Improved probability of detection of ecological "surprises"

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Ecological "surprises" are defined as unexpected findings about the natural environment. They are critically important in ecology because they are catalysts for questioning and reformulating views of the natural world, help shape assessments of the veracity of a priori predictions about ecological trends and phenomena, and underpin questioning of effectiveness of resource management. Despite the importance of ecological surprises, major gaps in understanding remain about how studies might be done differently or done better to improve the ability to identify them. We outline the kinds of ecological surprises that have arisen from long-term research programs that we lead in markedly different ecosystems around the world. Based on these case studies, we identify important lessons to guide both existing studies and new investigations to detect ecological surprises more readily, better anticipate unusual ecological phenomena, and take proactive steps to plan for and alleviate "undesirable" ecological surprises. Some of these lessons include: (*i*) maintain existing, and instigate new, long-term studies; (*ii*) conduct a range of kinds of parallel and concurrent research in a given target area; (*iii*) better use past literature and conceptual models of the target ecosystem in posing good questions and developing hypotheses and alternative hypotheses; and (*iv*) increase the capacity for ecological research to take advantage of opportunities arising from major natural disturbances. We argue that the increased anticipatory capability resulting from these lessons is critical given that ecological surprises may become more prevalent because of climate change and multiple and interacting environmental stressors.

discovery

Ecological "surprises" can be defined as unexpected findings about the natural environment (1–3). At the outset of every ecological investigation, a researcher will have a set of ideas or hypotheses about what is likely to happen, as well as a set of ideas of what is not likely. An ecological surprise occurs when what is found is outside of these two idea sets and, as we outline here, this surprise can lead to a fundamental shift in an ecological paradigm (4–6). Ecological surprises have been found in experiments and observations in many types of ecology (ecosystem, community, population ecology) as well as in many kinds of ecosystems: terrestrial, aquatic, and atmospheric (7–9).

Much has been written about ecological surprises, including recent developments on statistical aspects of data analysis and modeling (e.g., refs. 10, 11) as well as a broad classification of different kinds of dynamic-, pattern-, and intervention-based surprises (12). Yet major gaps in understanding remain about how ecological studies might be done differently or done better to improve the ability to identify and anticipate ecological surprises. Clearly, being able to anticipate a surprise is an oxymoron (as it contravenes the very definition of the term surprise), yet several authors have rightly called for ecologists to continue to develop new ways of better anticipating, predicting, and preparing for ecological surprises (e.g., refs. 9, 11, 13). This perceived need occurs because ecological surprises (*i*) provide one of the catalysts for questioning and reformulating views of the natural world and, at their strongest, promote a paradigm shift (12, 14); (*ii*) often are the trigger for subsequent studies that can lead to significant scientific discoveries (14); (*iii*) help shape assessments of the veracity of a priori predictions about ecological trends and phenomena, including the existence of tipping points or ecological thresholds (*sensu* refs. 15, 16); and (*iv*) underpin questioning of the validity and effectiveness of resource management activities like particular kinds of management interventions. Improved understanding and detecting of ecological surprises is also essential for developing human organizations and institutional arrangements that can better respond to unanticipated future events in positive ways (1).

Given the importance of surprises in ecology, we briefly outline the kinds of ecological surprises that have arisen from four long-term research programs we lead. These case studies are very different in nature and execution and have taken place in markedly different ecosystems around the world. Based on these case studies, we then draw together seven important lessons that might be used to guide existing studies and new investigations to detect ecological surprises more readily, better anticipate unusual ecological phenomena, and take proactive steps to plan for and alleviate "undesirable" ecological surprises. Our overarching aim is to identify and provide the kinds of studies that lead to an increased anticipatory capability in ecology, environmental science, and natural resource management. We believe that such an anticipatory capability is critical given that the prevalence of ecological surprises is predicted to increase as a consequence of climate change (17) and from the effects of multiple and interacting environmental stressors (9, 18). In addition, some ecological surprises are the unintended outcomes of management actions gone awry, and hence an enhanced anticipatory capability is important to resolving such problems (12).

