Observational approaches in ecology open new ground in a changing world

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Ecology has entered into a dynamic period, driven by both the urgency of large-scale ecological problems and startling new ecological findings that are being shared broadly beyond the scientific community. Both of these factors are well represented by observational approaches to ecology, which are re-emerging after a long period of deference to manipulative experimental approaches. These approaches examine ecological patterns and processes through data gathered in situations where nature has not been purposefully manipulated. The use of unmanipulated observational data reflects on the work of early naturalists, but is greatly enhanced by technological advances in remote sensing, microscopy, genetics, animal-borne sensors, and computing. Once dismissed as merely "exploratory", strictly observational approaches to ecology have demonstrated capability in testing hypotheses by correlating variables, comparing observed patterns to output from existing models, exploiting natural experiments, and simulating experiments within large datasets. These approaches can be used in a stand-alone fashion, but are strengthened when reconciled with experimental manipulations to isolate fine-scale ecological mechanisms.

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At its roots, ecology is an observational science, borne out of the field work of amateur naturalists and transformed in the late 19th and early 20th centuries to a professional discipline in universities and private laboratories (Fleischner 2005). With this transformation, however, began a gradual erosion of the prominence of natural history and holistic observation in academic ecology. From the late 19th century – when naturalist and future US President Theodore Roosevelt lamented of his studies at Harvard University, "the tendency was to treat as not serious, as unscientific, any kind of work that was not carried on with laborious minuteness in the laboratory" (Millard 2006) – to the late 20th century, when experimental and theoretical approaches to ecology were at their zenith, basic observational natural history has taken a backseat in academic life sciences. However, since the 1990s, several high-profile ecologists – even those who built their careers on seminal works in experimental and mathematical ecology – began to question the dominant focus on reductionist approaches in ecology (Dayton and Sala 2001; Greene 2005).

In a nutshell:

- Today's basic and applied ecological challenges demand approaches that work across broad scales of time and space, and in situations that are not easily manipulated
- New advances in technology and broader temporal and spatial datasets have made basic observational approaches in ecology far more powerful than at any point in scientific history
- This power is evident in recent observational-based studies that provide evidence of the effects of climate change on natural systems, challenge long-standing theoretical constructs, and lead to unexpected discoveries in situations that cannot be manipulated
- Observational approaches to ecology are increasingly accessible to non-scientists, because they easily translate to the general public and are amenable to the direct involvement of concerned citizens in data collection

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The temporal and spatial scale of global environmental problems and the increasing development of sophisticated technological tools to capture and analyze large datasets over the past few decades have provided new opportunities for approaches to ecology that do not rely on manipulated experiments. As environmental crises mount and ecologists are called upon to address conservation problems on large scales – such as forest fragmentation, biogeochemical alteration, fisheries collapse, and invasive species – these purely observational approaches were increasingly relied upon to provide relevant data. This resurgence consolidated in the 1990s, when observational studies began revealing for the first time responses of species and communities to climate warming in real-world settings (reviewed in Parmesan and Yohe 2003; Root *et al.* 2003). Of the 143 non-redundant papers cited as evidence in these two reviews, 132 (92%) are observational studies.

Shifting approaches to ecology also reflect changing philosophical views on achieving ecological understanding. Pickett *et al.* (2007) argue that ecologists have been

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Panel 1. Ecological understanding in a changing world

In Pickett *et al.*'s (2007) conceptualization, ecological understanding is built on two pillars: observable phenomena and conceptual constructs that are used to generate meaning out of the observations (Figure 1). The observable phenomena can be gleaned from manipulated experiments or unmanipulated observations of nature. Conceptual constructs range from simple ways of organizing observations, such as the use of the term "rocky intertidal" in categorizing all coastal areas dominated by rocky substrata, to complex, multilayered general theories, such as "top-down control imparts ecological stability". Constructs are refined as new observations are brought forward.

