area, because they were in subfields that were out of fashion, or simply because they were poorly expressed. The chairs moderated a discussion in which questions that were unlikely to make the final 100 were quickly excluded before a short list of 18 important questions to be taken to the plenary sessions were agreed. The latter were divided into three sets of six questions ranked 'bronze', 'silver' and 'gold' in the order of increasing importance. Chairs were asked to ensure the process was democratic with all views respected, and decisions were made by voting conducted as a show of hands.

The second stage of the workshop consisted of two sets of two parallel sessions each of which refined the questions from three of the initial working groups. Participants were first asked to examine the 18 (3 × 6) gold questions and remove any duplicates, improve the wording where necessary and demote to the silver section any which on further discussion were thought to be of less importance. The 18 bronze questions were then examined to see whether they contained any that should be elevated to the silver category. Finally, voting took place to identify the 20 top questions that formed a new gold group incorporating the existing gold questions and the most highly supported silver questions. Further discussion and voting chose from the old silver category (and sometimes the bronze) sets of five questions that formed new silver, bronze and a new category of 'nickel' questions.

In a final plenary session, the 80 (4 × 20) gold questions were considered in turn with further elimination of duplicates and major overlaps. Questions which on further consideration were thought not to be of the highest importance were demoted to silver, with further voting when there was no clear consensus. Using the same procedures, participants were then asked to identify whether any of the questions classified as nickel should be moved into bronze, and then whether those in the bronze and following that the silver category should be promoted or demoted. The final rounds of voting chose the most important silver questions to join the gold questions and so make up the final 100.

This voting process was devised so that at each stage the previous decisions were influential but could also be overruled. It also provided the opportunity to deal with similar questions that came from different initial parallel sessions. Furthermore, questions from different groups were compared against each other to ensure that they were of equivalent importance and to reduce possible artefacts, for example caused by a disproportionate number of questions initially suggested in one subject area.

Following the workshop, an extensive editing process was carried out which identified some overlooked ambiguities and duplications. A final email poll was conducted to decide the fate of the last few candidates for inclusion.

Table 1. The process used for reducing the submitted questions into the final list of 100. The first stage involved prioritizing the complete set of questions. Each subsequent stage used the ranking of the previous stage to influence the narrowing of the list

1.	754 questions categorized into 12 groups and ranked by voting before the meeting.
2.	Twelve sessions, each dealing with one group, identify 6 highest priority 'gold' questions, 6 'silver' and 6 'bronze'.
3.	Four sessions, each taking output from three sessions in stage (2), identifying 20 'gold' questions, 5 'silver', 5 'bronze' and 5 'nickel'.
4.	Plenary session identifying the top 100.

LIMITATIONS

Any undertaking such as this of course has limitations (Sutherland *et al.* 2011b). The most important caveat is that the questions posed and shortlisted are very likely to be influenced by the interests and expertise of the participants. Efforts were made to solicit questions and select attendees from across the full breadth of the subject, but inevitably biases will remain. In total, 388 people contributed questions, and there were 37 participants in the final workshop. The majority of the participants were from the UK, and hence, there is a geographical bias, although we did have attendees from continental Europe, the US, and Australia, and most participants have many collaborators and often conduct fieldwork around the globe. We also invited participants with experience in a range of taxa, including plants, animals and microbes from both aquatic and terrestrial systems, to reduce possible taxonomic biases.

The initial division into themes may have limited lateral thinking, and sometimes, it was not clear where questions should best be placed; the plenary session and final editing was designed to address this issue. As mentioned previously, there was a tendency to pose broad questions rather than the more focussed question we were aiming for. There is a tension between posing broad unanswerable questions and those so narrow that they cease to be perceived as fundamental. A possible solution to this in a further exercise might be to define sets of specific or tactical questions nested within overarching strategic questions.

Results

THE QUESTIONS

The questions here are presented by subject, but not in rank order. For some questions (e.g. 8, 9, 12, 23, 54), there may already be a good theoretical understanding but empirical support for the theory is still lacking.

