

Citizen Science as an Ecological Research Tool: Challenges and Benefits

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Abstract

Citizen science, the involvement of volunteers in research, has increased the scale of ecological field studies with continent-wide, centralized monitoring efforts and, more rarely, tapping of volunteers to conduct large, coordinated, field experiments. The unique benefit for the field of ecology lies in understanding processes occurring at broad geographic scales and on private lands, which are impossible to sample extensively with traditional field research models. Citizen science produces large, longitudinal data sets, whose potential for error and bias is poorly understood. Because it does not usually aim to uncover mechanisms underlying ecological patterns, citizen science is best viewed as complementary to more localized, hypothesis-driven research. In the process of addressing the impacts of current, global “experiments” altering habitat and climate, large-scale citizen science has led to new, quantitative approaches to emerging questions about the distribution and abundance of organisms across space and time.

Crowdsourcing:

getting an undefined public to do work, usually directed by designated individuals or professionals

CBC: Christmas Bird Count (USA; run by the National Audubon Society)

BBS: North American Breeding Bird Survey (run by USGS, Patuxent, MD)

INTRODUCTION

Volunteer participation in ecological studies has become a mainstay of research aimed at the conservation of biodiversity. Although observations of amateur naturalists have been important for centuries, citizen science projects have proliferated in the past decade, with the ability to track the ecological and social impacts of large-scale environmental change through the Internet (Lepczyk et al. 2009). Sophisticated internet applications effectively utilize crowdsourcing for data collection over large geographic regions (Howe 2006), offering opportunities for participants to provide, gain access to, and make meaning of their collective data (e.g., The Avian Knowledge Network). Today, public and professional ecologists alike have access to a growing number of tools to explore changes in the phenology, relative abundance, distributions, survival, and reproductive success of organisms across time and space. In the process, citizen science has influenced both the scale of ecological research that is being done and the relationship between ecologists and the public.

The fields of astronomy and ornithology have led the charge for citizen science with prominent efforts beginning at the end of the nineteenth century. In 1874, the British government funded the Transit of Venus project to measure the Earth's distance to the Sun. This project engaged the admiralty to support data collection all over the globe and recruited the services of the most prominent amateur astronomers of the Victorian period (Ratcliff 2008). Bird monitoring in Europe goes back even longer, with amateurs collecting data on timing of migration beginning in Finland in 1749 (Greenwood 2007). In 1900, the American Museum of Natural History's ornithologist, Frank Chapman, initiated the Christmas Bird Count (CBC) as an alternative to regular holiday bird-shooting contests; this project popularized ornithological monitoring in the United States and is now run by the National Audubon Society. The U.S. Geological Survey (USGS) began engaging the public in bird monitoring even earlier, in 1880, but became a major player in monitoring of birds with the well-known Breeding Bird Survey (BBS) launched in 1966. In recognition of the importance of phenological data for understanding impacts of global climate change, the USGS's North American Bird Phenology Program (focused on first arrivals of migrants) and the Cornell Lab of Ornithology's nest record card scheme (begun in 1965 and now online as NestWatch) have begun to engage the public to enter historic data online from scanned paper records. In 2005, the USA-National Phenology Network developed partnerships to collect and aggregate historic data to track seasonal timing of biological events for a broad range of taxa. Most of these data have been or will be made publicly available.

Although astronomy and ornithology have the largest body of amateur experts and the longest history of engaging volunteers in professional research, citizen science has expanded in the past decade to a point where we now have over 600 extant citizen science projects on the Cornell Lab of Ornithology's roster. Ecological projects range from local to global and monitor a broad range of taxa, including plants, fungi, earthworms, insects (including pollinators), crabs, fish, mammals, amphibians, and reptiles (Table 1). In addition to tracking a diversity of organisms, citizen scientists regularly contribute data on weather and habitat. Projects that engage the public in discovery research in astronomy (e.g., Galaxy Zoo) and protein folding (Foldit) or that engage people in computer games to facilitate machine learning and increase the search capabilities of the worldwide Web (GWAP) are pushing the envelope of what citizen science can do.

Citizen science invites the public to participate in both scientific thinking and data collection (Cooper et al. 2007a, Irwin 2001). Participants in ecological projects, typically outdoor hobbyists, are able to access learning materials and protocols, gather data, and enter them online into centralized, relational databases, where they can view results using interactive graphs and maps.

Development of new cell phone technologies is rapidly increasing the potential for immediate validation of observations and transmission of data as well as combining electronic sensor data with human observations (Burke et al. 2006).

The model of citizen science currently having the greatest influence on the field of ecology involves monitoring biodiversity at broad geographic scales. By allowing ecologists to move from local inference to inference at the scale of species ranges and ecosystems, citizen science accounts for growth in the fields of macroecology and geographical ecology, both of which explore spatial variation in colonization/extinction dynamics and environmental (niche) requirements across species' ranges (Bock & Lepthien 1975, Brown 1995). Similarly, it allows landscape ecology researchers to study the impact of land use change at large spatial scales, where important processes not detectable at local scales may dominate dynamics. Citizen science appears particularly effective at finding rare organisms, including new, invasive organisms and disappearing native species (e.g., The Lost Ladybug Project). The bang for the buck can be good; in the case of Cornell's Project FeederWatch (**Figure 1**), participants pay fees that support the project, while also contributing effort valued at \$3,000,000 per year (**Table 2**).

Citizen science is a good match for the new field of urban ecology and the perspective of coupled systems research (Lepczyk et al. 2009, McCaffrey 2005, Machlis et al. 1997). In urban and suburban environments, citizen science can match ecological monitoring data with data on human attributes, including educational/health statistics and participants' residential practices such as pesticide and water use, energy consumption, pet ownership, and residential habitat management, to better understand the impacts of cultural and behavioral practices on ecological response variables (Field et al. 2010).

In this review, we focus on the nature of citizen science research, its value to the field of ecology, and the challenges it presents. Using bird monitoring examples, we explore (*a*) the potential for citizen science to contribute to a wide range of ecological research questions and (*b*) the complex issues that arise in working with large, heterogeneous data sets. We do not cover the practice of developing citizen science projects, nor do we explore how to make citizen science projects better, because program development is a complex topic and is covered elsewhere (Bonney et al. 2009). Although we recognize that ecological literacy is a fundamental requirement in today's world, where people are asked to make personal and policy choices that influence the degree of ecological disturbance, we do not explore the impact of citizen science on ecological thinking or "habits of mind" (Jordan et al. 2009). Instead, we provide insight into the research value and constraints of citizen science data, the statistical expertise required to use the data, and the continuing requirement for biological insight, good questions, experiments, and strong inference.

CITIZEN SCIENCE AS A RESEARCH TOOL

We start with the premise that observing and defining ecological patterns, in the absence of questions that advance understanding of ecological processes, are largely descriptive. Once identified, however, patterns comprise initial observations, stimulating further investigation that will advance the field (**Figure 2**). So while identifying ecological patterns and trends is of considerable importance, investigating whether these patterns and trends conform to a competing set of alternative, *a priori* hypotheses is required for strong inference.