Surprises Versus Discoveries

As outlined earlier, we consider ecological surprises to be unexpected findings or outcomes that are well outside what is expected to happen or not happen and will sometimes lead to a major paradigm shift. Ecological surprises may often arise from pure serendipity (14).

In contrast, and for the purposes of this article, we consider an ecological discovery to be an insight that provides considerable new ecological understanding and that confirms what was hypothesized or postulated to occur. An ecological discovery will therefore often result from carefully executed science like a prolonged series of experiments or other kinds of tests. A discovery may lead to a surprise, although this is uncommon, whereas a discovery may start with a surprise (as in the case of

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the highly unexpected acidity of rainfall at the Hubbard Brook Experimental Forest; *Case Study 1*) but then require many years of scientific study to elucidate the underlying ecological mechanisms (examples in other locations detailed later).

Although we have distinguished between discoveries and surprises, we are acutely aware that there can be a continuum between them. In addition, there is a temporal dimension to the distinction between an ecological surprise and an ecological discovery. For example, the first detection of acid rain at Hubbard Brook Experimental Forest (*Case Study 1*) is an example of a true ecological surprise. However, now that it is well known, subsequent studies, for example in other locations, that find acid rain would be classified as discoveries.

Case Studies

In the following section, we briefly outline examples of ecological surprises from four major research programs that are very different in nature and execution and which have taken place in markedly different ecosystems around the world. These case studies are a prelude to a series of lessons for the design and implementation of investigations that we argue can promote the chances of ecological surprises being identified.

Case Study 1: Hubbard Brook Ecosystem Study, Northeastern United States. The Hubbard Brook Ecosystem Study is a multifaceted research program that has been running for nearly five decades in the northern hardwood forests in the White Mountains of New Hampshire, United States. A focus of the work has been on biogeochemical flux and cycling. Two major surprises among several resulting are discussed. The first was pure serendipity: the initial sample of rain (collected in July 1963) was very highly acidic (pH 3.7) (6). Decades of monitoring were then required to determine the long-term trend in precipitation acidity (19), to learn the reason for the acidity, whether it was unusual, and what the ecological effects were. A second surprise was that these forests in the White Mountains had stopped growing and, in fact, had begun to decline, thereby releasing rather than sequestering CO_2 to the atmosphere. Decades of acid rain that had fallen at the Hubbard Brook Experimental Forest had leached massive amounts of calcium and other base cations from the forest soil (6, 20, 21). The leaching reduced these vital nutrients in the root zone, reduced the buffering capacity, and made the ecosystem more sensitive to the continuing inputs of acid precipitation (21–24).

Case Study 2: Kluane Boreal Forest Ecosystem Study, Yukon, Canada. The Kluane Boreal Forest Ecosystem Study has been under way in the southwestern Yukon since 1973 (25), and two major surprises stand out. The first ecological surprise was that the red squirrel (*Tamiasciurus hudsonicus*) and Arctic ground squirrel (*Spermophilus parryii*) can be major predators of juveniles of the snowshoe hare (*Lepus americanus*) during the hares' first 2 wks of life (25). These squirrels are typically thought of as herbivores, and this finding produced another kink in the food web and added another set of predators to the already extensive list of species that prey upon the snowshoe hare in boreal forest. During the first 2 wks of life, 82% of juvenile hare losses were caused by predation, and red squirrels and ground squirrels accounted for a minimum of 58% of these losses (25). The second surprise was that adding food and restricting mammalian predation led to a 10-fold increase in hare density on a 1-km^2 plot, an effect much stronger than that produced by single factor manipulations of adding food alone or reducing predation alone. This surprise indicated an interaction between food supplies and predation, but signs of food shortage in hares could not be found. The answer appeared to lie in how feeding high-quality rabbit food to hares could reduce predation risk. Hares move less when provided with accessible high-quality food. This reduced predation risk, which, in turn, had effects on survival and reproduction (25). Predators thus have direct effects on survival and indirect effects on reproduction via predation risk. The interaction between food and predation in this experiment is not a direct result of food shortage but an indirect effect through predation risk.