EVOLUTION AND ECOLOGY

Ecology and evolution share a broad interface, with both fields recognizing the value of an inter-disciplinary perspective. Interest in the role of abiotic conditions and biotic interactions as drivers of natural selection (Questions 1, 3) is long standing (Darwin 1859) and remains an active area of research (Kingsolver *et al.* 2012). More recent, in light of evidence for very rapid evolution is a focus on eco-evolutionary dynamics (Schoener 2011). Population dynamic can influence selection from one generation to the next, but at the same, time life history may evolve and feedback upon population dynamics. This research programme is dissolving the distinction between evolutionary and ecological time-scales and is represented by several of the questions in this section that address aspects of the interplay between life-history evolution and population dynamics (5, 6, 8). Despite calls for ecologists to engage with the emergent field of epigenetics (Bossdorf, Richards & Pigliucci 2008), it is represented by a solitary question (4), the breadth of which highlights how just little is known from either a theoretical or empirical perspective. Reflecting some of the range of influences that evolution has on ecology, and *vice versa*, questions with an explicit evolutionary component also appear under the Populations (11, 14), Communities and Diversity (48, 56) and Human impacts and global change (74, 82) sections.

1 What are the evolutionary consequences of species becoming less connected through fragmentation or more connected through globalization?
2 To what extent can evolution change the scaling relationships that we see in nature?
3 How local is adaptation?
4 What are the ecological causes and consequences of epigenetic variation?
5 What are the relative contributions of different levels of selection (gene, individual, group) to life-history evolution and the resulting population dynamics?
6 What selective forces cause sex differences in life history and what are their consequences for population dynamics?
7 How should evolutionary and ecological theory be modified for organisms where the concepts of individual and fitness are not easily defined (e.g. fungi)?
8 How do the strength and form of density dependence influence feedbacks between population dynamics and life-history evolution?
9 How does phenotypic plasticity influence evolutionary trajectories?
10 What are the physiological bases of life-history trade-offs?

POPULATIONS

Understanding and predicting the spatio-temporal dynamics of populations remains a central goal in ecology (Davidson & Andrewartha 1948; Hanski 1998; Alexander *et al.* 2012). This requires detailed understanding of how demographic rates vary and covary through space and time as well as the underlying causes. Several questions reflect the drive to gain this understanding (e.g.17, 18, 23). The recent accumulation of evidence suggesting that evolutionary processes can occur rapidly enough to influence population dynamics at a range of spatial scales has resulted in renewed emphasis on joint analysis of population dynamics and life-history evolution (Pelletier, Garant & Hendry 2009; Schoener 2011), which is reflected in questions 20, 23). Dispersal is a key process determining spatial population dynamics and technological innovations have revolutionized our ability to measure individual movement trajectories (Cagnacci *et al.* 2010). Understanding the causes of variability in dispersal and their consequences for spatial dynamics across different spatial scales remains a major focus of ecological enquiry and future major challenges are emphasized in several of the questions (13–16). While we surmise that processes operating at fine spatial and/or temporal scales are likely to impact dynamics at large spatial scales such as species' ranges, there remains an urgent need for new methods that enable us to link local processes to large-scale spatial dynamics (12) (e.g. Helmuth *et al.* 2006). This linkage will help our understanding of how local population dynamics link to macroecological patterns and dynamics (11, 19), as well as improve predictions of population dynamics.

11 What are the evolutionary and ecological mechanisms that govern species' range margins?
12 How can we upscale detailed processes at the level of individuals into patterns at the population scale?
13 How do species and population traits and landscape configuration interact to determine realized dispersal distances?
14 What is the heritability/genetic basis of dispersal and movement behaviour?
15 Do individuals in the tails of dispersal or dormancy distributions have distinctive genotypes or phenotypes?
16 How do organisms make movement decisions in relation to dispersal, migration, foraging or mate search?
17 Do different demographic rates vary predictably over different spatial scales, and how do they then combine to influence spatio-temporal population dynamics?
18 How does demographic and spatial structure modify the effects of environmental stochasticity on population dynamics?
19 How does environmental stochasticity and environmental change interact with density dependence to generate population dynamics and species distributions?
20 To what degree do trans-generational effects on life histories, such as maternal effects, impact on population dynamics?
21 What are the magnitudes and durations of carry-over effects of previous environmental experiences on an individual's subsequent life history and consequent population dynamics?
22 What causes massive variability in recruitment in some marine systems?

23 How does covariance among life-history traits affect their contributions to population dynamics?
24 What is the relative importance of direct (consumption, competition) vs. indirect (induced behavioural change) interactions in determining the effect of one species on others?
25 How important is individual variation to population, community and ecosystem dynamics?
26 What demographic traits determine the resilience of natural populations to disturbance and perturbation?