Although citizen scientists can be recruited into question-driven and experimental studies (e.g., Jones et al. 1998), most large-scale citizen science projects provide long-term monitoring data. In spite of the connection between citizen science and exploratory research, these monitoring efforts occasionally come under scrutiny. Nichols & Williams (2006) highlighted the distinction between targeted monitoring, which is designed based on *a priori* hypotheses or conceptual models, and

Landscape ecology: study of importance of spatial variation in biological, physical, and social landscapes at a variety of scales

Coupled systems research: ecological research that includes human and ecological inputs in the same model

Table 1 Examples of citizen science programs and their associated Web sites

Organismal monitoring	Taxonomic group	Program name	Web site
	Fungi	MykoWeb (mushrooms, fungi, mycology)	http://www.mykoweb.com/articles/CitizenScience.html
	Plants	Plant Watch	http://www.naturewatch.ca
		Project Budburst (plant phenology)	http://www.windows.ucar.edu/citizen_science/budburst/
	Gastropods (snails) Annelids	Evolution MegaLab	http://www.evolutionmegalab.org
		Great Lake Worm Watch	http://www.nrri.umn.edu/worms
		Wormwatch (getting the dirt on earthworms)	http://www.icewatch.ca/english/wormwatch/
	Arthropods		
	Crabs	Invasive Tracers (marine invasive species monitoring)	http://massbay.mit.edu/exoticspecies/crabs/index.html
	Insects		
	Butterflies and moths	French Garden Butterfly Monitoring	http://noeconservation.org
		UK Butterfly Monitoring Scheme	http://www.ukbms.org
		The Monarch Larva Monitoring Project	http://www.mlmp.org/
	Bees (pollinators)	Garden Moths Count	http://www.mothcount.brc.ac.uk
		The Great Sunflower Project (pollinators)	http://www.greatsunflower.org/en/about-project
	Beetles		
	Fireflies	Firefly Watch	http://www.mos.org/fireflywatch
	Ladybugs	The Lost Ladybug Project	http://www.lostladybug.org/index.php
		FrogWatch USA	http://www.nwf.org/frogwatchUSA
	Amphibians	North American Amphibian Monitoring Program	http://www.pwrc.usgs.gov/naamp/
		USGS Frog Quizzes	http://www.pwrc.usgs.gov/frogquiz/
	Fish	REEF (coral reef fish)	http://www.reef.org/programs/volunteersurvey
	Reptiles	Nature North (reptiles and amphibians)	http://www.naturenorth.com/Herps/Herps_Atlas_Proposal.html
	Birds	Audubon's Christmas Bird Count	http://www.audubon.org/Bird/cbc/
		Big Garden Bird Watch	http://www.rspb.org.uk/birdwatch/
		Britain's Common Birds Census	http://www.bto.org/survey/complete/cbc.htm
		Cornell Lab of Ornithology's eBird	http://www.ebird.org/

Environmental monitoring	Mammals	Cornell Lab of Ornithology's NestWatch	http://www.nestwatch.org
	Environmental variable	Cornell Lab of Ornithology's Project Feeder Watch	http://www.feederwatch.org/
	Habitat	Monitoring Häufige Brutvöge	http://www.vogelwarte.ch/home.php?lang=e
	Weather	North American Breeding Bird Survey	http://www.pwrc.usgs.gov/BBS/
	Water quality	Road Watch (mammals)	http://www.rockies.ca/roadwatch/about.php
Nonecological projects	Field of inquiry	Program name	Web site
	Astronomy	The YardMap Network	http://www.yardmap.org
	Crowdsourcing machine learning	Citizen Weather Observer Program	http://www.wxqa.com/
	Protein folding	NASA's Earth Observatory	http://earthobservatory.nasa.gov/Experiments/CitizenScientist/WaterQuality/
Citizen Science gateways/portals	Field of inquiry	Program name	Web site
	Astronomy	Galaxy Zoo	http://www.galaxyzoo.org/
	Crowdsourcing machine learning	GWAP	http://www.gwap.com/gwap/
	Protein folding	Foldit	http://fold.it/portal/
	Field of inquiry	Program name	Web site
	Astronomy	Avian Knowledge Network	http://www.avianknowledge.net/content/
	Crowdsourcing machine learning	North American Bird Phenology Program	https://www.pwrc.usgs.gov/bpp/index.cfm
	Protein folding	USA-National Phenology Network	http://www.usanpn.org/
	Field of inquiry	British Trust for Ornithology	http://www.bto.org/
	Astronomy	Citizen Science Projects	http://citizensci.com/
	Crowdsourcing machine learning	Citizen Science Central	http://www.citizenscience.org/
	Protein folding	Cornell Citizen Science	http://www.birds.cornell.edu/NetCommunity/Page.aspx?pid=708
	Field of inquiry	Historical bird monitoring data	http://www.pwrc.usgs.gov/birds/histdata.html
	Astronomy	Science Cheerleader	http://www.sciencecheerleader.com/2009/01/calling_all_citizen_scientists/
	Crowdsourcing machine learning	Open Air Laboratories	http://www.OPALexplore.nature.org
	Protein folding	Citizen Science Canada	http://www.ccmn.ca/english/
	Field of inquiry	National Biodiversity Network	http://www.nbn.org.uk
	Astronomy	Swedish Species Gateway	http://www.artportalen.se/
	Crowdsourcing machine learning	North American Breeding Bird Atlas Viewer	http://www.pwrc.usgs.gov/bba/index.cfm?fa=bba.About

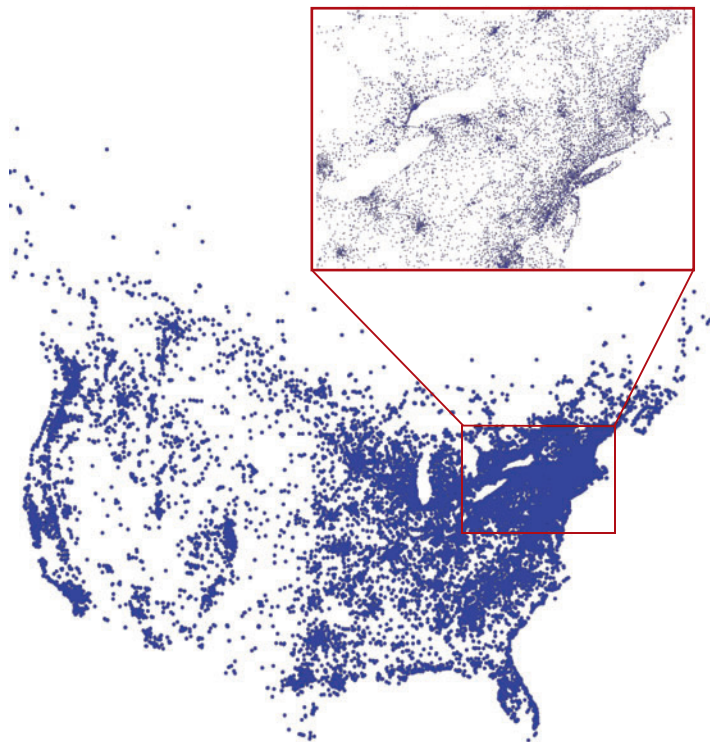


Figure 1

FeederWatch map of North America with all details of the map “drawn” simply by placing participants’ locations (latitude and longitude) as points in two-dimensional space. Cities, towns, and population centers become obvious, because FeederWatch data are typically gathered in backyards. (Inset: closer view of Northeastern North America).

surveillance monitoring, which is conducted without specific hypotheses in mind. Most citizen science programs involve surveillance monitoring of numerous species over broad geographic regions, with the idea that data will ultimately be useful for a broad spectrum of questions. In general, targeted monitoring puts less emphasis on finding and estimating patterns and trends, and instead emphasizes the monitoring of priority species based on taxonomic status, endemism, sensitivity, immediacy of threats, public interest, and other factors (Yoccoz et al. 2001). In general, it is easier to evaluate alternative hypotheses when data collection is designed with specific predictions in mind; however, surveillance monitoring is perhaps the only means of addressing unanticipated threats to biodiversity.