Constructs and observable phenomena are linked by tools – causal explanation, generalization, and testing – and these tools are amenable to both manipulated experiments and unmanipulated observations of nature, to varying extents. What is changing in ecology is the mechanism that filters the phenomena that are brought to bear on concepts. In Pickett *et al.*'s (2007) construct, this filter is called "domain", or the scale of objects, relationships, and dynamics that are studied. Climate change and widespread alterations in biodiversity are forcing ecologists to expand the domain in which classical manipulative studies are carried out (typically at the population or community level, and rarely at the ecosystem level). This in turn is shifting the weight of inquiry toward phenomena that can be observed at a wide range of scales, that are multiply interactive, and that expressly include anthropogenic forces.

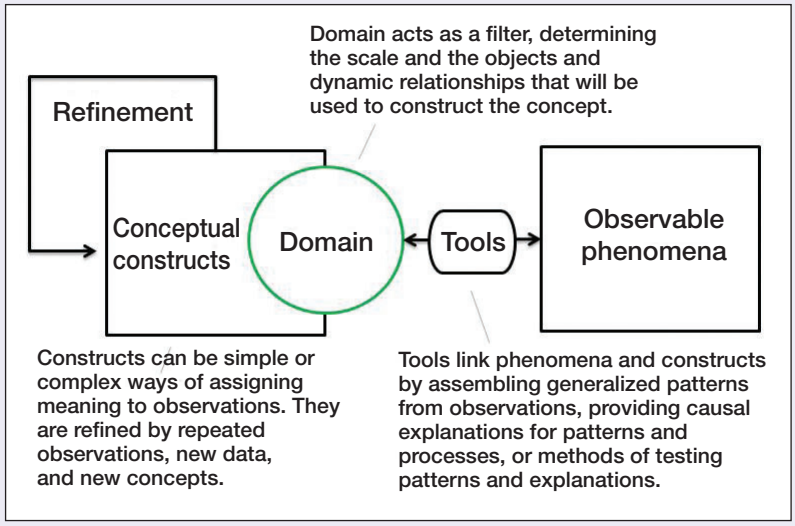


Figure 1. *The linked components of ecological understanding. Human alteration of ecological systems is pushing ecologists to expand the* domain *of ecological* constructs *or theories, leading to a renewed emphasis on observational-focused tools to link* phenomena *to* constructs *and establish understanding. Adapted from Pickett* et al. *(2007).*

As applied to an example from classical experimental ecology, Paine's (1966) manipulations of the predatory starfish *Pisaster ochraceus* in rocky intertidal shores in the Pacific Northwest fed into the conceptual construct, "predators maintain diversity in rocky intertidal shores", which subsequently spread into a general theory of "keystone predation" that has been applied in multiple ecological systems. However, later historical observational work by Sagarin *et al.* (1999) revealed that climate change was rearranging intertidal communities regardless of individuals' trophic status, and observations and manipulations by Sanford (1999) demonstrated that keystone predation by *P ochraceus* was conditional on upwelling patterns, which are expected to be altered by climate change. Although these studies were carried out in limited spatial locations, they pushed subsequent investigators to expand the domain of classic manipulations of the rocky intertidal zone to a greater portion of the geographic range of *P ochraceus* (Menge *et al.* 2004). These expanded studies revealed that: (1) experiments conducted in one part of the species range could not be adequately replicated throughout the entire range because other extrinsic factors (especially habitat differences) could not be controlled; and (2) *P ochraceus* does not act as a keystone predator in much of its range. This example illustrates that, on occasion, conceptual constructs borne out of limited scale experimental work are expanded out of proportion to their respective observable phenomena and new tools must be applied (in this case, observations of pattern and process at larger geographic scales, at longer time frames, and under altered biophysical conditions) to achieve ecological understanding that is relevant to contemporary questions.

unduly influenced by a focus on "falsifiability" (the idea, championed by the 20th-century philosopher Karl Popper, that a statement is only scientifically valid if its inverse can be tested and rejected) as the demarcation of scientific versus non-scientific inquiry. In place of this approach, Pickett *et al.* (2007) have promoted an integrated ecological philosophy that includes both falsification of specific hypotheses through targeted manipulations, and confirmation of theory through multiple layers of observations. Although falsification works well for testing specific, narrowly scoped hypotheses, confirmation is necessary for broad-scale questions that reflect multiple underlying causes and probabilistic, rather than absolute, answers (Pickett *et al.* 2007). The latter set of criteria almost certainly describes today's ecosystems and ecological problems, which are globally interconnected and heavily influenced by the complex social, economic, and political behavior of humans. In the integrated framework, multilayered observational approaches are not only firmly in the realm of scientific activity, but are also a key component of ecological understanding (Panel 1). Regardless of the extent to which this more holistic philosophy is adopted in the ecological community, the ubiquity and urgency of human alteration of ecosystems are increasingly driving ecologists to adopt observation-focused approaches.