DISEASE AND MICRO-ORGANISMS

While the study of infectious disease is often seen as a branch of medical science, the way that all micro-organisms (from parasites to commensalists to mutualists) interact with their hosts and their environment clearly fits within the remit of ecology. Indeed, for many years, the study of infectious diseases (e.g. Anderson & May 1992) has used ecological concepts to improve our understanding of public-health issues. Furthering understanding of the regulation of disease continues to require knowledge of basic microbiology and there is growing realization within the discipline of ecology that the abundance, diversity and function of micro-organisms have fundamental roles in shaping ecosystems. This view appears to be borne-out by the selected questions, which tend to focus on interactions between micro-organisms and larger organisms (e.g. 28–31). The rapid development and application of molecular techniques continues to reveal a previously hidden diversity of micro-organisms, particularly in complex environments such as soils (Rosling *et al.* 2011). Population genomics has provided insight into the genetic mechanisms using which micro-organisms interact with, and help shape, their environment (e.g. Martin *et al.* 2008, 2010), and this calls for a better understanding of the importance of microbial genotypic diversity for ecosystems (Johnson *et al.* 2012; 29, 30). The questions also reveal the need to test the suitability of general ecological theory to microbial systems (35), and to determine how experimental microbial systems can inform and develop ecological theory (36) that has often been derived from or applied to macroorganisms (Prosser *et al.* 2007).

27 How important are multiple infections in driving disease dynamics?
28 What is the role of parasites and mutualists in generating and maintaining host species diversity?
29 How does below-ground biodiversity affect above-ground biodiversity, and *vice versa*?
30 What is the relationship between microbial diversity (functional type, species, genotype) and community and ecosystem functioning?
31 To what extent is macroorganism community composition and diversity determined by interactions with micro-organisms?
32 What is the relative importance of biotic vs. abiotic feedbacks between plants and soil for influencing plant growth?
33 How do symbioses between micro-organisms and their hosts influence interactions with consumers and higher trophic levels?
34 In what ecological settings are parasites key regulators of population dynamics?
35 Do the same macroecological patterns apply to micro-organisms and macroorganisms, and are they caused by the same processes?
36 What can we learn from model communities of micro-organisms about communities of macroorganisms?
37 How does intraspecific diversity contribute to the dynamics of host-parasite and mutualistic interactions?

COMMUNITIES AND DIVERSITY

Some of the most challenging questions in ecology concern communities: sets of co-occurring species. For much of the last century, ecologists have typically interpreted the diversity and composition of communities as the outcome of local-scale processes, both biotic (e.g. competition and predation) and abiotic (e.g. temperature and nutrients). However, some have challenged this view, and emphasize the importance of chance (e.g. Hubbell 2001) and large-scale biogeography and evolutionary history (e.g. Ricklefs 2008) and many issues remain (e.g. 47, 48, 50, 52). Ecologists need to resolve the extent to which the structure and dynamics of ecological communities can be predicted from the traits of their component species (38–40). Understanding the nature and ramifications of the networks of interactions among species remains a major priority (e.g. 41, 42), as does understanding the role of environmental variability through space and time (39, 43, 45). A developing area of emphasis – interfacing with questions listed under the 'ecosystems' heading–is on the functioning of ecological communities in relationship to their diversity, composition and structure. A large body of experimental research has explored these relationships, but most experiments are necessarily restricted to small sets of species, often drawn from a single trophic level. Many important questions about the attributes of 'real' ecological communities in relation to their functioning remain unanswered (e.g. 39, 44, 49).

38 How can we use species' traits as proxies to predict trophic interaction strength?
39 How well can community properties and responses to environmental change be predicted from the distribution of simple synoptic traits, e.g. body size, leaf area?
40 How do species traits influence ecological network structure?
41 When, if ever, can the combined effect of many weak interactions, which are difficult to measure, be greater than the few strong ones we can easily measure?
42 How widespread and important are indirect interactions (e.g. apparent competition, apparent mutualism) in ecological communities?
43 How do spatial and temporal environmental heterogeneity influence diversity at different scales?