Case Study 3: Wet Forest Biodiversity Study, Victoria, Southeastern Australia. Work in the montane ash forests of the Central Highlands of Victoria, Australia, has examined a wide range of research questions since 1983 (26). A key part of the work has centered on the abundance, condition, and population dynamics of large diameter cavity trees, which are the sole nesting and denning sites for an array of species of hollow-dependent vertebrates, including a species-rich assemblage of arboreal marsupials. Two major ecological surprises are outlined. The first was that individual arboreal marsupials occupied as many as 20 different trees with hollows within a given 18-mo period, and it was possible to predict intertree movements on any given day (27). Neither past extensive literature nor natural history gave a hint of this result, especially as previous studies had indicated that animals have specific requirements for particular kinds of trees with hollows and many species construct complex nests in these trees (28). Indeed, it was widely believed that any given individual animal selected a single hollow tree or only a small number of such trees for denning, nesting, or both. A second major surprise was that large cavity trees contributed significantly to the carbon storage capacity of montane ash forests, with some measured sites supporting more than 2,000 tons of above-ground carbon biomass per hectare. These are the highest values for any forest in the world (29) and they indicated that the default average carbon biomass values for temperate forests may have been underestimated by as much as 30% (29). Furthermore, forests with a history of wildfire had the greatest values for above-ground biomass. This was found because burnt and killed trees remained standing and subsequent regenerating young stands created two major cohorts of trees that together significantly increased levels of above-ground carbon biomass (29).

Case Study 4: Serpentine Grassland Dynamics Study, Northern California. A study of serpentine grassland dynamics in northern California commenced in 1983 to examine the impacts of faunal disturbance and herbivory. A series of replicated plots was established including areas fenced to exclude above-ground mammalian herbivores (predominantly rabbits and deer), other areas fenced to exclude fossorial mammals (pocket gophers), and control areas open to both. The first major surprise was the highly variable and spatially contiguous nature of the disturbance caused by gophers. Earlier results indicated that gopher disturbance was relatively ubiquitous and led to distinct vegetation patterning (30). However, long-term work revealed that disturbance rates varied greatly from year to year and also spatially (31). This result led to very uneven disturbance impacts between plots, and this problem was further exacerbated by the inability of the exclosures to exclude gophers for more than a few years. In addition, an unexpectedly strong interaction between gophers and above-ground herbivores meant that the above-ground exclosures were subject to considerably more gopher disturbance than the control plots. Hence, the experimental treatments provided a variation in level and frequency of disturbance rather than clear exclosure effects per se. A second major surprise was the large variation in relative abundances of the constituent plant species over time. Nearly all species showed dramatic variations in abundance, with extreme examples of species that were relatively rare early in the study reaching high abundance levels in subsequent periods. Because of the dramatic differences in species abundances from year to year, early observational and modeling studies

(30, 32) provided, at best, only a partial picture of the overall grassland dynamics.

"Increasing the Odds:" Ways to Improve the Probability of Detecting Ecological Surprises

We have touched briefly upon a small subset of the more notable ecological surprises that have arisen in each of four long-term research programs we lead. Some of these surprises were pure serendipity, whereas others resulted from careful experimentation, careful observation, or both. Nevertheless, we believe the four case studies have some common attributes that increased the chances of ecological surprises being detected. Based on this concordance, we outline below seven key lessons on how ecological studies might be done to increase the probability of detecting surprises and hence better position such studies in times of increasing environmental uncertainty. We present these lessons separately, although it is clear that some—like the posing of good scientific questions, the maintenance of long-term studies, and the value of multifaceted research programs—will often be strongly interlinked.

