PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2012) **367**, 191–199
doi:10.1098/rstb.2011.0176

Research

Biodiversity in the context of ecosystem services: the applied need for systems approaches

Ken Norris*

Centre for Agri-Environmental Research, University of Reading, Earley Gate, PO Box 237, Reading RG6 6AR, UK

Recent evidence strongly suggests that biodiversity loss and ecosystem degradation continue. How might a systems approach to ecology help us better understand and address these issues? Systems approaches play a very limited role in the science that underpins traditional biodiversity conservation, but could provide important insights into mechanisms that affect population growth. This potential is illustrated using data from a critically endangered bird population. Although species-specific insights have practical value, the main applied challenge for a systems approach is to help improve our understanding of the role of biodiversity in the context of ecosystem services (ES) and the associated values and benefits people derive from these services. This has profound implications for the way we conceptualize and address ecological problems. Instead of focusing directly on biodiversity, the important response variables become measures of values and benefits, ES or ecosystem processes. We then need to understand the sensitivity of these variables to biodiversity change relative to other abiotic or anthropogenic factors, which includes exploring the role of variability at different levels of biological organization. These issues are discussed using the recent UK National Ecosystems Assessment as a framework.

Keywords: biodiversity; ecosystem function; ecosystem services; systems ecology

1. INTRODUCTION

The year 2010 was the International Year of Biodiversity. It served mainly to highlight the ongoing loss of global biodiversity despite commitments to the contrary [1]. A range of pressures and drivers that adversely affect biodiversity continue to worsen. At the same time, limited progress has been made even in areas in which significant public funding has been invested, such as improving the biodiversity value of UK and European agro-ecosystems [2–5]. As a consequence, there are ongoing debates about policy reform and new targets emerging for the future [6].

Over the past decade in particular, we have become increasingly aware of ecosystem loss (a decrease in the spatial extent of an ecosystem) and degradation (a structural change within an ecosystem that adversely affects its function), and the potential implications for ecosystem services (ES) and human well-being [7–9]. The exploitation and management of ecosystems has led to significant increases in provisioning services (food, fuel and fibre), but at the expense of a range of other supporting (e.g. nutrient cycling), regulating (e.g. clean air and water) and cultural services. Human impacts on terrestrial and marine ecosystems are widespread, and ongoing environmental change has implications for ecosystems that are currently remote and sparsely populated. These realizations have led to the concept of multi-functional ecosystems and recognition of the need to quantify and manage trade-offs between ES in relation to drivers of ecosystem change (e.g. land-use change, species exploitation, etc.) [10–12].

Biodiversity loss and ecosystem loss/degradation are inextricably linked. It is well established that biodiversity plays an important functional role in the processes that underpin ES [13–15]. The loss and degradation of ecosystems is a major driver of biodiversity loss. Furthermore, similar sets of pressures and drivers cause biodiversity loss and ecosystem loss/degradation—land-use change, pollution, invasive species, exploitation, etc. These links are increasingly being recognized in the policy arena. For example, at the Nagoya Summit in 2010 signatories of the Convention on Biological Diversity agreed that conservation had to recognize and protect the role that biodiversity plays in ES.

These are clearly major societal issues to which the science community needs to respond. How should we do this? Do we have the approaches we need or are novel ones needed? Are systems approaches likely to be an important part of this response or simply an intellectual luxury we can do without? This paper aims to address these broad questions. It begins by exploring the role systems approaches have or might have in traditional biodiversity science and

*k.norris@reading.ac.uk

One contribution of 16 to a Discussion Meeting Issue 'Predictive ecology: systems approaches'.

conservation. It then goes on to consider biodiversity in the context of ES. For the purposes of this discussion, a systems approach is defined as one in which some characteristics of one level in a hierarchy are explored as emergent properties of processes lower down in the hierarchy. For example, population dynamics as an emergent property of individual-level process; or ecosystem functions as an emergent property of community-level dynamics.

2. BIODIVERSITY SCIENCE AND CONSERVATION

Although community and ecosystem perspectives are becoming increasingly important for biodiversity conservation, population perspectives still play the dominant role. Population status and trends are key components of most biodiversity indicators and the criteria used to assess endangerment [16,17]. As a result, a wide range of population-level approaches are used to provide evidence to inform conservation decisions [18]. These include statistical approaches that link population density or trends to habitat or other variables of conservation interest and demographic models that explore how various human activities might affect population growth or viability through their impacts on demography. While it is always possible to identify key gaps in knowledge or understanding that must affect these approaches to some extent, there are examples of successful conservation action being generated by their use. A classic example is the ongoing recovery of the corncrake (*Crex crex*) population in the UK [19–21].

By comparison, systems approaches have been much less conspicuous in either their use or impact. Most attention has been given to understanding the emergent population consequences of individual-level processes. Applications have included the management of agricultural habitats for biodiversity [22], assessing the impacts of natural resource use on biodiversity [23] and endangered species management [24]. Studies on wild bird populations dominate this area presumably because it is relatively straightforward to obtain the individual-level data needed to parametrize individual-based models for wild populations.

Why have systems approaches played such a limited role? This question is explored in the following section using a case study of a formerly critically endangered bird population. This is a potentially valuable case study example because both more traditional population-level and systems approaches have been applied to the population, and because the conservation issues it faces and its priority are fairly typical of many threatened species.

(a) *Case study. Seychelles magpie robins*

The Seychelles magpie robin (*Copsychus seychellarum*) is an endemic bird species in the Seychelles archipelago in the Indian Ocean. It is believed to have been widespread within the central granitic islands at the onset of continuous human settlement at the end of the eighteenth century, but was reduced to a single relic population on the island of Frégate by the middle of the twentieth century. The population may have been as small as eight individuals in the 1960s.