44 How does species loss affect the extinction risk of the remaining species?
45 What is the relative importance of stochastic vs. deterministic processes in controlling diversity and composition of communities, and how does this vary across ecosystem types?
46 How do we predict mechanistically how many species can coexist in a given area?
47 To what extent is local species composition and diversity controlled by dispersal limitation and the regional species pool?
48 What are the contributions of biogeographical factors and evolutionary history in determining present day ecological processes?
49 To what extent is primary producer diversity a driver of wider community diversity?
50 How relevant are assembly rules in a world of biological invasion?
51 What is the relative importance of trophic and non-trophic interactions in determining the composition of communities?
52 How important are dynamical extinction-recolonization equilibria to the persistence of species assemblages in fragmented landscapes?
53 Which mechanisms allow the long-term coexistence of grasses and woody plants over a wide range of ecosystems?
54 How do resource pulses affect resource use and interactions between organisms?
55 How important are rare species in the functioning of ecological communities?
56 What is the feedback between diversity and diversification?
57 What are the functional consequences of allelopathy for natural plant communities?

ECOSYSTEMS AND FUNCTIONING

Our understanding of how biotic and abiotic factors drive the functioning of ecosystems has advanced rapidly over the last two decades, in part as a consequence of a growing degree of integration of community-level and ecosystem-level ecology. As such, we now have a much better understanding of how community diversity and composition influence ecosystem processes, the resistance and resilience of ecosystems to environmental perturbations, and feedbacks between the producer and decomposer components of ecosystems. There is also growing awareness of how ecosystems respond to global environmental changes, their capacity to regulate fluxes of carbon and nutrients, and their interactions with the Earth climate system, but challenges remain (e.g. 61, 69, 72). Future challenges for ecosystem science, as reflected in the questions, include being able to make predictions about ecosystems undergoing catastrophic transitions (e.g. 58–60, 71) (Scheffer *et al.* 2009), better understanding the role of spatial scale in driving ecosystem processes (e.g. 63), and extending our rapidly growing knowledge of ecological networks (Bascompte 2009) to study the functioning of ecosystems (e.g. 65). Another major challenge is to better understand the responses of ecosystems to realistic scenarios of biodiversity change through the simultaneous processes of extinction (Cardinale *et al.* 2012) and invasion (Simberloff *et al.* 2012) (e.g. 61–63, 68).

58 Which ecosystems are susceptible to showing tipping points and why?
59 How can we tell when an ecosystem is near a tipping point?
60 Which factors and mechanisms determine the resilience of ecosystems to external perturbations and how do we measure resilience?
61 Which ecosystems and what properties are most sensitive to changes in community composition?
62 How is ecosystem function altered under realistic scenarios of biodiversity change?
63 What is the relative contribution of biodiversity at different levels of organization (genes, species richness, species identity, functional identity, functional diversity) to ecosystem functioning?
64 What are the generalities in ecosystem properties and dynamics between marine, freshwater and terrestrial biomes?
65 How does the structure of ecological interaction networks affect ecosystem functioning and stability?
66 How does spatial structure influence ecosystem function and how do we integrate within and between spatial scales to assess function?
67 How do nutrients other than nitrogen and phosphorus (and iron in the sea) affect productivity in ecosystems?
68 To what extent is biotic invasion and native species loss creating ecosystems with altered properties?
69 Are there globally significant ecosystem functions provided by poorly known ecosystems (e.g. deep oceans, ground water)?
70 Which, if any, species are functionally redundant in the context of stochastic or directional environmental changes?
71 Is hysteresis the exception or the norm in ecological systems?
72 Can we predict the responses of ecosystems to environmental change based on the traits of species?

HUMAN IMPACTS AND GLOBAL CHANGE

It is increasingly recognized that current ecological dynamics and ecosystem function occurs within the context of a human-dominated planet (Marris 2011) and that many ecosystems have been altered and affected by humans since pre-history (Gill *et al.* 2009; Doughty, Wolf & Field 2010). Human impacts on ecosystems include direct impacts on habitats such as land conversion and fire use, habitat modification (such as selective logging or changing in drainage of wetlands), changes in connectivity (fragmentation or globalization) as well as changes in species composition through removal (due to harvesting or pest control) or introduction (accidental or otherwise) of species. These impacts generate many important questions (73–75, 85, 86, 88, 89). Another suite of human impacts is more indirect but perhaps even more pervasive; through our alteration of the climate (both its mean state and variability; IPCC 2007; Hannah 2011) and changes in the biogeochemistry of the atmosphere and oceans (Heimann & Reichstein 2008; Doney *et al.* 2009). These alterations raise questions about what determines how and how fast particular species respond to such change (82, 83), how communities of species interact and respond to change (80, 81, 87), and whether past rates of change can yield insights into likely ecological responses to current and future change (84). Another set of global change ecology questions is centred on how the functioning of the biosphere as a whole is affected by global change, and what role the biosphere plays in the response of the atmosphere to human impacts, through the carbon and water cycles and other major biogeochemical cycles (76–79).