Throughout this review, we highlight the requirement for expertise in working with large, messy, spatial data sets and the need to entertain competing, alternative hypotheses to make good use of citizen science data. We also argue that omnibus surveillance of multiple species throughout a region has an important role to play as a first line of attack; it can illuminate unexpected or even counterintuitive patterns and trends as the starting point for intensive, targeted monitoring or theoretically driven research. For example, in England, multigenerational observations of flowering time by garden hobbyists were used to document large phenological shifts of plant species in response to climatic warming (Hepper 2003). Moving from surveillance monitoring to

Table 2 Comparison of eight monitoring projects focused on measuring bird occurrence and abundance

Results from these programs have been used in over 1000 scientific publications										
Project	Method	Sample	Placement	Effort ^a	Extent	Interval	Period	Participants	Data ^b	Pubs
Audubon Christmas Bird Count	Count circle (24-km diameter)	2,113 (2008–2009)	Opportunistic	V (party hours)	International	Annual (Dec. 14–Jan. 5)	1900–	59,918 (2008–09)	O	~310
North American Breeding Bird Survey	Roadside survey (39.4 km; 50 stops)	3,036 (2009)	Stratified random	S (3 min count)	International	Annual (Variable; May–June)	1966–	2,749 (2009)	O/A	~490
Monitoring Häufige Brutvögel (MHB)	Bird survey (1-km blocks; 3–6-km transect)	267 blocks	Regular grid	S (2–4 hr)	Switzerland	Annual (mid–April–mid–July)	1999–	209 (2009)	O/A	~50
Project FeederWatch	Feeder counts	9,986 (2009)	Opportunistic	V (2-days, Hours, Days)	International	Annual (Nov.–April)	1987–	9,750 (2009)	O/A	~20
eBird	Online checklists	934,363 (2009)	Opportunistic	V (Hours, Distance, Area)	International	Continuous	2002–	18,053	O/A	~10
North American Amphibian Monitoring Program	Roadside survey (~24.1 km; 10 stops)	500 (2009)	Stratified random	S (5 min. listening period)	Multistate (20 states)	Three periods (Region specific)	2001–	500 (2009)	O	~50
Bird Atlas	Systematic grid (100-km ² blocks; 4-km ² tetrads)	3,879	Regular grid	S/V (roving, timed visits)	Britain and Ireland	Two visits (Winter: Nov./Dec. & Jan./Feb.; Breeding: April/May & June/July)	1968–76 1988–93 2007–11	10,000–20,000	O/A	~60
Common Birds Census	Census plots (Farmland: 70 ha; Woodland: 20 ha)	200	Stratified random	S (territory mapping)	Britain	Annual (8–10 visits; late March–early July)	1962–2000	250–300	O/A	~120

^aEffort is considered standardized (S) or variable (V). When standardized, we present the protocol specifications; when variable, we present the effort variables that are reported during sampling.

^bO, binary occurrence data; A, data that can reflect relative abundance (e.g., counts, number of territories per sampling unit).

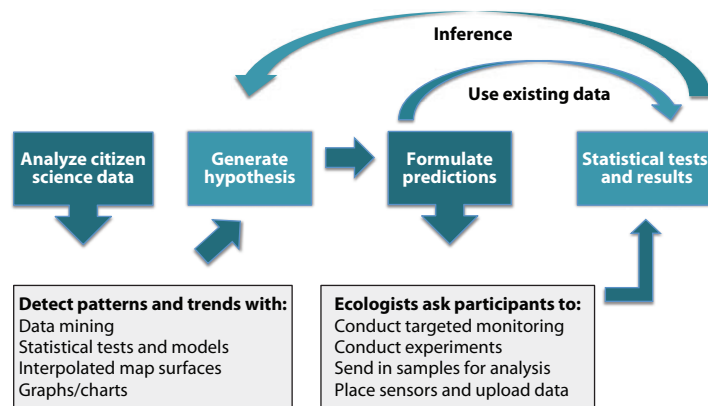


Figure 2

Citizen science and its relation to more traditional approaches to ecological research. Citizen science research includes both preliminary analysis to examine patterns and trends, which are often of significance to conservation and management, and generation of a priori hypotheses and predictions, which lead to strong inference. When used to generate hypotheses, patterns and trends become analogous to the initial field observations ecologists make, fitting within a hypothetico-deductive framework. Predictions can be tested with existing data, new samples and observations, or citizen science experiments.

targeted monitoring can lead to observational tests of hypotheses that require data at the macroscale or recruitment of a subset of participants for more specific, high-effort or short-term studies directed at specific questions (**Figure 2**). The latter approach has been successful in a variety of research contexts, including cases where observers have been recruited to conduct manipulative experiments (Hames et al. 2002), collect and upload data from electronic sensors (Cooper & Mills 2005), or collect and mail biological samples to researchers (Koenig et al. 2009). This process also works in reverse, where ecologists involved in detailed, local studies can recruit citizen scientists to conduct experiments at larger scales, tapping existing groups like the Boy Scouts (Jones et al. 1998).

The following sections summarize the benefits and challenges of using citizen science data, beginning by assessing the growing impact of citizen science research. We use ornithological research as the primary example, because ornithology has a long history of embracing citizen science and therefore has a large number of research examples that can be evaluated. Even within ornithology, the greatest research impact has been achieved in the past decade using long-term monitoring databases designed at a time when many of the questions posed were not even on the table. We then review issues of data quality, emphasizing the challenges of working with data whose potential for error and bias is usually poorly understood. Our goal is to focus on large-scale citizen monitoring efforts, because other means of involving volunteers in research, e.g., EarthWatch, are not very different from the typical practice among ecologists of engaging undergraduate field assistants.

CONTRIBUTIONS TO BASIC AND APPLIED ECOLOGY

Below we present examples of a variety of questions that have been addressed with citizen science data on birds. The data sets come from citizen science efforts in North America and Europe (**Table 2**). We begin with global climate change effects and macroecology, because these are areas of research for which citizen science data are indispensable.

Global Climate-Change Effects on Birds

Recent changes in global temperatures have spurred significant interest in documenting and predicting ecological responses to climate change, with increased reliance on citizen science projects such as the CBC (Canterbury 2002, Repasky 1991, Root 1988). Large, spatial data sets with long time series are rare, even for birds, and have proven crucial for studying the role of recent climate change in driving shifts in species ranges (Thomas & Lennon 1999), onset of egg laying (Winkler et al. 2002), and migratory timing (Hüppop & Hüppop 2003).