From 1988 onwards, a programme of research and conservation has seen the population recover from 23 individuals on Frégate to over 120 individuals on five islands in recent years (figure 1*a*) [24,26]. Ecological studies provided the basic evidence to support a package of conservation measures including predator removal, habitat restoration, supplementary feeding, nest-site provision and the translocation of birds to other potentially suitable islands. The Seychelles magpie robin was downlisted from *Critically Endangered* to *Endangered* in 2003 on the basis of the International Union for Conservation of Nature (IUCN) criteria [24].

Despite this apparent success, a number of conservation issues remain—poor breeding success on a number of territories and islands without any obvious deterioration in habitat quality or other problems (e.g. the presence of non-native predators), supplementary feeding strategies and their continuation on Aride Island and a need to assess additional islands for future translocations. All these issues are being addressed using a system approach. Recent work has shown that territorial conflict can significantly reduce breeding success. Magpie robins have a territory-based social system. Each territory consists of a social group composed of a dominant breeding pair plus various numbers of adult subordinates and juveniles from previous breeding attempts. Only the dominant pair is able to breed, so there is aggression between breeding individuals and other adult subordinates for breeding positions. This conflict reduces the frequency of breeding on territories (figure 1*b*) [24]. Furthermore, subordinates are more common on the best-quality territories, increasing territorial conflict and reducing breeding success to levels associated with the poorest quality territories (figure 1*c*) [24,25]. Not surprisingly, territorial conflict has implications for population growth (figure 1*d*) [24]. This is a clear example of how decisions that benefit individuals in the wild can have detrimental population consequences.

Although the further work is clearly needed, what practical value do these insights have as they stand? These studies show that poor breeding success can simply result from social conflict with no other changes in the wider environment. This implies that enhancing the quality of poorer quality territories is likely to reduce conflict in the short term by spreading the conflict more evenly between territories, thereby improving breeding success and population growth. The studies also suggest that providing supplementary food only in the best-quality territories, as currently happens on Aride Island, is likely to exacerbate conflict with detrimental effects on breeding success, which is opposite to the desired impact. A key goal for supplementary feeding strategies, therefore, should be to reduce and not to increase variation in territory quality. The patterns and processes illustrated in figure 1 could also be used to help assess the suitability of additional islands for translocation by using initial data on potential territory qualities to parametrize an individual-based model that is then used to explore potential population growth and viability. Such a model could also be used to explore the value of management options. There is utility, therefore, in using a systems approach in a traditional biodiversity conservation context.

If they have value, why are systems approaches not more widely used to inform biodiversity conservation? The magpie robin case study provides some insights. First, although not extensive, the historical and contemporary data available in the early stages of the programme were sufficient to design remedial management measures. These were then implemented and the population's response monitored to assess its impact. This suggests that systems approaches are not necessarily critical to the design of initial conservation action. Second, the analyses and the modelling shown in figure 1 were based on relatively long-term (i.e. a number of years), individual-based data. Although data requirements will vary depending on the ecological processes being investigated, long-term data were important in the magpie robin case in order to explore territorial conflict and its consequences in space and time. Systems approaches are inevitably more data demanding than the basic ecological approaches typical of conservation biology. Third, the development of a systems approach in the magpie robin programme was driven by individual scientists with relevant knowledge and expertise. This knowledge and expertise are frequently lacking from conservation programmes, suggesting that even when data are potentially available, opportunities to employ systems approaches are likely to be missed.

Despite these issues, the magpie robin is not an isolated example of the application of systems approaches in conservation biology. For example, in group-living mammals, such as the African wild dog (*Lycaon pictus*), there is clear evidence that the behavioural dynamics of individuals in social groups have important implications for population persistence, recovery and management [27–29]. Furthermore, recent modelling work has concluded that understanding the population dynamics of cooperatively breeding species requires the explicit consideration of population structure [30]. Put another way, population dynamics need to be considered as an emergent property of the interactions between individuals.

Taken together, these insights suggest that there is a role for systems approaches in population management for conservation, particularly where answers are required to questions that are difficult or impossible to address in any other way. However, this role will be constrained by available data, knowledge and expertise, and needs to be balanced against the urgency for action. Despite these constraints, there are long-term, individual-based datasets, particularly from vertebrate conservation programmes, that could be more fully explored using a systems approach; there must be a range of opportunities to build in systems thinking and approaches to ongoing conservation management and monitoring programmes; and there is a need to bring a wider range of quantitative skills into conservation biology.

3. BIODIVERSITY IN THE CONTEXT OF ECOSYSTEM SERVICES

(a) *Concepts*

It has long been recognized that biodiversity plays an important functional role in ecosystems [14,31–33]. Recent research has begun to reveal the details of this role, particularly through the use of studies on experimental (e.g. grassland mesocosms) and wild ecosystems (e.g. crop pollination) in which biodiversity and function are relatively straightforward to quantify [34–39]. Nevertheless, there is still much to learn about the quantitative relationships between biodiversity and ecosystem function, leading to calls for further work on the links between biodiversity and ES and scepticism about the relevance of highly contrived ecosystem experiments to the real world [13,40].

In parallel to the science, there have been an increasing number of ecosystem assessments, following the Millennium Ecosystem Assessment (MA) published in 2005 [41]. The MA showed very clearly that ecosystem loss and degradation caused by human activities have favoured some ES (provisioning services) at the expense of others (regulating and cultural services). In so doing, it raised the profile of ecosystems and ES with both decision-makers and the research community. The MA viewed biodiversity loss within a framework of ecosystem function linked to ES. This is a subtle but important shift in emphasis away from the species perspective that has tended to dominate biodiversity science and conservation to date. What implications does this have for the way we should think about systems approaches in biodiversity science and conservation?