73 What is the magnitude of the 'extinction debt' following the loss and fragmentation of natural habitats, and when will it be paid?

74 What is the role of evolution in recovery from exploitation and responses to other forms of relaxed selection?

75 What are the indirect effects of harvesting on ecosystem structure and dynamics?

76 What are the major feedbacks and interactions between the Earth's ecosystems and the atmosphere under a changing climate?

77 What are the key determinants of the future magnitude of marine and terrestrial carbon sinks?

78 How will atmospheric change affect primary production of terrestrial ecosystems?

79 How will ocean acidification influence primary production of marine ecosystems?

80 To what extent will climate change uncouple trophic links due to phenological change?

81 How do natural communities respond to increased frequencies of extreme weather events predicted under global climate change?

82 In the face of rapid environmental change, what determines whether species adapt, shift their ranges or go extinct?

83 What determines the rate at which species distributions respond to climate change?

84 To what extent can we extrapolate from palaeoecological range shifts to understand 21st-century change?

85 Under what circumstances do landscape structures such as corridors and stepping stones play important roles in the distribution and abundance of species?

86 To what extent will the breakdown of biogeographical barriers (e.g. the more permanent opening of the Northwest Passage) lead to sustained changes in local diversity?

87 How do interspecific interactions affect species responses to global change?

88 What are the ecosystem impacts of world-wide top predator declines?

89 What is the legacy of Pleistocene megafauna extinctions on contemporary ecosystems?

METHODS

Over the past two decades, the practice of ecology has been revolutionized by the development of new technologies, and further developments will continue to be an important stimulus to new research. Important advances include the increase in the availability and speed of computers, new molecular approaches for resolving diversity and dispersal, barcoding techniques that permit rapid identification and even phylogeny building at the community level, the development of new statistical methods (e.g. mixed models and Bayesian statistics, e.g. Bolker *et al.* 2009), monitoring tools such as remote sensing (Asner *et al.* 2008) and geo-tagging of individuals (Block *et al.* 2001). There is also increasing use of citizen science to conduct ecological and evolutionary studies (e.g. Worthington *et al.* 2012).This set of questions reflects on the methods used to conduct research in ecology and the lessons that can be drawn from previous ecological studies, for example whether previous predictions have been successful or erroneous (91, 92, 94). It encompasses new technology (95, 96), as well as the development of new tools and inter-disciplinary links (90, 99, 100). The development of new tools for measuring and monitoring is an important focus (96, 98), and this includes developing methods to model the observation process itself (99).

90 What unexploited theories used by other disciplines could inform ecology, and vice versa?

91 How do we best develop and exploit empirical model systems for understanding natural systems?

92 How successful have past ecological predictions been and why?

93 What is the nature of published ecological errors and how do errors affect academic understanding and policy?

94 How is our understanding of ecology influenced by publication bias?

95 What new technologies would most advance ecological understanding?

96 How do we combine multiple scales and types of monitoring (from field to earth observation) to make robust ecological inferences?

97 To what extent are widely studied ecological patterns (species-abundance distribution, species-area relationship, etc.) the outcomes of statistical rather than ecological processes?

98 What are the most appropriate baselines for determining the magnitude and direction of ecological changes?

99 How much does modelling feedbacks from the observation process, such as the responses of organisms to data collectors, improve our ability to infer ecological processes?

100 How can the feedbacks between human behaviour and ecological dynamics be accounted for in ecological models?

Discussion

KNOWLEDGE GAPS IN ECOLOGY

Collaborative projects to highlight and prioritize unanswered research questions allow researchers to review and reflect on the current state of a discipline, and how it is likely to develop in the future. Our list of 100 unanswered questions includes many that address the nature of fundamental concepts and principles in ecology. For example, some questions reveal profound knowledge gaps regarding the central mechanisms driving ecosystems [61, 63, 64, 75, 76, 77], communities [42, 45, 47, 48, 51], and even population dynamics [11, 19].