Here, we discuss six key strengths and opportunities of observation-driven approaches to ecology that relate to the nature of observational data and the questions to which they can be applied. We then consider some of the limitations and challenges of relying on unmanipulated observational data and discuss ways to truly reintegrate pathways toward ecological understanding.

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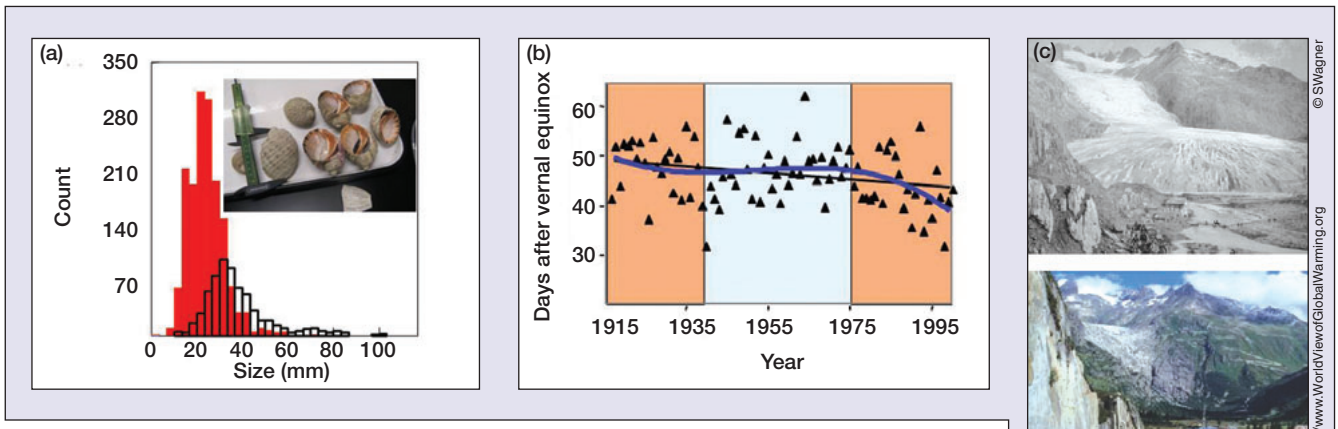


Figure 2. *Observational approaches to study change across large temporal scales. (a) Museum lots of the intertidal Muricid gastropod* Plicopurpura columellaris *from Pacific and Gulf of California, Mexico, collected in the early and mid 20th century, contain far larger individuals (outlined bars, n = 633) than those currently found in the field (red bars, n = 1599; Sagarin unpublished data). (b) Data on the exact minute of spring melt on an Alaskan river – kept for the "Nenana Ice Classic" betting contest over 85 years – reveal a 5.5-day-earlier melt on average (black line) and multi-decadal warm and cool periods that coincide with the Pacific Decadal Oscillation (blue line and background shading; Sagarin and Micheli 2001). (c) Snapshot observations have been critical in revealing climate-related changes. A lithograph from the Rhone Glacier, Switzerland, made in 1859, is compared with a 2001 photograph of the glacier, revealing an almost complete retreat.*

Data can come from anywhere

Observational approaches to ecology allow far more openness in data assimilation than do controlled experiments. Data collected by independent parties (eg non-scientists, enthusiasts) can have unexpected implications when they are analyzed under larger conceptual frameworks. For example, an Alaskan gambling contest that has been focused on guessing the exact minute of spring ice break each year since 1917 proved to be an excellent record of multidecadal climate variation (Sagarin and Micheli 2001; Figure 2). Likewise, one of the best phenological records in the US – spanning nearly 100 years – combines consistently recorded weather data with phenological records of 24 plant and animal species taken by a private family, and later by private reserve managers (Cook *et al.* 2008). Museum records and photographs are similarly being "rediscovered" as an essential window into ecologies of the past (Figure 2).