The UK National Ecosystems Assessment (NEA) is used as a framework to address this question. The NEA was developed around a conceptual framework in a comparable way to the MA (figure 2). This framework is not intended to act as an ecosystem model with dependencies and feedbacks, but as a basis for recognizing the components of an ecosystem that need to be considered in an assessment. The assessment itself focused on the output of *final ES* from a range of ecosystem types, and the *goods* and their *values* associated with these services. The term 'goods' in this sense means anything that has value, irrespective of whether the value is monetary or non-monetary. The conceptual framework also recognizes that final ES are underpinned by a range of ecosystem processes (figure 2). It also recognizes the functional role played by biodiversity (figure 2).

The way biodiversity is represented in this conceptual framework is, however, misleading. It implies that biodiversity is only really important in terms of the processes that underpin final ES. In fact, biodiversity can be a key part of an *ecosystem process*, a *final ecosystem service* or a *good*. Consider the following examples. The Seychelles magpie robin is an example of biodiversity as a *good*. This is because the birds themselves have conservation value owing to their status as a threatened species. This status may reflect a range of specific 'cultural' values, but the important point is that biodiversity itself (i.e. a living organism) is valued. Contrary to concerns often expressed by the biodiversity conservation community, this example shows that species of conservation value are very much part of an ES framework rather than peripheral to it. Biodiversity can be a final ecosystem service without necessarily being a good. An example of this would be an oilseed rape crop that is then processed to produce rapeseed oil. Finally, biodiversity can be part of several key ecosystem