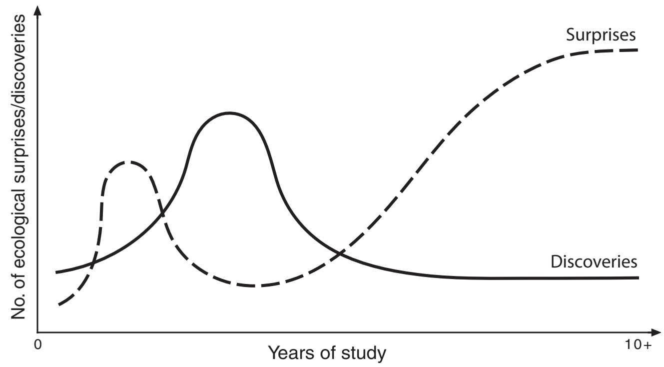

Fig. 1. Hypothetical plot of temporal changes in the number of ecological surprises derived from an investigation. Based on our experience, the early phases of a research study may lead to ecological discoveries, primarily with initial learning about the target ecosystem, population, or process, but there also may be some ecological surprises (including those identified if work is instigated soon after a major event like a high-severity natural disturbance; *Lesson 7*). After 7 to 10 y of work, we believe there might be fewer discoveries but more ecological surprises as a result of greater experience in working in an ecosystem and realization of the cumulative or interactive effects of multiple ecological drivers and multiple ecological patterns (*Lesson 1* and *Lesson 2*).

Lesson 1: Long-Term Studies. Each of the case studies we have summarized has been running for more than 25 y. We strongly believe that long-term investigations are critically important for increasing the probability of detecting ecological surprises. There are good reasons for this conclusion. First, as illustrated in all four case studies, time is a major driver of change (e.g., time following major natural disturbances) and some key phenomena do not become apparent unless targeted entities like populations, ecosystems, and ecological processes are studied for a prolonged period (19, 33) (Fig. 1). Second, increasing experience with a target ecosystem increases the chance that appropriate ecological questions can be posed (e.g., *Lesson 3*) and important new insights subsequently found, including ones that are unexpected (34). Such increasing experience can include cumulative knowledge of a system that draws together multiple avenues of learning and enables multiple strands of work to be completed and then integrated (e.g., *Lesson 2*), thereby increasing the chances that unanticipated interrelationships among different subcomponents of an ecosystem might be uncovered. Experience with an ecosystem, ecological community, or population heightens the potential to notice when something unusual or different occurs. A third reason why long-term studies are important for detecting ecological surprises is that longitudinal research will often allow the identification, quantification, and deeper understanding of important phenomena that are not detectable with a cross-sectional approach (35–37). Such important phenomena include: (*i*) the key ecological processes that underlie ecological patterns, (*ii*) relationships between different ecological patterns, and (*iii*) links between sets of interrelated ecological processes.

Lesson 2: Conducting a Range of Kinds of Parallel and/or Concurrent Research. Following from *Lesson 1*, the collective experience from our four case studies has been that ecological surprises were often found by interrelating the results of sets of parallel or concurrent studies. For example, the unexpected effect of acid rain on forest biomass in the research at the Hubbard Brook Experimental Forest emerged only because of concurrent studies of watershed biogeochemistry and forest structure and vegetation composition (22, 23). Similarly, parallel bodies of work on animal use of cavity trees and on vegetation structure led to ecological surprises associated with the quantities of carbon biomass in the wet forests of Victoria (26). These examples highlight the value for detecting ecological surprises of (*i*) group research in one ecosystem and (*ii*) the completion of a range of different kinds of studies in one area (i.e., ecosystem-based research and species-based research). We acknowledge, however, that not every kind of research can be done (or is appropriate) within a single study program. Nevertheless, for a given investigation, it can be critical to consider which kinds of research might have been overlooked and what the consequences might be (e.g., the paucity of work on soils in the forests of Victoria and its implications for calculations of carbon storage values).

There are other reasons why parallel and concurrent studies have an increased probability of detecting ecological surprises. One is that such research can make it easier to quantify interactions between and among multiple factors (including the unintended consequences of management actions in already modified ecosystems), which are a common cause of ecological surprises (4, 9, 12). Another is that factors at multiple spatial and temporal scales can have important influences on key ecosystem processes as well as on the distribution and abundance of animals and plants (38–40).

The value of accumulated knowledge from an ecosystem (*Lesson 1*), coupled with the need to be alert to the effects of interacting factors, highlights the potential for missing ecological surprises arising from excessive reductionism in ecological science.