Additionally, public participation in, and awareness of, ecological discoveries are greatly facilitated by the simplicity and accessibility of basic observational approaches. For instance, "citizen-science" programs, where the public can participate in data collection through supervised programs at specific locations or independent activities that can be reported on the internet, can provide data while helping the public appreciate the role of ecological science in the larger world. Such programs are gathering useful data on patterns of migration (eg The Journey North, www.learner.org/jnorth), phenology of terrestrial plants (eg Project Budburst, www.windows.ucar.edu/cirizen_science/budburst), and intertidal communities (eg Long-term Monitoring Program and Experiential Training for Students, http://limpetsmonitoring.org/index.php), among many other examples around the world.

Technology enhances the power of observation

New technological advances – undreamed of in Charles Darwin's time – are providing the opportunity for basic observations to contribute disproportionately to our conceptual understanding of changing ecological systems. Pop-off satellite tags, archival data recorders, and cameras are effectively turning thousands of organisms into natural historians, providing unprecedented and surprising records of animal behavior and the environment (eg marine animals diving far below their physiological thresholds, as determined in models and laboratory studies; Moll *et al.* 2007). These observations often carry key management implications; tags on Atlantic bluefin tuna (*Thunnus thynnus*) revealed that these animals routinely cross stock management boundaries (Figure 3), raising major doubts about the existing management regime, which considered the species to be divided into western and eastern Atlantic stocks (Block *et al.* 2005). Remote sensing and Geographic Information Systems (GIS) applications – which greatly exceed humans' innate visual field, as well as visual frequency – are providing global-scale observations that can be combined with current constructs about land-use change and climate change to provide understanding of the impact of human beings on Earth (eg human modification of land cover; Ellis and Ramankutty 2008). Population genetics is also a technology-enhanced observational approach that has made vital contributions to basic and applied ecological questions. For example, genetic data have revealed that historical gray whale (*Eschrichtius robustus*) populations

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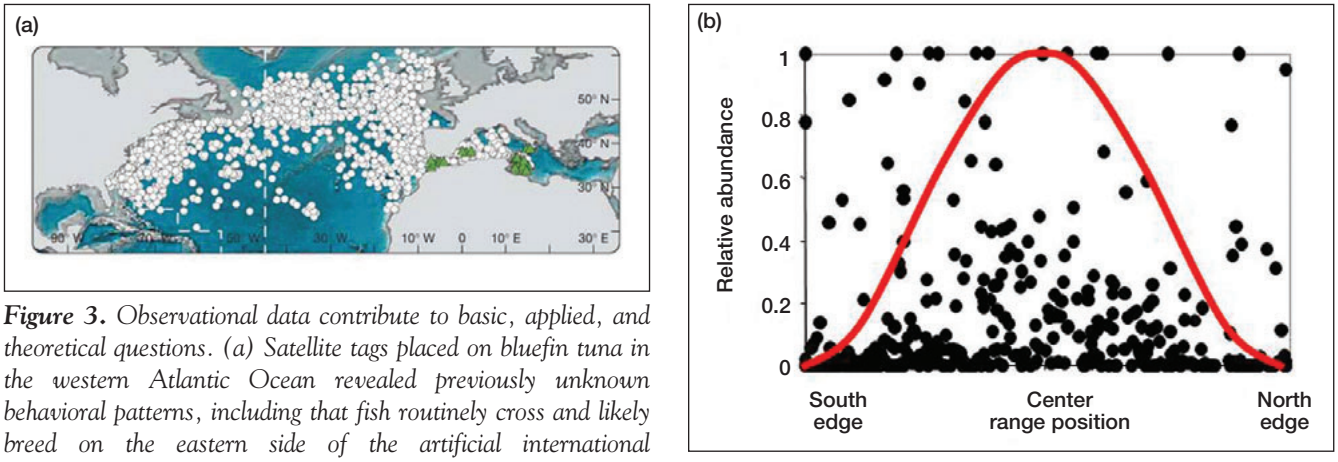