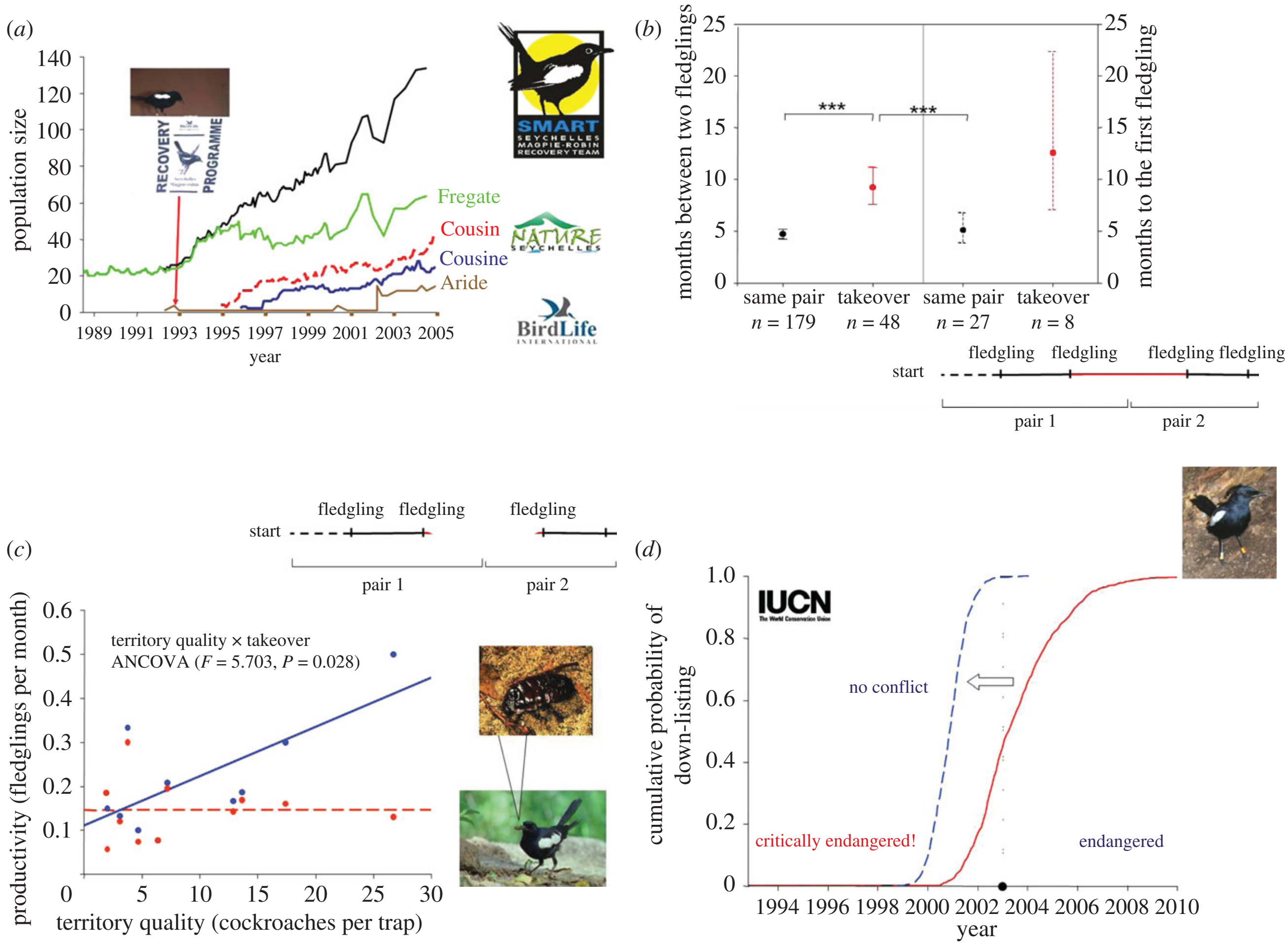

Figure 1. Social conflict and the population dynamics of the Seychelles magpie robin [24,25]. (*a*) Changes in the number of magpie robins between 1989 and 2005. The solid black line shows total population size, and the coloured lines show the population size for specific islands (named at the side of the graph). (*b*) Impact of territory takeovers on reproductive success. Magpie robins produce only a single chick, so the interval between two fledglings is a measure of reproductive output. The timeline in the bottom right-hand corner shows fledgling events through a territory takeover. The graph shows that when a takeover occurred, the interval between successive fledglings significantly increased. The left-hand plot shows the data for all fledglings; the right-hand plot shows only the time interval until the first fledgling was produced by a pair. (*c*) Relationship between territory quality measured as the abundance of an important food resource (cockroaches) and reproductive success. The red symbols and line show all data; the blue symbols and line exclude territory takeovers (as illustrated by the timeline in the top right-hand corner). These relationships are significantly different as shown by the test statistic on the graph. The graph shows that territory takeovers reduce reproductive success on the best-quality territories, so that all territories effectively have the same low levels of reproductive success. This occurs because takeovers reduce breeding success and there is greater social conflict and hence takeovers on the best-quality territories. (*d*) Predicted probability that the population will have grown sufficiently to be down-listed from critically endangered to endangered based on IUCN red-list criteria with and without social conflict and the associated territory takeovers. The graph shows that territory conflict reduces population growth. The predictions are based on an individual-based model parametrized with empirical data from the magpie robin population.

processes without being part of the final ecosystem service or good underpinned by these processes. Drinking water (the good) is an example of this. It is derived from a water supply (the final ecosystem service), which is underpinned by a range of ecosystem processes of which biodiversity is part.

These concepts have several important and related implications for systems thinking in biodiversity science. First, it is perhaps obvious but nevertheless important to state that if we want to explore the relationships between ecosystem processes, services and goods, it is difficult to imagine how we do this without treating it as a complex systems problem. Although this statement is relatively obvious, exactly how we should address the complexities in the context of a changing environment is less clear. Ecosystem science typically uses trophic structuring to explore the role of biodiversity in ecosystem processes [43]. What is less typical is to consider ecosystem processes, such as the flow of nutrients, as an emergent property of the dynamics of the population and communities involved. Recent work has begun to show that changes in these dynamics can have a demonstrable impact on ecosystem function [44]. This suggests that we need to move away from thinking of an ecosystem as a series of boxes linked by functions that describe the relationships between them, to a more dynamical representation in which certain properties or functions of an ecosystem are considered as emergent properties of the underlying population and community dynamics.

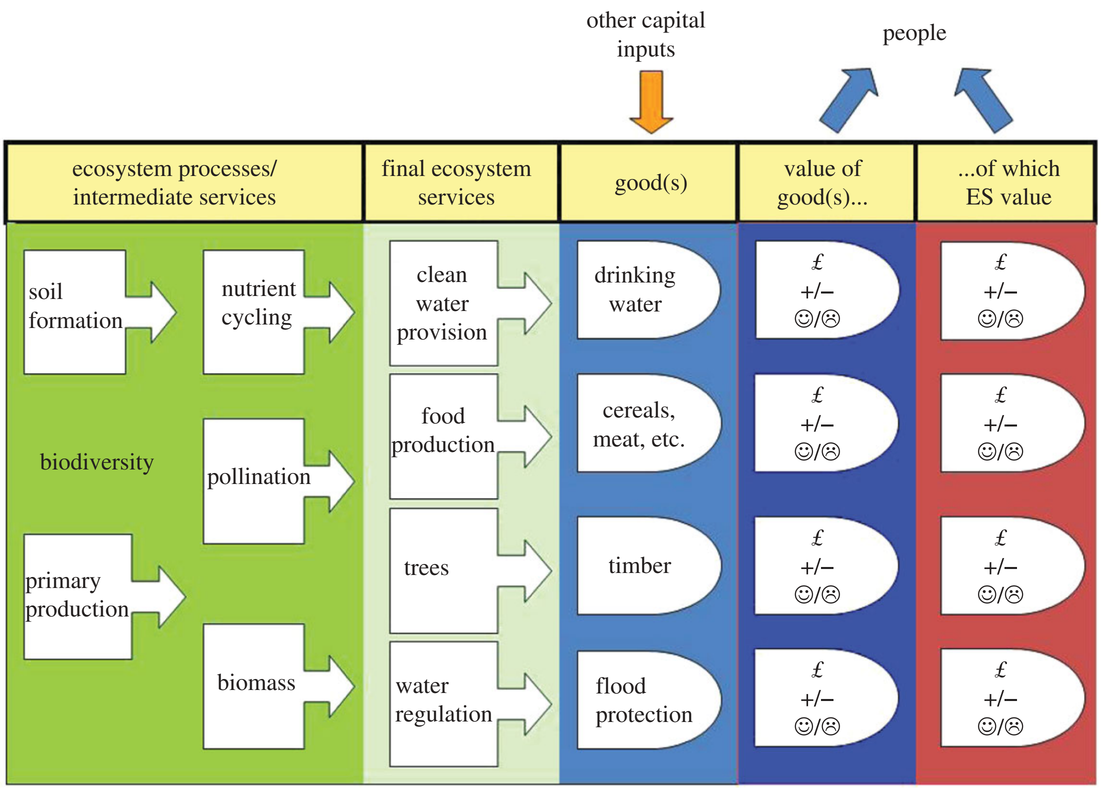

Figure 2. Part of the conceptual framework developed for the UK National Ecosystem Assessment (NEA). The diagram illustrates the links between *ecosystem processes*, *ecosystem services* (ES) and the *goods* and *values* people derive from these services. The term 'good' is used to identify anything derived from ES that has value to people, irrespective of the type of value involved. Goods are not necessarily just dependent on ES, but also other capital inputs (see text for examples). The value of goods can be monetary (£) or non-monetary (☺/☹). To value ES appropriately requires values to be partitioned into those attributable to other capital inputs and those attributable to ES. The functional role of biodiversity is recognized in the left-hand panel of the diagram, although this represents part of its role within the framework (see text). The framework was adapted from Fisher & Turner [42].