Species range shifts: shifts in the geographical area occupied by a species

Species range shifts. In response to warming, populations should shift poleward and higher in elevation, with the most dramatic shifts occurring along range boundaries. Because breeding bird atlases have relatively even sampling effort and are often repeated at relevant intervals, they are useful for examining range boundary shifts (Lemoine et al. 2007, Zuckerberg et al. 2009b). Thomas & Lennon (1999) analyzed Britain's two breeding bird atlases (1968–1972 and 1988–1991) and found shifts in the northern range margins of 59 southerly species, concluding that climate change was the most likely explanation. These shifts were unidirectional and not matched by shifts in the southern range boundaries of northerly bird species. In Finland, Brommer (2004, 2008) found similar patterns and also suggested that shifts were larger for small-bodied and wetland birds. Northward range shifts have been documented for waders in Western Europe (Charadrii) (Maclean et al. 2008) as well as wintering and breeding birds in North America (Butler et al. 2007, Hitch & Leberg 2006, La Sorte et al. 2009, La Sorte & Thompson 2007). Since the 1930s, half of 24 bird species banded in the Netherlands, mostly short-distant migrants, have gradually begun to winter closer to their breeding grounds (Visser et al. 2009). In sum, citizen science data have been critical for documenting poleward range shifts for numerous taxa across the world, providing some of the strongest evidence that species are responding to recent climate change (Hickling et al. 2006, Parmesan & Yohe 2003, Walther et al. 2002).

Phenology. With growing interest in phenology (e.g., The USA-National Phenology Network), data from constant-effort banding operations, many of which rely upon citizen scientists, provide critical information. In Europe and North America, migratory arrival times appear variously tied to cycles of the North Atlantic Oscillation (NAO), the El Niño Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and local temperatures (Hüppop & Hüppop 2003, Macmynowski et al. 2007). Both long- (trans-Saharan) and short-distance migrants showed advancing autumnal departure dates based on a 42-year study in western Europe, but the effect was smallest for short-distance migrants wintering north of the Sahara (Jenni & Kery 2003). In regions of North America that have not experienced warming, arrival times have not shifted, although timing and speed of migration appear plastic and change with weather encountered en route (Marra et al. 2005). Challenges confronting the use of banding data to examine phenological shifts include heterogeneity in banding, recapture, and resighting efforts as well as temporal changes in land use, habitat, and supplemental feeding (Fiedler et al. 2004). Ideal data come from banding stations that follow standardized protocols covering the entire migration period (Hüppop & Hüppop 2003). Breeding phenology may be especially sensitive to climate change; a study of breeding phenology based on 2,881 nest record cards for Tree Swallows, *Tachycineta bicolor*, across the United States revealed that laying dates have advanced by about 9 days in just over 30 years (Winkler et al. 2002).

Changes in species richness and community composition. Although citizen science is often used to examine effects of environmental change on individual species, it is rarely used to examine

impacts on communities. We should be concerned about disruptive impacts of large shifts in community composition; lack of information on these shifts certainly weakens population-level projections. Lemoine et al. (2007) used atlas data collected an average of 12 years apart to examine the response of 21 European bird communities to climate change. They found that by 1992 species richness and community composition had already responded with an increase in the frequency of long-distance migrants and a reduction in the frequency of short-distance migrants, suggesting that warming increases the relative survival and reproductive success of more vagile species. This study points to a need for new citizen science research focused on geographic changes in community-level interactions.

Macroecology

Macroecology, the study of relationships between organisms and their environment over broad spatial scales, is more dependent than any other area of ecology on data collected by citizen scientists (Brown 1995, Gaston & Blackburn 2000). For example, the abundance-occupancy rule predicts that species with high average densities will be widely distributed, whereas species that are less abundant will have more restricted ranges (Gaston et al. 2000). Researchers have examined abundance-occupancy relationships over large geographic regions, both at a single point in time (interspecific relationships) and over multiple years (intraspecific relationships) (e.g., Blackburn et al. 1998; Freckleton et al. 2005, 2006; Gaston et al. 1998; Gaston & Curnutt 1998). Britain's Common Birds Census (**Table 2**), which ran from 1962 to 2000, produced detailed territory maps for nearly one million birds. This survey, carried out by 250 to 300 dedicated volunteers, used the same methods on the same plots year after year. The mean sampling duration was seven consecutive years, but a few observers surveyed the same sites for more than 30 years. Analysis of data for 73 farmland and 55 woodland bird species demonstrated that abundance-occupancy relationships have weakened over time, particularly for rare and declining species (e.g., Webb et al. 2007). More and more we are seeing a need for studies addressing the anthropogenic disruption of macroecological processes (Kuhn et al. 2008).

Landscape Ecology: Habitat Loss and Fragmentation

Citizen science data are particularly suitable for studying the effects on biodiversity of habitat loss and fragmentation, providing sufficient coverage for landscape-scaled, fragmentation studies. Using georeferenced data and broad geographic sampling of a large number of species with varying life-history characteristics (e.g., migratory status, vagility, habitat specificity, etc.), scientists are able to test predictions for which species will be more or less affected by fragmentation across a diversity of geographic regions. Ecologists have used both roadside surveys (Boulinier et al. 1998, 2001; Flather & Sauer 1996) and atlas data (Vallecillo et al. 2009, Venier et al. 2004, Villard et al. 1999, Zuckerberg & Porter 2010) to quantify the effects of habitat loss and fragmentation on wildlife populations. By and large, these studies showed that habitat loss and fragmentation reduce the probability that a species will occupy a landscape and increase variability in abundance (over twenty or more years), especially for habitat specialists (e.g., area-sensitive species).

Population and Community Ecology

Life-history evolution. Life-history theory makes explicit predictions about variation in survival and reproductive strategies of organisms, which can be tested by examining geographic variation within and among species. Citizen science data, such as those gathered on nest record cards and

through Cornell's NestWatch program, provide information on reproductive success of birds at the continental scale. These data have been used to test thermal constraints on hatching success by examining the geographic predictions of the egg viability hypothesis (Stoleson & Beissinger 1997). Because high ambient temperatures trigger embryonic development, leading either to early onset of incubation or to loss of early-laid eggs, increased ambient temperatures should result in increased hatching failure, especially for larger clutches, clutches laid closer to the equator, and clutches laid later in the breeding season. These predictions were supported by data on eastern bluebirds, *Sialia sialis*, for 32,567 eggs from 7231 nests in North America (Cooper et al. 2006). Future integration of citizen-generated bird-banding and recovery information with nest monitoring data would provide full demographic data, allowing ecologists to study the spatial ecology of population viability and life-history trade-offs.