Figure 3. *Observational data contribute to basic, applied, and theoretical questions. (a) Satellite tags placed on bluefin tuna in the western Atlantic Ocean revealed previously unknown behavioral patterns, including that fish routinely cross and likely breed on the eastern side of the artificial international management boundary (dashed line) in the middle of the Atlantic (from Block* et al. *2005). (b) Empirical tests of long-standing theory were made by observing patterns of population density in 12 intertidal invertebrates across their geographic range on the Pacific coast of North America, revealing that few conform to the widely assumed "abundant center" distribution, with highest abundances in the center of the range (Sagarin* et al. *2006).*

are likely to have been much larger than expected from fishery records alone (Alter *et al.* 2007). Combining these approaches, Kozak *et al.* (2008) showed that geographic patterns in population genetics are better explained when fitted to GIS-based environmental data rather than the commonly used Euclidean distance between populations.

Observations can be made and analyzed on multiple scales

Patterns and processes that manifest at one scale can be completely different, or even contradictory, at broader or finer scales (emergent properties), because they are driven by different mechanisms (Levin 1992). For example, the controversy over the negative or positive relationship between native and non-native species richness appears to be based on observations made at completely different scales. At microscales (~1 m^2 spatial resolution), a negative relationship is explained by competition, whereas at larger spatial scales, heterogeneity increases both native and non-native diversity (Davies *et al.* 2007). Yet, because of logistical and conceptual constraints, most ecological studies tend to be single scaled, limiting the generalization of their results to very specific circumstances. For example, for a study of plant diversity, a single plot size (typically < 1 m^2 in manipulative experiments) yields limited results, because it only covers a particular set of patterns and processes.

Recently, studies have increasingly adopted multiscale approaches based on observational data (Pauchard and Shea 2006). Multiscale studies operate in a hierarchical framework that acknowledges that a particular phenomenon cannot be explained based solely on the observations made at a single scale. In plant ecology, field data and remote-sensing techniques can be used to identify phenomena at a wide range of scales and to explore relationships between dependent and independent variables at multiple scales (Figure 4). Multiple temporal scales of variation (eg diurnal, seasonal, annual, multidecadal) can also be captured through monitoring plots studied at different temporal intervals within a single sampling protocol, to shed light on which processes and mechanisms dominate at each temporal scale (Nichols and Williams 2006).

Observations work in situations that cannot be manipulated

Many changes to ecological systems – especially those operating over large temporal (Figure 2) or spatial (Figure 3) scales – simply cannot be studied with manipulative experimental approaches. In some cases, repeating well-designed experiments across a species range is not possible, because variability in key environmental attributes (eg habitat type, weather conditions) may confound experimental design (Panel 1). Ethically, it may be inadvisable to replicate ecological changes in experimental field treatments. For example, intentionally transplanting species beyond the boundaries of their normal geographic range – to test why those boundaries act as such – may lead to accidental range extension if those species escape. In cases where ecological change may have serious but unreplicable consequences for humans and ecosystems (eg radiation effects from Chernobyl; Bradbury 2007), the use of detailed observational analogies to past events of a similar nature may be the only available option in determining likely outcomes of a given perturbation (Turner *et al.* 1998). Citing the logistical and ethical limitations of experimental manipulations for identifying ecological drivers of human disease, Plowright *et al.* (2008) propose using criteria derived from epidemiology (which rely on large-scale observational datasets) to establish causation.

Observations can challenge long-held assumptions

Several key assumptions in ecology, developed within fairly narrow conceptual "domains" (see Panel 1) and reinforced by models and experiments that operate within those domains, have recently fallen in the face of

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observational studies. The assumption that species are most abundant in the center of their range and decline in numbers toward the edges (which has implications for population gene flow, responses of species to climate change, and where to situate habitat reserves, for example) was shown in a literature review to have little empirical support, spawning a wide range of new observational studies that also failed to find the pattern (Sagarin *et al.* 2006; Figure 3). Even classic, experimentally supported theories, such as the island colonization theory in island biogeography, are being radically revised as a result of evidence obtained through unmanipulated observation. Bellemain and Ricklefs (2008) used data from geography and molecular phylogeny to suggest that reverse colonization from islands may be an important and neglected process. Nonetheless, wide-scale observation can also provide much-needed empirical support for theory. For example, Rietkerk and van de Koppel (2008) have assembled numerous visual examples of regular pattern formation in nature that lend credence to theories of spatial self-organization.