This view opens up a much richer array of biodiversity–ecosystem function questions than we currently address. At present, the biodiversity–ecosystem function literature focuses on variability at the species-level [14,45], but it is not necessarily the case that function is most sensitive to variability at this level. Recent work has shown that changes in individual traits within populations can affect ecosystem function [44]. This raises important questions about the sensitivity of ecosystem function to variation at different levels of biological organization, and how variation at different levels affects the resilience of ecosystem function to environmental change.

Second, the response variables of interest may not necessarily be measures of biodiversity. It might be more appropriate to consider chemical, physical, economic or social endpoints rather than biodiversity *per se*. In ecology, systems approaches are often considered as a means to explore interactions across levels of biological organization—for example, the population consequences of individual-level processes [22–24,46]. In this sense, the important response variables are always measurements related to some aspect of biodiversity, such as a vital rate or population growth. In the wider context of ES, this might not necessarily be the case.

Third, in the context of ES, the main goal of biodiversity science becomes to understand the sensitivity of response variables to biodiversity change relative to other factors including the abiotic environment and human processes [47]. Where the response variable is a measurement related to some aspect of biodiversity (e.g. population size and population growth), it is likely that ecology will play the dominant role; but where the response variable is a non-biodiversity measure, the science becomes inherently multidisciplinary. The latter requires a regime shift in the way biodiversity science is done. It is interesting to note that the biodiversity research community has focused to a large extent on ecosystem functions in which biodiversity plays a dominant role (e.g. primary productivity, pollination, pests and diseases) [35,36,38,48]. By contrast, the biodiversity community is much less involved than it should be in certain key areas of ecosystem science, such as major biogeochemical cycles, the water cycle and biosphere–atmosphere interactions that underpin a wide range of ES.

(b) *Concerns, gaps and emerging activities*

Viewing biodiversity in the context of ES is clearly challenging. A major concern about addressing the complexities involved is the importance of stochasticity in ecological systems. Unlike other areas of science in which a systems approach has been developed

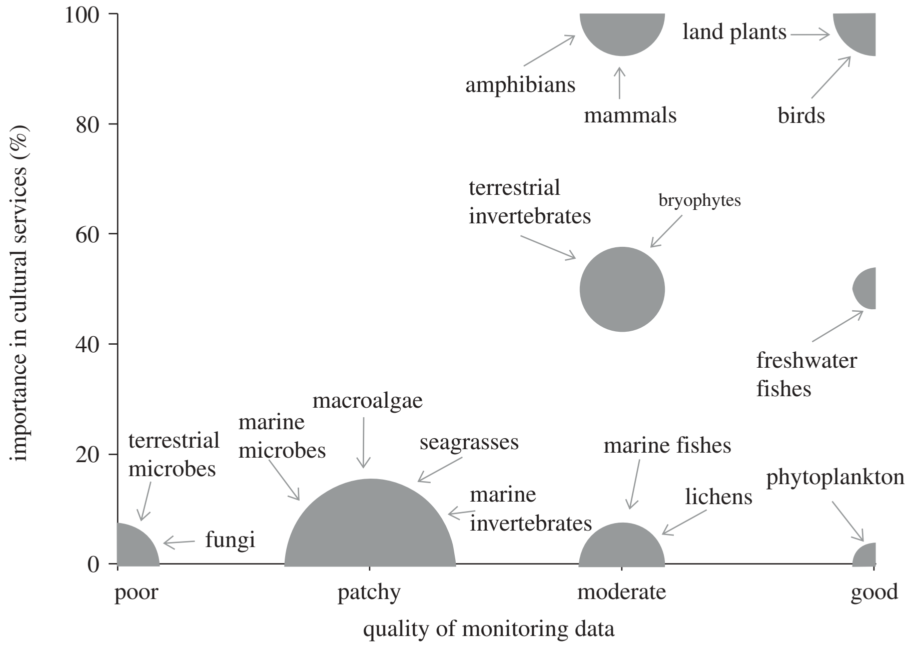

Figure 3. The relationship between the quality of biodiversity monitoring data in the UK and the importance of each biodiversity group in the cultural services examined by the UK National Ecosystems Assessment (NEA). Biodiversity groupings represent those recognized by biodiversity monitoring programmes in the UK. The status and trend information available in the UK for each biodiversity group were classified as 'good' (UK-wide data on distribution, abundance and population trends over a 20-year or more time period), 'moderate' (UK-wide data on distribution, but limited data on abundance and population trends owing to spatial or temporal coverage), 'patchy' (only localized data available on distribution or trends) or 'poor' (negligible data available on distribution or trends). The y-axis represents the percentage of cultural services for which each biodiversity group was assessed as having high importance using a simple scale of low, medium or high. Both the quality of monitoring data and the importance of each biodiversity group in cultural services were assessed by a team of experts. The size of the circles represents the number of biodiversity groups associated with each point. The relationship can be described by the simple linear model: $y = a + bx$, in which x takes integer values from 1 (poor) to 4 (good). This model is statistically significant ($R^2_{adj} = 0.30$, $p = 0.016$).