HFDS: House Finch Disease Survey (run by the Cornell Lab of Ornithology)

MG: *Mycoplasma gallisepticum*

Ecology of infectious disease. Citizen science has considerable potential for helping to detect and track infectious disease (Crowl et al. 2008). The most striking example of this is the early detection and monitoring of the house finch eye disease, caused by a novel strain of the bacteria, *Mycoplasma gallisepticum* (MG), and first detected in North American finches in 1994. Infected house finches, *Carpodacus mexicanus*, show visible symptoms, including swollen eyes with excretions and lethargic behavior, which make a reliable diagnosis relatively simple, even for the novice observer (Dhondt et al. 1998). Recruiting volunteers from an existing network of citizen scientists involved in Project FeederWatch, the House Finch Disease Survey (HFDS) launched quickly and immediately began to collect data on the number of sick and healthy finches.

Citizen scientists not only tracked the geographic spread of MG in house finch populations, but they confirmed the spread to alternate host species, helping researchers identify possible modes of transmission (Hartup et al. 1998). Analysis established that high disease prevalence in house finches was associated with increased spread of MG to secondary hosts (Hartup et al. 2001). Data from BBS, CBC, and HFDS revealed that house finch numbers rapidly decreased and then stabilized at lower levels in areas of outbreaks, indicating a density-dependent process (Hochachka & Dhondt 2000). Disease dynamics were primarily a function of interactions among finches at individual sites with little evidence of habitat, regional, or weather effects (Hochachka & Dhondt 2006). This ability to take advantage of opportunities to recruit citizen scientists from general to targeted monitoring projects is an intrinsic value of citizen science.

In a second example, citizen science data have proven crucial for studying the recent spread of West Nile virus (WNV) in North America, particularly for the highly susceptible American Crow, *Corvus brachyrhynchos* (Bonter & Hochachka 2003, Hochachka et al. 2004) and California's endemic Yellow-billed Magpie, *Pica nuttalli* (Crosbie et al. 2008). Citizen science monitoring provides ready support both for new, direct measures of disease prevalence and for indirect analysis of disease impacts using population trends.

Interspecific competition and the ecology of invasive species. Invasive species are drivers of global environmental change, particularly in plant communities and aquatic systems (Sala et al. 2000), but environmental change is also likely to drive new invasions. Citizen science has tracked changes in distributions of invasive birds colonizing new habitats, including the rate of population growth in the invasive mute swan, *Cygnus olor*, in North America (Petrie & Francis 2003) and the extent of range expansion by the Eurasian collared-dove, *Streptopelia decaocto*, in both North America and Europe (Eraud et al. 2007, Rocha-Camarero & DeTrucios 2002). Going beyond distribution mapping, Bonter et al. (2009) linked the abundance and distribution of Eurasian collared-doves in Florida with remotely sensed land cover data, showing that urban and suburban sites were more likely to be occupied by this invasive bird.

Negative interactions between non-native, invasive species of birds that share an ecological niche with native species are widely assumed, but evidence of rangewide impacts is limited (Bonter et al. 2009, Koenig 2003). Data from the BBS and CBC demonstrated negative population-level effects of the house finch on established populations of the house sparrow (*Passer domesticus*, itself non-native) and purple finch (*Carpodacus purpureus*) as the house finch expanded into eastern North America (Wootton 1987). Revisiting data from BBS, CBC, and Project FeederWatch two decades later, after house finch populations were reduced by disease, Cooper et al. (2007b) demonstrated that house sparrow population declines slowed or ceased, further suggesting interspecific competition between house finch and house sparrow populations.

Potential effects of non-native starlings (*Sturnus vulgaris*) on native cavity-nesting birds in North America are of great interest to ornithologists (Cabe 1993), but incontrovertible evidence is limited. Using CBC and BBS data, Koenig (2003) failed to detect population declines that could be attributed to starlings for nearly all of 27 species examined with the exception of the sapsuckers (*Sphyrapicus* sp.). Similarly, Bonter et al. (2009) did not detect population-level effects of the invasive Eurasian collared-dove on native Columbids in Florida. However, data from the North American BBS suggest that outbreaks of the invasive gypsy moth, *Lymantria dispar*, provide a trophic subsidy for some native bird species (Barber et al. 2008).

Citizen science data have allowed researchers to identify hotspots of nonindigenous birds in the continental United States and Hawaii and to see how these hotspots relate to various biotic and abiotic factors (Crowl et al. 2008, Stohlgren et al. 2006). Creation of continental-scale networks may improve understanding of invasions and their consequences (Crowl et al. 2008). Although a number of networks have already been developed for this purpose (Meyerson & Mooney 2007), new tools for merging biodiversity databases would facilitate integrated research on ecological invasions.

Biocontaminants, Biogeochemistry, and Ecosystem Ecology

Biocontaminants have regained visibility in recent years as a major source of bird declines, largely through citizen science data. Hames et al. (2002) coupled monitoring data (BBS and Birds in Forested Landscapes) with smaller-scale studies to link acid deposition, low pH soils depleted of calcium, and a shortage of calcium-rich invertebrates to declines in the wood thrush, *Hylocichla mustelina*. In a detailed study, citizen participants placed moist cardboard squares out in the forest to quantify calcium-rich invertebrates, demonstrating an association between acid deposition and lower abundance of calcium sources required for successful breeding. Ongoing studies in New York State continue to involve these citizen scientists in collecting calcium-rich invertebrates to look for high concentrations of methyl mercury as a secondary impact of acidification. Meanwhile, researchers continue large-scale analysis linking declines in abundance based on BBS data to acid rain and heavy mercury deposition.

This approach to citizen science, recruiting dedicated individuals to help ask specific questions about environmental stressors, combines the spatial coverage of citizen science with more detailed, hypothesis-driven research to develop a deeper understanding of how a particular ecological system functions. Following up on this research, another group of ecologists conducted a local field experiment, demonstrating positive effects of calcium supplementation (liming) on both snail and ovenbird, *Seiurus aurocapillus*, abundance in Pennsylvania (Pabian & Brittingham 2007). Expanding upon citizen science research with rigorous, detailed field experiments leads to stronger inference and illustrates how ecologists might think about integrating citizen science into

large, collaborative endeavors, such as at Long Term Ecological Research sites and the National Ecological Observatory Network (NEON) (see **Figure 2**).

The previous examples notwithstanding, ecosystem studies have been slow to take advantage of the potential for gathering citizen science data. Plans for NEON include augmenting data collected at observatory sites with data from surrounding landscapes for broader understanding of spatial variation in ecological and biogeochemical processes (Lowman et al. 2009). NEON program developers should consider the possibility that citizen scientists may be tapped to carry mobile sensing devices into a broad range of environments (Burke et al. 2006) with particularly robust coverage in urban and suburban landscapes (**Figure 1**).

Ecosystem studies will benefit from both observational monitoring and engaging participants in collecting physical samples over broad regions. For example, a primary concern of ecosystem ecology is climate forcing, which describes the feedback loop in which climate-induced changes in ecosystems in turn produce changes in regional climate (Torn & Harte 2006). Research on climate forcing would certainly benefit from citizen science approaches, because dispersed citizen science observations could be used to ground truth remote sensing data, add spatial coverage to coordinated observational and experimental data sets, and provide critical sampling coverage for parameters such as weather, water table depth, soil moisture, phenology, and herbivory (Kueppers et al. 2007). The potential impact on climate forcing of changes in abundance and distributions of animal and plant species is currently addressed with crude categorical measures, suggesting an important role for biodiversity monitoring in this area of ecosystem research as well.