Lesson 3: Good Questions and the Use of a Conceptual Model of the Target Ecosystem, Community, or Population. It is almost trite to state that good questions are fundamental to the conduct of good ecological science. A conceptual model of an ecosystem or particular entity being studied (e.g., a population) is a valuable tool for guiding the development of good ecological questions (41). Yet ecologists have often been poor at developing and posing good ecological questions and forming well framed hypotheses and alternative hypotheses (42). Furthermore, many studies are not guided by a conceptual model (34). We believe these deficiencies have led to many studies being poorly framed or designed (*Lesson 4*) and hence poorly positioned to detect ecological surprises when they do occur.

Lesson 4: Use of Past Literature in Developing Questions, Hypotheses, and Alternative Hypotheses. A deep understanding of the past ecological literature is an obvious and critically important part of framing good hypotheses and alternative views of ecosystems and, in turn, developing ecological research. Indeed, without this step, everything would (inappropriately) be an ecological surprise. However, it is notable that a very large number of ecological studies have ignored past research and recycled earlier ideas (43). It has been argued that the ecological sciences have been guilty of fickleness, with important themes going in and out of fashion, resulting in "…the same issues resurfacing decades later under a different rubric and a guise of novelty, often without reference to the previous work" (44). Familiarity with previously published research represents a truly major challenge to modern science because of an "information superglut" reflected by the sheer volume (and rapidly increasing numbers) of journal articles and books, which no single research scientist can hope to digest fully.

Important as it is to be cognizant of past ecological literature in framing hypotheses, we also argue that it is also critical for researchers to question their preconceptions about ecosystems; otherwise, there is a risk that they will find only what they are looking for (14), and as a consequence important ecological surprises will be missed.

Just as past literature is an important archive of information (*Lesson 4*), so too are field samples and specimens, which can be stored for later analysis to enable new questions to be pursued when, for example, new technology becomes available (e.g., refs. 45, 46). Comparative analyses of radioactivity in long archived and recent crop samples at Rothamsted in the United Kingdom is one of many examples (47).

Lesson 5: Good Experimental Design. Careful attention to experimental design is a recurrent theme in all four case studies in this article and was critical for identifying ecological surprises. Good experimental design is needed to answer robustly well framed ecological questions (*Lesson 3*) and therefore lies at the heart of good science (48). It can lead to valuable and robust outcomes from a given study, even when unexpected things occur, as in the case of the serpentine grassland ecosystems in California (31). Good experimental design is an inherently statistical process, and when it is ignored or done poorly, it can lead to studies failing (48, 49). This deficiency makes it difficult to obtain robust results and reduces the likelihood that ecological surprises will be detected. In the work in the Central Highlands of Victoria (*Case Study 3*), the experimental design underpinning the different research studies is overseen by a panel of accredited, professional statistical scientists (26).

Lesson 6: Field-Based Empirical Work. All four case studies we have presented are field-based, empirical research programs. and we believe that the discovery of surprising ecological phenomena was strongly underpinned by a keen interest in, and appreciation of the value of, natural history on the part of each of the principal investigators and their coworkers. Thus, we argue that field-based empirical work and natural history skills are an integral part of good research, and particularly the kind of long-term research likely to lead to ecological surprises. This approach is the antithesis of current trends in many resource management and related kinds of organizations, in which there has been a widespread loss of natural history skills (50), as well as in western society per se, which is characterized by an increasing disconnect between people and the natural environment (51–53). There also has been a tendency to replace ground-based work with remote approaches like the use of new generations of satellites. However, we argue that ground-based work is important for calibrating remote measures and verifying key results (e.g., see ref. 14).

We argue that the researchers at the Hubbard Brook Experimental Forest, as well as those in the three other case studies, further increased their chances of detecting ecological surprises because they had time to think long and deep about the phenomenon they were observing in the field. This is the antithesis of much of modern scientific culture, which we argue is often afflicted by an "epidemic of busyness" (54) created by cell phones, e-mail, and other rapid communication technology, as well as the comparative ease of travel to meetings worldwide. Although these innovations can assist the scientific enterprise in many ways, this epidemic can restrict time for clear thinking, thoroughness, and creativity (34).

Although field-based empirical research is clearly of paramount importance, particularly when it is guided by good experimental design, we do not discount the potential contribution of other kinds of work. For example, various kinds of computer modeling have been an adjunct activity in each of the four case studies outlined here, but it is notable that early modeling studies in three of them—the Hubbard Brook Experimental Forest (55), Victoria (56), and California (32)—did not provide an accurate picture of actual longer-term system dynamics. This problem highlights the fact that good-quality modeling is dependent on good-quality long-term field-derived empirical data to parameterize models (57).