around a core of essentially deterministic chemical or physical relationships, the individuals, populations and communities that make up ecosystems are affected by a wide range of stochastic processes owing to environmental variation. This stochasticity inevitably means there will be uncertainties in how processes at one level of organization (e.g. individual decisions) might affect processes at another (e.g. population demography and growth). It is important, however, to recognize the distinction between stochastic dynamics in an essentially stable system and the substantial changes in the state of a system experiencing environmental change. It is now well established that the loss (or decline) of biodiversity in response to environmental change (e.g. habitat loss and exploitation) is remarkably deterministic. Habitat loss or degradation disproportionately affects species that are habitat specialists [49]; exploitation disproportionately affects relatively large-bodied species with slow life histories [50]. Traits at various levels of organization, therefore, provide insights into how communities might respond to environmental change and also the potential functional consequences [51,52]. Uncertainties owing to stochasticity may be less important than we might otherwise think.

Understanding the sensitivity of ecosystem processes, services or goods to biodiversity change is hampered by fundamental gaps in our knowledge and understanding. One of these is our knowledge about biodiversity change itself. The NEA examined the quality of monitoring data on status and trends for a range of biodiversity groups in the UK and found that data quality was correlated with cultural importance (figure 3). Better quality data are available for biodiversity groups that have cultural value. It is tempting to speculate that the interests of the biodiversity research community also reflect this cultural bias, at least to some extent. The corollary of this is that we have little information on the status and trends of micro-organisms, fungi, lower plants and micro-invertebrates that play important roles in the basic processes (e.g. nutrient cycling, decomposition, etc.) supporting all ecosystems. This is a major gap that needs to be addressed.

Finally, ES are recognized because of the values and benefits people derive from them. This means that people are affected by changes in ES, but also modify ES through the decisions they make. The need to understand ecosystems as coupled socio-ecological systems has been recognized for some time [12,53], and conceptual frameworks being developed around an ecosystems approach include feedbacks between people and ecosystems [54]. Nevertheless, there are still relatively few examples of studies that treat people as an integral part of the system in biodiversity and ecosystem science. Developments in the social sciences provide opportunities to improve this integration [55].

There is evidence that the research community is responding to the above challenges. Ambitious integrated research programmes are developing. Examples include the Stability of Altered Forest Ecosystems (SAFE) project in South East Asia (www.safeproject.net) and the National Ecological Observatory Network (NEON) in the USA (www.neoninc.org). There is a need to extend these approaches to other ecosystems and regions. In doing so, we need to be mindful of key gaps in our knowledge (e.g. previous paragraph) and consistent in our approach (e.g. in the properties of ecosystems we measure). Research funding organizations are also responding through new ecosystem scale programmes such as the Biodiversity and Ecosystem Service Sustainability (BESS) programme sponsored by the Natural Environment Research Council (NERC) in the UK (www.nerc.ac.uk/research/programmes/bess/) and the Macrosystems Biology programme sponsored by the National Science Foundation (NSF) in the USA (www.nsf.gov/pubs/2010/nsf10555/nsf10555.htm). Finally, in developing future activities, we have to guard against the temptation to re-badge existing activities where these offer neither the scale nor level of integration required to move the science forwards.

4. CONCLUSIONS

Are systems approaches important, or likely to be important, in biodiversity science? The available evidence suggests that the properties of a particular level in an ecological hierarchy are an emergent property of processes occurring at lower levels. Put simply, the traits of individuals, and the way these vary in space and time, have consequences that are propagated through ecosystems. They affect the populations of which they are part, and the wider ecosystem within which their populations occur. As the environment changes, these individual traits, as well as other components of the system, change; this in turn has a series of consequences for populations, communities and the wider ecosystem. It is clear from this argument that a mechanistic understanding of biodiversity change and its consequences for ES can only be addressed using systems approaches [45].

Given this argument, why is a systems approach less evident in biodiversity science than it should be? A major reason for this is that biodiversity science has been largely retrospective to date; attempting to understand how and why biodiversity has been lost in the recent past, and how we might halt and reverse these losses. In this context, the past is a useful guide to what might happen in the future in response to conservation interventions targeted in particular at individual or small groups of species. This is very different to understanding how multiple, concurrent future changes in the environment might impact on biodiversity and ES owing to the complex nature of the interactions involved, the need to embed human behaviour in our understanding and because future environmental conditions may be novel, limiting the value of past observations. It is in this prospective sense that system approaches have potential utility. Realizing this potential will be challenging, but ecology needs to embrace the complexities involved rather than simplify them into abstraction. This is critically important if we are to tackle applied problems relating to biodiversity and ES, not least because the functional consequences of variability at different levels of biological organization are likely to be key to understanding the resilience of ecosystems to environmental change.