CHALLENGES IN WORKING WITH CITIZEN SCIENCE DATA

Citizen science data are often subject to a wide range of analysis methods with varying results. Take, for example, declines in neotropical migrants, which have concerned conservation biologists for nearly half a century (Carson 1962). Although declines, based on BBS data, were first attributed to tropical deforestation (Robbins et al. 1989), subsequent analysis suggested that they were a statistical artifact (James et al. 1996, Villard & Maurer 1996), that they were real, but caused by brown-headed cowbird (*Molothrus ater*) parasitism in North America (Böhning-Gaese & Bauer 1996), that they were an artifact of reduced detectability due to increased anthropogenic noise (Simons et al. 2007), and, most recently, that they were real and caused by widespread use of pesticides and other biocontaminants (Stutchbury 2007). This example shows not only that different approaches to the same data set can lead to different results and conclusions, but that achieving a best fit between analytical techniques, a data set, and a particular question is an active area of research.

Ecologists should anticipate a significant learning curve in working with any particular data set, in terms of both data management and developing an understanding of how to work with the data to minimize error and bias for particular research projects. Data quality issues are not unique to citizen science, and very large sample sizes will tend to lessen sampling error (that is, increase precision); however, issues of bias must be addressed in a question-specific manner with advanced statistical approaches, biological insight, and recognition that samples unbiased for one question are not necessarily unbiased for another.

Error and Bias Due to Variation in Observer Quality

An early concern regarding citizen science data was observer quality, that is, skill of participants compared to professional biologists. Like ecological field assistants, citizen scientists vary in ability,

NEON: National Ecological Observatory Network

Sampling error: the variation in the numerical spread of observations collected by citizen scientists and the associated parameter estimates that are computed through repeated samples (also known as precision)

Observer quality: relates to inter-observer variation in the ability to collect data and may result from age, education, collection skills, and length of program participation

experience, and type of training. Training deficits may certainly lead to increased error or bias, but it is not yet clear whether allowing citizen scientists to teach themselves how to follow protocols, as is typical for Internet-based projects, is less effective than personalized training.

One study demonstrated that trained volunteers were not as good as professionals at detecting low densities of woolly adelgids (Hemiptera), an insect pest of eastern hemlock (*Tsuga Canadensis*) (Fitzpatrick et al. 2009). Volunteers performed better when accompanied by professionals, suggesting that ongoing, personalized training is important. This study did not differentiate the importance of training from that of experience, leaving open the possibility that trained volunteers, left to their own devices, would provide professional quality data with more experience.

Acoustical monitoring has been used for birds and other taxa, but its efficacy for volunteer-based monitoring is best studied in amphibians. The North American Amphibian Monitoring Program and other anuran surveys employ hundreds of volunteers to keep track of frogs and toads (Table 2). Using anuran call surveys, researchers found that observer skill and inter-observer variation vary widely with species and should be controlled for, either in sampling design or in data analysis (de Solla et al. 2005, Genet & Sargent 2003, Lotz & Allen 2007, Pierce & Gutzwiller 2007, Weir et al. 2005). Coordinators of this program deemed this sampling issue so important that starting in 2006 they required program participants to pass an online “Frog Quiz” to ensure that they know how to identify species by their vocalizations.

Age of observers can also be an important determinant of data quality. Delaney et al. (2008) assessed the accuracy of data collected by over 1,000 citizen scientists to document the occurrence of invasive and native crabs within the intertidal zone of seven coastal states of eastern North America. Students in grades three and seven had the ability to differentiate between species of crabs with over 80% and 95% accuracy, respectively, but older volunteers with at least two years of university education were better able to correctly identify both the species and the age of crabs.

Several studies of volunteer-based monitoring programs conducted over many years have documented “learner” or “first-year” effects, where observers become better data collectors over time (Bas et al. 2008, Jiguet 2009, Kendall et al. 1996, Sauer et al. 1994, Schmeller et al. 2009). Improvement is expected with increased familiarity with protocols, improved identification skills, and increased awareness of where and when certain species occupy certain areas. Cognitive issues inherent in development of a “search image” may also play a role (Duncan & Humphreys 1989). In the French Breeding Bird Survey, Jiguet (2009) estimated the average increase in the detected abundance of bird species between the first and all subsequent years at about 4.3%. For many programs, new participants account for most of the variation in observer ability.

In general, we see a clear need for wider assessment of data quality and clarification of the independent effects of professional training, task training, experience with the task, observer age, training duration, mode of training (in person versus via the Internet), and variation in species detection probability with habitat or background composition of other, nontarget species. Some studies suggest that long, arduous, or repetitive tasks, complex methods, or difficult taxonomic identifications are not suitable for citizen scientists (Darwall & Dulvy 1996, Newman et al. 2003, Penrose & Call 1995). Most research has compared novice participants with professionals, the latter having both extensive experience and background, including experience on the focal project (Fitzpatrick et al. 2009, Galloway et al. 2006). Ecologists working with long-term monitoring data and projects delivered over the Internet should be concerned with such issues as: (a) whether training at a distance works, (b) whether cognitive biases lead to chronic data biases, (c) whether certain attributes or species are particularly difficult to measure or tell apart, and (d) how much experience is required before data are reliable.

Tools for Dealing with Observer Error

Data validation is an integral component of citizen science research. Major sources of error and bias, if identified, can be added to the metadata for a project and considered during analysis. Some avian monitoring projects vet data using varying combinations of local coordinators and Internet applications. Applications developed for eBird and FeederWatch use more than 600 geographic and numeric data quality filters, which allow rapid data review and electronic communication with observers to validate questionable observations. For example, in 2008–2009, Project FeederWatch received 1,342,633 observations. Biologists reviewing the 0.01% of reports flagged as “unexpected” determined that 378 records required supporting evidence in order to be accepted into the database. They received 291 responses (77%) to emails requesting validating evidence. Of the 291 responses, 158 records were confirmed (54%), 45 identifications were corrected in the database (16%), and 88 provided too little evidence to confirm the report (30%).

Sampling Bias

Citizen science data gain research value with increased understanding of their inherent biases. Bias is a complex issue that requires serious investigation, because it varies with sampling method, effort, species, and habitats sampled; usually there is potential for complex interactions among these variables.

Variation in sampling effort (time). Attempts to standardize sampling effort vary from regular-interval, repeated-visits protocols to flexible guidelines and benchmarks that participants are encouraged to reach (**Table 2**). Because protocols that are too rigid or demanding will reduce the number of volunteers, some program managers scaffold participation, recruiting a large number of participants to collect incidental observations while funneling a subset of very committed volunteers into stricter, more labor intensive protocols. When programs have no prerequisites for minimum effort (that is, any amount of effort is allowed), samples may be highly biased, resulting in over-reporting of rare species, under-reporting of common species, and failure to report repeated sightings, because they are not deemed as “interesting” by the observer. Further, people may simply stop sampling when there are no interesting organisms to be seen. In general, this can lead to analyses and conclusions that reflect variation in effort more than actual biological patterns and processes.