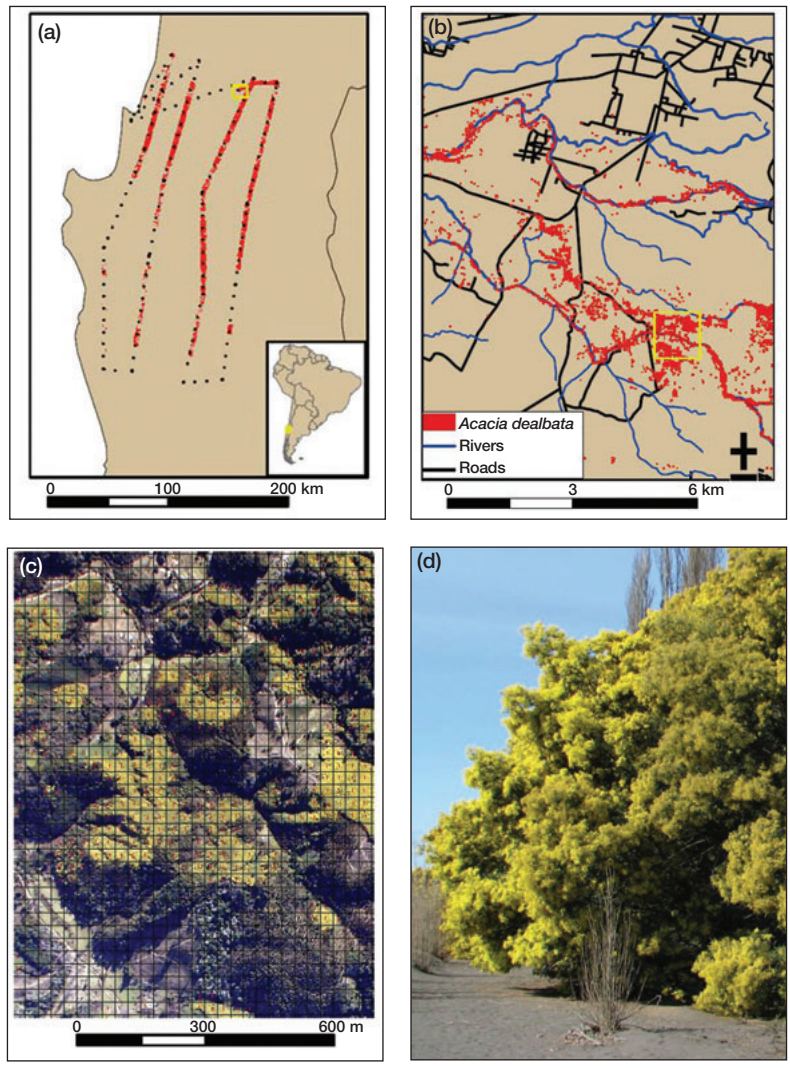


Figure 4. *Detection of the invasive species* Acacia dealbata *(Fabaceae) at multiple scales. (a) Regional scale: presence of the species in flight lines showing aggregation at large spatial scales. (b) Landscape scale: the species is associated with rivers and roads. (c) Stand scale: the species forms dense monotypic stands. (d) Individual* A dealbata*, showing the intense yellow flowering that allows stands to be detected by winter aerial photography. Predicting the distribution of* A dealbata *at landscape scales benefits from the use of independent variables (eg road/river density, temperature) at multiple scales. Similarly, the dependent variable (presence of the species) can also be studied at different scales of resolution (eg pixel size), in order to model specific phenomena (eg habitat invasibility, speed of spread).*

Observations work with – and without – experiments

The oft-repeated criticism that "correlation does not indicate causation" has reinforced the idea that observation-based studies are less scientific than experimental manipulation. Yet, Hewitt *et al.* (2007) argue that the correlational nature of observational studies neither disqualifies them as unscientific nor prevents them from assigning causality in ecology, noting that major advances in medicine, physics, and oceanography have been made via correlational data and analogies. Indeed, some of the most robust theories in ecology, on natural selection, extinction, habitat fragmentation, and biogeography, have emerged from analysis dominated by multiple layers of correlations (eg the large impact theory of the Cretaceous–Tertiary extinction).