REFERENCES

1 Butchart, S. H. M. *et al.* 2010 Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168. (doi:10.1126/science.1187512)

2 Butler, S. J., Brooks, D., Feber, R. E., Storkey, J., Vickery, J. A. & Norris, K. 2009 A cross-taxonomic index for quantifying the health of farmland biodiversity. *J. Appl. Ecol.* **46**, 1154–1162. (doi:10.1111/j.1365-2664.2009.01709.x)

3 Butler, S. J., Vickery, J. A. & Norris, K. 2007 Farmland biodiversity and the footprint of agriculture. *Science* **315**, 381–384. (doi:10.1126/science.1136607)

4 Kleijn, D. *et al.* 2006 Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* **9**, 243–254. (doi:10.1111/j.1461-0248.2005.00869.x)

5 Kleijn, D. & Sutherland, W. J. 2003 How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* **40**, 947–969. (doi:10.1111/j.1365-2664.2003.00868.x)

6 Rands, M. R. W. *et al.* 2010 Biodiversity conservation: challenges beyond. *Science* **329**, 1298–1303. (doi:10.1126/science.1189138)

7 Balmford, A. & Bond, W. 2005 Trends in the state of nature and their implications for human well-being. *Ecol. Lett.* **8**, 1218–1234. (doi:10.1111/j.1461-0248.2005.00814.x)

8 Carpenter, S. R. *et al.* 2009 Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. *Proc. Natl Acad. Sci. USA* **106**, 1305–1312. (doi:10.1073/pnas.0808772106)

9 Mooney, H. A., Cropper, A. & Reid, W. 2004 The Millennium Ecosystem Assessment: what is it all about? *Trends Ecol. Evol.* **19**, 221–224. (doi:10.1016/j.tree.2004.03.005)

10 Chan, K. M. A., Shaw, M. R., Cameron, D. R., Underwood, E. C. & Daily, G. C. 2006 Conservation planning for ecosystem services. *PLoS Biol.* **4**, 2138–2152. (doi:10.1371/journal.pbio.0040379)

11 Foley, J. A. *et al.* 2005 Global consequences of land use. *Science* **309**, 570–574. (doi:10.1126/science.1111772)

12 Kareiva, P., Watts, S., McDonald, R. & Boucher, T. 2007 Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science* **316**, 1866–1869. (doi:10.1126/science.1140170)

13 Raffaelli, D. G. 2006 Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Mar. Ecol. Prog. Ser.* **311**, 285–294. (doi:10.3354/meps311285)

14 Hooper, D. U. *et al.* 2005 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35. (doi:10.1890/04-0922)

15 EASAC 2009 Ecosystem services and biodiversity in Europe. EASAC policy report 09. European Academies Science Advisory Council. See http://www.easac.eu/fileadmin/PDF_s/reports_statements/Ecosystems.pdf.

16 Balmford, A., Green, R. E. & Jenkins, M. 2003 Measuring the changing state of nature. *Trends Ecol. Evol.* **18**, 326–330. (doi:10.1016/S0169-5347(03)00067-3)

17 Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akcakaya, H. R., Leader-Williams, N.,

Milner-Gulland, E. J. & Stuart, S. N. 2008 Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* **22**, 1424–1442. (doi:10.1111/j.1523-1739.2008.01044.x)

18 Norris, K. 2004 Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *J. Appl. Ecol.* **41**, 413–426. (doi:10.1111/j.0021-8901.2004.00910.x)

19 Green, R. E. 1996 Factors affecting the population density of the corncrake *Crex crex* in Britain and Ireland. *J. Appl. Ecol.* **33**, 237–248. (doi:10.2307/2404746)

20 Green, R. E. & Stowe, T. J. 1993 The decline of the corncrake *Crex crex* in Britain and Ireland in relation to habitat change. *J. Appl. Ecol.* **30**, 689–695. (doi:10.2307/2404247)

21 Green, R. E., Tyler, G. A., Stowe, T. J. & Newton, A. V. 1997 A simulation model of the effect of mowing of agricultural grassland on the breeding success of the corncrake (*Crex crex*). *J. Zool.* **243**, 81–115. (doi:10.1111/j.1469-7998.1997.tb05758.x)

22 Butler, S. J., Mattison, E. H. A., Glithero, N. J., Robinson, L. J., Atkinson, P. W., Gillings, S., Vickery, J. A. & Norris, K. 2010 Resource availability and the persistence of seed-eating bird populations in agricultural landscapes: a mechanistic modelling approach. *J. Appl. Ecol.* **47**, 67–75. (doi:10.1111/j.1365-2664.2009.01750.x)

23 Stillman, R. A. *et al.* 2001 Predicting shorebird mortality and population size under different regimes of shellfishery management. *J. Appl. Ecol.* **38**, 857–868. (doi:10.1046/j.1365-2664.2001.00644.x)

24 Lopez-Sepulcre, A., Norris, K. & Kokko, H. 2009 Reproductive conflict delays the recovery of an endangered social species. *J. Anim. Ecol.* **78**, 219–225. (doi:10.1111/j.1365-2656.2008.01475.x)

25 Lopez-Sepulcre, A., Kokko, H. & Norris, K. 2010 Evolutionary conservation advice for despotic populations: habitat heterogeneity favours conflict and reduces productivity in Seychelles magpie robins. *Proc. R. Soc. B* **277**, 3477–3482. (doi:10.1098/rspb.2010.0819)

26 Norris, K. & McCulloch, N. 2003 Demographic models and the management of endangered species: a case study of the critically endangered Seychelles magpie robin. *J. Appl. Ecol.* **40**, 890–899. (doi:10.1046/j.1365-2664.2003.00840.x)

27 Gusset, M., Jakoby, O., Muller, M. S., Somers, M. J., Slotow, R. & Grimm, V. 2009 Dogs on the catwalk: modelling re-introduction and translocation of endangered wild dogs in South Africa. *Biol. Conserv.* **142**, 2774–2781. (doi:10.1016/j.biocon.2009.07.007)

28 Gusset, M., Slotow, R. & Somers, M. J. 2006 Divided we fail: the importance of social integration for the re-introduction of endangered African wild dogs (*Lycaon pictus*). *J. Zool.* **270**, 502–511. (doi:10.1111/j.1469-7998.2006.00168.x)