Atlases are relatively labor-intensive forms of citizen science in which volunteers are asked to collect data on the occurrence (and sometimes abundance or breeding status) of hundreds of species in thousands of designated sampling blocks (**Table 2**) (Dunn & Weston 2008, Gibbons et al. 2007). To achieve consistent coverage, many atlas programs have standard benchmarks based on the number of species sampled within a given block or the hours of effort. With repeated atlases, often spanning twenty years or more, effort and the change in effort for individual blocks are critical sources of variation that should be accounted for. Blocks differ in land cover composition such that equal time spent surveying two atlas blocks does not necessarily mean equivalent probabilities of detecting species when they are present; however, large differences in effort are particularly problematic when making analytical comparisons (McGowan & Zuckerberg 2008).

Citizen science programs with few or no formal guidelines for standardizing effort, such as the CBC, often employ teams that vary widely in terms of number of participants and count duration (**Table 2**). The amount of effort expended in producing a CBC is generally considered an important variable that should be accounted for in analysis (e.g., Link & Sauer 1999). One of the main challenges with citizen science data could be resolved by standardizing sampling effort.

Species detectability:

the probability of detecting a species if it is present, also called detection probability

Stratified sampling:

study design that involves grouping individuals or locations into subgroups before sampling

Random within-strata sampling:

study design that involves sampling at random within predesignated subgroups

Sampling bias:

the difference between the expected value of an estimate and the true value of the parameter of interest

Collecting the appropriate data on effort expended is also helpful in disentangling variation in effort from variation related to true biological patterns and processes; however, it still does not address the interaction between which birds are seen and the propensity of the observer to keep watching, a relationship that requires further study.

When sampling effort is standardized, occupancy modeling allows researchers to estimate abundance, occurrence, and species richness while accounting for species detectability (Royle et al. 2005, 2007). Sampling frameworks based on repeated visits to the same site quantify variation in the ability to detect particular species (MacKenzie 2006). For example, the Swiss Common Breeding Bird Survey (“Monitoring Häufige Brutvögel”) (**Table 2**) relies on over 200 skilled volunteers to survey 150 breeding bird species in 267 1-km squares laid out as a representative grid across Switzerland. Using a simplified territory mapping protocol and a specified transect route, each square is surveyed three times during the breeding season. Such standardized field protocols based on repeated visits allow researchers to develop precise estimates of population trends for most common species while accounting for individual observers’ and site-level differences in ability to detect species. In the process of documenting biological patterns and trends with citizen science data, statisticians have pushed the field to adopt new, more rigorous methods of data analysis and a deeper understanding of sources of variation inherent in all ecological data.

Variation in sampling effort (space). Like temporal heterogeneity, spatial heterogeneity of sampling effort results in biased estimates. Large, multispecies citizen science projects like the North American BBS and eBird ask people to report counts for all of the species they see or hear; researchers then code as “absent” locations reporting birds other than the target species. This strategy works best when projects sample a broad range of species or include monitoring of a smaller number of very common species to provide reasonable background data on sampling effort.

Even when citizen science programs use some form of stratified sampling, random within-strata sampling, or random sampling design, data analysts are charged with determining whether the samples are representative of the surrounding region (that is, unbiased). In general, if the habitat types surrounding sampling sites are not representative of the larger regional landscape, then differences in species occurrences or abundance may reflect spatial sampling bias rather than true geographic differences in population size (Bart et al. 1995, Lawler & O’Connor 2004, Niemuth et al. 2007).

Sampling from roads, such as with the BBS, means that roadless areas are left out of the data set completely. Several researchers have attempted to quantify whether roadside surveys are representative of the surrounding regions with mixed results (Bart et al. 1995, Hanowski & Niemi 1995, Harris & Haskell 2007, Keller & Yahner 2007, Niemuth et al. 2007). In one such study, Betts et al. (2007) analyzed changes in mature forest cover immediately adjacent to BBS routes (150 m on either side of the road) compared to the larger region within which the route was embedded (one surrounding degree block; 8,758 km²). Although they did not detect a difference in the rate of change in forest cover between 1974 and 2001, BBS routes were less representative of the regional landscape during certain decades.

Although roadless areas may be undersampled, residential landscapes, which tend to have higher levels of habitat degradation, are often oversampled (**Figure 1**). Corrections can be made if data from uninhabited areas are sufficient; however, if they are sparse, this can lead to biased estimates of population size, a mistaken view of the relationship between habitat and species abundance or occupancy, and flawed distribution maps.

Methods for Improving Data Analysis

There is generally a steep learning curve both for working with a particular database, which gains value with increased documentation of potential sources of error and bias (that is, with metadata), and for individual scientists, who may require considerable time to become familiar with a particular data set. Over time, analysts discover ways to filter large data sets, using informed rules for eliminating error and bias, such as excluding data from (*a*) first-year participants, (*b*) people who submit erratically, and (*c*) participants who have submitted erroneous reports. Continued refinement and advancement of spatiotemporal modeling (e.g., Fink et al. 2010) will likely help to improve the quality and accessibility of citizen science research for a broader swath of researchers.

CONCLUSIONS

We are just beginning to see the benefits of combining data from separate, independent citizen science programs to monitor changes in populations, communities, and ecosystems (Freeman et al. 2007, Link & Sauer 2007, Link et al. 2008, Zuckerberg et al. 2009a). In the rush to meet the requirements of ecologists, managers, and government agencies, new, collaborative efforts seek to combine and federate monitoring data, linking them to environmental data and analysis tools (Kelling et al. 2009). Simultaneously, there is interest on the part of government and funding agencies to build national databases and cyberinfrastructures for large-scale ecological research. These are positive steps toward recognizing the value of understanding ecological processes and addressing applied problems at large geographic scales (e.g., NEON, the USA-National Phenology Network, Data.gov, and new National Science Foundation funding initiatives). But in the scramble for resources, it is important to recognize that the scientific and conservation goals are best served through partnership with existing projects toward ensuring that data sets can be combined and that historic data are digital and accessible online. Somewhat ironic is the fact that in the midst of a flurry of project development it has been difficult to obtain funding to digitize historic citizen science data, a problem that is currently being addressed with more economical attempts at crowdsourcing data entry.

To be successful, efforts to create and use citizen science data for the public good will require bringing historic data into national databases, while taking advantage of existing knowledge about how to make citizen science projects work. If species ranges warrant it, citizen science projects must (and most do) cross national boundaries, necessitating partnerships between governmental and nongovernmental organizations to achieve relevant geographic scope. Education specialists and information scientists have led much of the development of citizen science projects. Increased involvement of top ecological researchers in the design of citizen science projects is necessary to take monitoring to the next level. In the best of all possible worlds, this would focus efforts on a strategic set of questions of critical importance to the fields of basic and applied ecology.