Lesson 7: Rapid Response to Major Natural Disturbance Events. Studies commenced immediately following major natural disturbances often result in ecological surprises as well as offer important opportunities for ecological and management learning (58, 59). This opportunity occurred in two of our case studies: following the extensive and high-severity 2009 wildfires in the Central Highlands of Victoria (26) and major ice storms in the Hubbard Brook Experimental Forest (60). The lead researchers in both these research programs were able to position their investigations to take advantage of the scientific opportunities created by major natural disturbance events and such subsequent work quickly led to very surprising new findings. For example, it was recently demonstrated that even the most severely burned forests in the 2009 Victorian wildfires that were remote from unburned "green forest" continued to support residual populations of small mammals and that these individuals have underpinned a highly unexpected process of nucleated postfire population recovery (61).

Concluding Comments

Ecological surprises can be prevalent in a wide range of ecosystems, and several authors have highlighted the need to develop ways to understand them better and increase the chances of detecting them early (11). This capacity is critically important as it can (*i*) provide opportunities to improve management responses to ecological surprises, (*ii*) stimulate early intervention in ecological systems and improve the chances of management success such as in the management of fish stocks (62, 63) and in the control of invasive species (64), and (*iii*) avoid unexpected perverse outcomes of management interventions (e.g., refs. 4, 5), which are often a major source of ecological surprises (12, 65).

We fully recognize that some ecological phenomena will be well outside the history of past observations and have no prospective predictive ability (as hypothesized in Black Swan theory for economic systems) (65, 66). We also argue in this article that some ecological surprises will occur because of key oversights like inadequate duration of a study, insufficient attention to natural history, and failure to think more broadly about population/ecosystem function and processes, including taking account of past research. As an antidote to these problems in the design, execution, and duration of ecological investigations, we have outlined seven lessons we believe may increase the probability of detection of ecological surprises. On this basis, we therefore make the following recommendations:

Greater efforts must be made to maintain existing long-term ecological research studies and instigate new ones. This plea is far from new (reviewed in refs. 34, 48, 67), but we add increasing the probability of detecting ecological surprises to the long list of reasons why they are critically important and why science policy makers, funders, and managers need to be strongly encouraged to avoid the temptation to suspend long-term ecological research studies (14, 34).

The quality of long-term studies needs to be improved because, in many of them to date (particularly long-term monitoring programs), it has been poor (34). The studies can be enhanced through the development of good scientific questions and associated conceptual models, increased awareness of past ecological research, rigorous experimental design, and stronger collaboration between ecologists and expert statistical scientists. Long-term studies often can be strengthened when they go beyond simple "passive" monitoring of the target system (*sensu* ref. 34) to include quantification of changes associated with experimental interventions. Finally, long-term studies can be enhanced if an adaptive monitoring approach is embraced in which the entities being measured can be altered in response to what is being learned (68).

As part of long-term studies, researchers need to be more cognizant of the potential for increasing the probability of detecting ecological surprises arising from undertaking different kinds of studies concurrently or in parallel in the target area. For example, complementarities and synergies can arise from conducting both ecosystem-based and species-based research in a given area.

There is a need for far greater appreciation of the importance of field-based empirical work, and particularly the contribution of natural history skills, in uncovering ecological surprises. We argue that ongoing losses in natural history skills, coupled with current trends away from field-based empirical work in many organizations (e.g., the Commonwealth Scientific and Industrial Research Organisation in Australia), urgently need to be reversed.

There is a need for researchers to maintain flexibility and rapid response capability to take opportunities to increase the probability of detecting ecological surprises and deriving important ecological and management learning that arise from ecological events like major natural disturbances.

There is a need for greater awareness of the role that serendipity plays in detecting ecological surprises by ensuring that at least some of the scientific endeavor in ecology is curiosity-driven rather than tightly constrained by reporting against narrowly focused milestones and producing results in line with preordained deliverables.

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