What is less well appreciated is that unmanipulated observations can be used to rigorously test and reject alternative hypotheses that are envisioned under different conceptual constructs. Natural observational experiments can be constructed out of large-scale and long-term observational datasets, which provide multiple axes to compare given "control" and "experimental" conditions. Useful comparative axes may isolate characteristics of organisms (eg species interactions in dense versus sparse populations), physical habitat (eg foraging behavior on open ground versus in closed-canopy forests), climatic conditions (eg community composition in warm versus cold climate regimes), or even regulatory environments (eg species size structure in protected reserves versus unprotected sites). Sax *et al.* (2007) show that invasive species can be used as natural experiments to test both classic ecological hypotheses (eg what are the causes of species range limits?) and provide new insights (eg competition seldom causes global extinction). The authors note that such experiments using observed data on invasive species (whether generated naturally or by human transport) can be conducted on spatial and temporal scales untenable in manipulative experiments while

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avoiding the ethical constraints of deliberately introducing a potentially detrimental species.

Nonetheless, even among proponents of an increased focus on observational approaches, there is still debate on the extent that a priori hypotheses should drive observational work. Some argue that hypotheses impart scientific rigor to natural history and prevent the waste of resources (Lovett *et al.* 2007; Moll *et al.* 2007). Others make the point that open-ended journeys of discovery have merit in training and inspiring naturalists, even as they also address the great dearth of ecological observations (Dayton and Sala 2001; Greene 2005). Astonishing new discoveries stemming from rather simple questions, such as "Does anything live in the deep sea?", as well as serendipitous results that have nothing to do with the original research questions, provide retrospective evidence that structured, hypothesis-driven studies are not a prerequisite for ecological advances. Serendipitous discoveries are becoming the norm with observational data. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) records, for example, which were originally designed and implemented in the 1950s to gather data on the causes of California's sardine collapse, have been far more valuable for their ability to reveal climate-mediated changes to California's entire current ecosystem (McGowan *et al.* 1998). As Dayton and Sala (2001) note, creative and orthogonal (ie not related to the original line of inquiry) discoveries are not a matter of "luck", but rather are a result of a holistic conceptualization of a system, which is built from careful observation at a range of scales.

Limitations of strictly observational approaches to ecology

Unfortunately, the data we need to answer today's most pressing ecological questions are missing. In reconstructing community changes at Stanford University's Hopkins Marine Station, the oldest marine biology laboratory on the US west coast, Sagarin *et al.* (1999) were forced to go back to a single study conducted by a graduate student in the 1930s to find any comprehensive survey of the local intertidal community. Even long-term datasets like CalCOFI suffer from unfortunate data gaps, such as during the mid-1970s, when the most important Pacific climatic regime shift in the 20th century was occurring. The data situation is especially concerning in developing countries, where funding for research is more erratic over time and is usually directed to solve very specific questions. This can be clearly seen in the amount of research directed to invasive species by regions (Pysek *et al.* 2008), where more developed countries account for much of the published information. Promising new international networks of research efforts (eg regarding invasive species in mountains; Pauchard *et al.* 2009) may help to reduce disparities in data collection. Yet, even as this is occurring, aging museum specimens – incredibly valuable for a range of ecological studies (Wandeler *et al.* 2007) – and even relatively modern satellite data are decaying or becoming inaccessible (Loarie *et al.* 2007).