29 Somers, M. J., Graf, J. A., Szykman, M., Slotow, R. & Gusset, M. 2008 Dynamics of a small re-introduced population of wild dogs over 25 years: allee effects and the implications of sociality for endangered species' recovery. *Oecologia* **158**, 239–247. (doi:10.1007/s00442-008-1134-7)

30 Bateman, A. W., Coulson, T. & Clutton-Brock, T. H. 2011 What do simple models reveal about the population dynamics of a cooperatively breeding species? *Oikos* **120**, 787–794. (doi:10.1111/j.1600-0706.2010.18952.x)

31 Palumbi, S. R. *et al.* 2009 Managing for ocean biodiversity to sustain marine ecosystem services. *Front. Ecol. Environ.* **7**, 204–211. (doi:10.1890/070135)

32 Worm, B. *et al.* 2006 Impacts of biodiversity loss on ocean ecosystem services. *Science* **314**, 787–790. (doi:10.1126/science.1132294)

33 Benayas, J. M. R., Newton, A. C., Diaz, A. & Bullock, J. M. 2009 Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* **325**, 1121–1124. (doi:10.1126/science.1172460)

34 Diaz, S., Fargione, J., Chapin, F. S. & Tilman, D. 2006 Biodiversity loss threatens human well-being. *PLoS Biol.* **4**, 1300–1305. (doi:10.1371/journal.pbio.0040277)

35 Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. 2001 Diversity and productivity in a long-term grassland experiment. *Science* **294**, 843–845. (doi:10.1126/science.1060391)

36 Tilman, D., Reich, P. B. & Knops, J. M. H. 2006 Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632. (doi:10.1038/nature04742)

37 Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. & Tscharntke, T. 2007 Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* **274**, 303–313. (doi:10.1098/rspb.2006.3721)

38 Kremen, C. *et al.* 2007 Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* **10**, 299–314. (doi:10.1111/j.1461-0248.2007.01018.x)

39 Kremen, C., Williams, N. M., Bugg, R. L., Fay, J. P. & Thorp, R. W. 2004 The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.* **7**, 1109–1119. (doi:10.1111/j.1461-0248.2004.00662.x)

40 Srivastava, D. S. & Vellend, M. 2005 Biodiversity-ecosystem function research: is it relevant to conservation? *Annu. Rev. Ecol. Evol. Syst.* **36**, 267–294. (doi:10.1146/annurev.ecolsys.36.102003.152636)

41 Millennium Ecosystem Assessment 2005 *Ecosystems and human well-being, synthesis*. Washington, DC: Island Press.

42 Fisher, B. & Turner, R. K. 2008 Ecosystem services: classification for valuation. *Biol. Conserv.* **141**, 1167–1169. (doi:10.1016/j.biocon.2008.02.019)

43 Hairston, N. G. 1993 Cause-effect relationships in energy-flow, trophic structure, and interspecific interactions. *Am. Nat.* **142**, 379–411. (doi:10.1086/285546)

44 Bassar, R. D. *et al.* 2010 Local adaptation in Trinidadian guppies alters ecosystem processes. *Proc. Natl Acad. Sci. USA* **107**, 3616–3621. (doi:10.1073/pnas.0908023107)

45 Loreau, M. 2010 Linking biodiversity and ecosystems: towards a unifying ecological theory. *Phil. Trans. R. Soc. B* **365**, 49–60. (doi:10.1098/rstb.2009.0155)

46 Sutherland, W. J. & Norris, K. 2002 Behavioural models of population growth rates: implications for conservation and prediction. *Phil. Trans. R. Soc. Lond. B* **357**, 1273–1284. (doi:10.1098/rstb.2002.1127)

47 Luck, G. W. *et al.* 2009 Quantifying the contribution of organisms to the provision of ecosystem services. *Bioscience* **59**, 223–235. (doi:10.1525/bio.2009.59.3.7)

48 Keesing, F., Holt, R. D. & Ostfeld, R. S. 2006 Effects of species diversity on disease risk. *Ecol. Lett.* **9**, 485–498. (doi:10.1111/j.1461-0248.2006.00885.x)

49 Owens, I. P. F. & Bennett, P. M. 2000 Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl Acad. Sci. USA* **97**, 12 144–12 148. (doi:10.1073/pnas.200223397)

50 Jennings, S., Greenstreet, S. P. R. & Reynolds, J. D. 1999 Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* **68**, 617–627. (doi:10.1046/j.1365-2656.1999.00312.x)

51 Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K. & Robson, M. 2007 Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl Acad. Sci. USA* **104**, 20 684–20 689. (doi:10.1073/pnas.0704716104)

52 Sekercioglu, C. H., Daily, G. C. & Ehrlich, P. R. 2004 Ecosystem consequences of bird declines. *Proc. Natl Acad. Sci. USA* **101**, 18 042–18 047. (doi:10.1073/pnas.0408049101)

53 Tallis, H. M. & Kareiva, P. 2006 Shaping global environmental decisions using socio-ecological models. *Trends Ecol. Evol.* **21**, 562–568. (doi:10.1016/j.tree.2006.07.009)

54 Rounsevell, M. D. A., Dawson, T. P. & Harrison, P. A. 2010 A conceptual framework to assess the effects of environmental change on ecosystem services. *Biodivers. Conserv.* **19**, 2823–2842. (doi:10.1007/s10531-010-9838-5)

55 Rounsevell, M. D. A., Robinson, D. T. & Murray-Rust, D. 2012 From actors to agents in socio-ecological systems models. *Phil. Trans. R. Soc. B* **367**, 259–269. (doi:10.1098/rstb.2011.0187)