All vibrant fields of science have unanswered questions, but are there characteristics of ecology as a discipline that might explain why some large knowledge gaps remain after 100 years of intensive research? One explanation of barriers to progress in ecology maintains that it is a science of middle numbers (Allen & Hoekstra 1992). In small-number systems like the solar system, the relationships between the components, and the state of the system, can often be adequately described by a simple set of equations. In contrast, in large-number systems such as chemical interactions in fluids, the behaviour of the system can usually be adequately described using statistical averages because of the large number of components and the simple nature of their interactions. Ecological systems unfortunately belong to the study of middle numbers: they are too complex to describe individually, yet their components are too few and their interactions too complex to be described by statistical dynamics. Compounding this problem is the long time-scale of ecological dynamics: many interesting phenomena, especially those involving ecosystems, have decadal time-scales making their study difficult and leading to a lack of long-term data. Although great progress has undoubtedly been made in the last 100 years, we must continue the task of observing, experimenting and modelling, anticipating the expected, and unexpected, steady progress and great leaps forward which will result. It would be interesting to repeat this exercise in 10 or 15 years' time to monitor progress.

Ecology has its origins in natural history and early publications tended to be very descriptive and site-specific. Modern ecology has progressed through the incorporation of highly sophisticated numerical methods, as well as becoming underpinned by a set of strong theories. Some of the questions identified here are moderately well understood from a theoretical perspective but require more empirical research. It is instructive to note that volume 1, issue 1 of *Journal of Ecology*, the oldest ecological journal, contained only a single paper that referenced statistics (Smith 1913) and no paper in that first issue of the journal tested a hypothesis. Modern ecology is a hugely collaborative discipline. Many of the questions listed here link to other disciplines within biology including genetics, epidemiology and evolutionary biology. Furthermore, while for clarity we have organized the questions into themes, it is notable that many of the unanswered questions cut across these rather arbitrary divisions.

FUTURE DIRECTIONS

There have been intermittent calls over the decades for the development of a general theory of ecology. The desirability and feasibility of this has been debated extensively (Scheiner & Willig 2005; Roughgarden 2009). We would agree with Loreau (2010) that the way forward is not a single monolithic theory, but increasing the process of merging-related disciplines to generate new principles, perspectives, and questions at the interfaces, thus contributing to the emergence of a new ecological synthesis transcending traditional boundaries. The range of questions presented here reflects the diversity of modern ecology. There is a balance of questions best answered by theoretical approaches, experiment and observation and all these approaches will continue to be important. Global environmental change provides an important context for current ecological research. Much past ecological theory was derived for systems that fluctuated very little around an average state, but global change is leading to both long-term shifts in average conditions as well as potentially dramatic changes in environmental variation. Many of the questions identified are concerned with understanding how systems will respond to such changes.

It is encouraging that there was a general consensus that some areas viewed as hot topics over the last few decades did not need to be included in our list; evidence that the discipline is progressing. It was clear from discussions that questions once considered important had not been definitively answered; but rather that the focus had shifted in the light of improved understanding and experience. If this exercise had been conducted 40 years ago then many of the questions would have involved density dependence and whether or not it was present in the field. Today there is a consensus that density dependence is pervasive, but also that it may take very different forms and sometimes be very hard to detect. Looking back, much of the heat of the discussion involved people misunderstanding each other. Some questions set 25 years ago would have involved the search for dynamical deterministic chaos. We now know that intrinsic and extrinsic (stochastic) forces act together to determine observed dynamics and looking for pure deterministic chaos has little meaning (in as much as weather affects population dynamics all species have chaotic dynamics).

In communities and ecosystems, questions of community equilibria have evolved into questions about resilience and perturbation of communities, or indeed whole ecosystems, and such thinking has been incorporated in the study of phylogenetic diversity patterns through time (e.g. Rabosky & Glor 2010).

CONCLUDING REMARKS

Both the science of ecology and the British Ecological Society have come a long way over the last 100 years. In 1913, the BES was made up of a relatively small group of mostly British scientists with a focus on studying natural history in natural environments. Today, it is a dynamic international organization with members representing academia, industry, education and NGOs, and coming from more than 80 countries. These members conduct pure research, answer applied questions concerning restoration and management, and influence government policy. They work in protected areas as well as farmland, post-industrial landscapes and the urban environment. Despite expanding its initial remit and reaching out far beyond its membership, the science of ecology remains at the heart of the BES. In this paper, a large group of ecologists have prioritized 100 questions they think are the most important remaining questions for the science of ecology to tackle. We do not claim this list to be definitive but hope that it stimulates discussion and exciting new research.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. A list of the 754 submitted questions.