As lamentable as the situation is with biophysical data, we have even fewer data from the social sciences side of ecology. A recent study correlating a proxy record of Asian monsoon variability over the last 1800 years with major periods of political upheaval in China is a startling reminder of the inseparable link between large-scale ecological forces and society, and an indication of the power of observational studies to make this link explicit (Zhang *et al.* 2008). As "ecosystem-based" approaches to science and management become increasingly popular, socioeconomic data, including information on corporate behavior and social justice, become increasingly relevant (Bundy *et al.* 2008).

Finally, reintegration of ecology with other fields of societal interest means that entirely new users are becoming interested in ecological data. This supports a commitment to compiling large datasets and making them easily available for researchers of all types, in all parts of the world, as espoused by the "open access" movement. In turn, ensuring that these widely available data are used sensibly will require renewed attention to ecological education at the early and advanced levels. This education, as with the science of ecology itself, should begin with simple observations of nature.

Integration

Approaches to ecology based on unmanipulated observations are by no means a complete substitute for either theoretical or experimental manipulative ecology. All approaches to ecology will, in fact, benefit from integrative approaches that utilize the relative strengths of one approach to overcome the weaknesses of another. Hewitt *et al.* (2007) proposed an approach that integrates observational and experimental manipulations, beginning with observational natural history, to identify the likely scale of the problem, potential causal variables, and feedbacks. Depending on the scale and complexity of the problem, experimental manipulations are either built into a large-scale observational/correlational framework or applied in an alternating fashion with correlational studies, with each type of study providing information to better focus the next iteration of the other.

Good examples of this approach are emerging in ecology. Using the example of a reed invasion into farmed salt hay fields, Bart (2006) presented a case for integrating "local ecological knowledge" – which often provides excellent historical observational insights but has little power to resolve causal mechanisms – with experimental manipulations. At larger scales, ecological physiologists are successfully applying experimentally calibrated physiological indicators to field studies to test questions such as, "What is the cause of a species range limit?" and "How will this species respond to climate warming?" Norkko *et al.* (2006) argue that integrating physiological indicators honed in controlled laboratory experiments

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with broad population sampling across ecological gradients can elucidate linkages between mechanisms and ecological patterns. Some experimental manipulations have now been carried out for a long enough period of time to be combined usefully with observational data to resolve key hypotheses, such as the relative role of natural versus artificial selection (eg size-selective harvesting) in driving microevolutionary change in fish (Coltman 2008).

Further integration is possible with synthetic approaches, such as meta-analysis, pattern finding, and comparative case studies that can be used to generalize concepts that are first elucidated in either smaller scale experimental manipulations or individual observational investigations. The value of this approach is exemplified by the success of the National Center for Ecological Analysis and Synthesis (NCEAS) in Santa Barbara, California, which is a nexus for multi-investigator, multidisciplinary projects that attempt to derive new insight through combining and analyzing existing datasets and revising existing conceptual constructs. Although only founded in 1995, NCEAS has risen to the top 1% of over 39 000 ecological institutions worldwide based on impact factor (Hackett *et al.* 2008) and has become a model for at least 17 new ecological institutions internationally (S Hampton pers comm).

The resurgence of purely observational approaches has had impacts on all levels of the study of ecology, but has also pushed the science further into the public realm than at almost any time since Charles Darwin and Alfred Russel Wallace used basic observations and holistic synthetic analysis to introduce the concept of evolution by natural selection. Advances in observational technologies have documented new species and even new phyla of organisms and have revealed surprising new discoveries about species as familiar as ground squirrels (*Spermophilus beecheyi*; Rundus *et al.* 2007), as valued as bluefin tuna (Block *et al.* 2005), and as revered as whales (Alter *et al.* 2007). Observations get people intrigued about nature, and the anthropological impacts on nature, in a way that laboratory and field experiments – and mathematical models – cannot. When these observations are made firsthand, as afforded by citizen-science programs, they not only add to scientific knowledge but also help new constituencies appreciate ecological problems. Moving ecology in this direction will fulfill both the call of early ecologists, such as Edward Ricketts, to study systems holistically, as well as modern projections of the role of natural history in 21st-century science, as expressed by Grant (2000):

> "To be a naturalist is to ask questions directly about organisms in nature and to seek answers wherever they are to be found (macroecology, population genetics, etc), by whatever means are available (field experimentation, analysis of DNA, etc)."

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