To the extent that citizen science is valuable as a research tool, there is need for funding agencies to ensure that citizen science is on their radar as a developing field, requiring training programs and ecologists' engagement in development of projects and cyberinfrastructures. Although the pool of scientists competent to use the growing array of sophisticated spatial analysis tools is still quite small and the tools themselves are challenging to master, we are beginning to see Ph.D. theses in ecology based primarily or even exclusively on citizen science data. Programs and funding to support combined training and collaboration in ecology, computational biology, and advanced geospatial statistics have been lacking; these are essential to ensure full and accurate use of the large spatial data sets that are rapidly becoming available for birds and other organisms. As concerns

about changes in environmental quality increase, we expect citizen science, with its broad spatial and temporal reach, to play an increasingly important role.

SUMMARY POINTS

1. A large suite of applied and basic ecological processes occur at geographic scales beyond the reach of ordinary research methods.
2. Citizen science is perhaps the only practical way to achieve the geographic reach required to document ecological patterns and address ecological questions at scales relevant to species range shifts, patterns of migration, spread of infectious disease, broad-scale population trends, and impacts of environmental processes like landscape and climate change.
3. Citizen science methodologies are diverse and often lead to varying levels of error and bias that are poorly understood; this has necessitated development of new, more sophisticated approaches to the analysis of large data sets, including innovations in geospatial statistics, exploratory data-mining, hierarchical modeling, and computational biology.
4. As the use of large citizen science databases grows, additional resources are required for data management, training in analytical techniques, and the development of macroecological theory.
5. The value of citizen science to applied and basic ecology has not been fully realized and articulated; increasing involvement of leading ecologists in prioritizing research goals, evaluating data quality, and informing sampling methodologies will advance the field.

FUTURE ISSUES

1. Cyberinfrastructure: Concomitant with expansion of citizen science is development of new sensor technologies, mobile and stationary, that will automate collection of large volumes of ecological data. It is unrealistic to believe that we can automate collection of all ecologically important data; making sense of diverse data sets will require increasingly advanced cyberinfrastructures to take in, vet, and federate data on a wide range of biotic and abiotic factors.
2. Data quality: Citizen science would benefit from increased emphasis on data quality, including adopting increasingly rigorous protocols such as repeated sampling at predetermined intervals, improved strategies for reducing spatial biases, use of quizzes and games to evaluate observer skill, and tools for inclusion of data on observer quality in the database.
3. Research and training: Data-intensive ecology will require research and training in new computational and statistical modeling approaches to working with large, spatial data sets, including tools for exploration, analysis, and displaying results.

4. Minimal collaborative units: Identification of critical skill sets required to make sense of large, complex ecological data sets will be vital; we suggest that the minimal trio should include a field ecologist, a geospatial ecologist, and a trained statistician. Collaborations will become increasingly cross-disciplinary (www.computational-sustainability.org) involving fields such as computer science, information science, operations research, applied mathematics, and statistics.
5. Real-time synthesis with environmental and social data: Associating citizen science data with ancillary data sets is critical, but can be complex and computationally intensive. Online data warehouses will play a critical role in linking citizen science data with other databases containing information on land cover, topography, census data, LIDAR (Light Detection And Ranging), and NDVI (Normalized Difference Vegetation Index). Further, historical data sets must be digitized and integrated with contemporary citizen science platforms.

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LITERATURE CITED

- Barber NA, Marquis RJ, Tori WP. 2008. Invasive prey impacts the abundance and distribution of native predators. *Ecology* 89:2678–83
- Bart J, Hofschien M, Peterjohn BG. 1995. Reliability of the breeding bird survey: effects of restricting surveys to roads. *Auk* 112:758–61
- Bas Y, Devictor V, Moussus JP, Jiguet F. 2008. Accounting for weather and time-of-day parameters when analyzing count data from monitoring programs. *Biodivers. Conserv.* 17:3403–16
- Betts MG, Mitchell D, Dlamond AW, Bety J. 2007. Uneven rates of landscape change as a source of bias in roadside wildlife surveys. *J. Wildl. Manag.* 71:2266–73
- Blackburn TM, Gaston KJ, Greenwood JJD, Gregory RD. 1998. The anatomy of the interspecific abundance-range size relationship for the British avifauna: II. Temporal dynamics. *Ecol. Lett.* 1:47–55
- Bock C, Lepthien L. 1975. A Christmas count analysis of woodpecker abundance in the United States. *Wilson Bull.* 87:355–66
- Böhning-Gaese K, Bauer H-G. 1996. Changes in species abundance, distribution, and diversity in a central European bird community. *Conserv. Biol.* 10:175–87
- Bonney R, Cooper CB, Dickinson J, Kelling S, Phillips T, et al. 2009. Citizen science: a developing tool for expanding science knowledge and scientific literacy. *BioScience* 59:977–84
- Bonter D, Hochachka W. 2003. Widespread declines of chickadees and Corvids: Possible impacts of West Nile virus. *Am. Birds* 103:22–25
- Bonter DN, Zuckerberg B, Dickinson JL. 2009. Invasive birds in a novel landscape: habitat associations and effects on established species. *Ecography* (DOI: 10.1111/j.1600-0587.2009.06017.x)

- Boulinier T, Nichols JD, Hines JE, Sauer JR, Flather CH, Pollock KH. 1998. Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proc. Natl. Acad. Sci. USA* 95:7497–501
- Boulinier T, Nichols JD, Hines JE, Sauer JR, Flather CH, Pollock KH. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* 82:1159–69
- Brommer JE. 2004. The range margins of northern birds shift polewards. *Ann. Zool. Fenn.* 41:391–97
- Brommer JE. 2008. Extent of recent polewards range margin shifts in Finnish birds depends on their body mass and feeding ecology. *Ornis Fenn.* 85:109–17
- Brown JH. 1995. *Macroecology*. Chicago: Univ. Chicago Press. xiii, 269 pp.
- Burke J, Estrin D, Hansen M, Parker A, Ramanathan N, et al. 2006. *Participatory sensing*. Presented at World Sensor Web Workshop, ACM SenSys '06, Boulder, CO
- Butler JR, MacMynowski DP, Laurent C, Root TL. 2007. Temperature-associated dynamics of songbird winter distributions and abundances. *AMBIO* 36:657–60
- Cabe PR. 1993. European Starling (*Sturnus vulgaris*). In *The Birds of North America Online*, ed. A Poole. Ithaca: The Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/048>
- Canterbury G. 2002. Metabolic adaptation and climatic constraints on winter bird distribution. *Ecology* 83:946–57
- Carson R. 1962. *Silent Spring*. Boston: Houghton Mifflin
- Cooper CB, Dickinson J, Phillips T, Bonney R. 2007a. Citizen science as a tool for conservation in residential ecosystems. *Ecol. Soc.* 12:11 [online] <http://www.ecologyandsociety.org/vol12/iss2/art11/>
- Cooper CB, Hochachka WM, Dhondt AA. 2007b. Contrasting natural experiments confirm competition between House Finches and House Sparrows. *Ecology* 88:864–70
- Cooper CB, Hochachka W, Phillips TB, Dhondt AA. 2006. Geographic and seasonal gradients in hatching failure in eastern bluebirds reinforce clutch size trends. *Ibis* 148:221–30
- Cooper CB, Mills H. 2005. Software to quantify incubation behavior from time series recordings. *J. Field Ornithol.* 76:352–56
- Crosbie S, Koenig W, Reitem W, Kramer V, Marcus L, et al. 2008. Early impact of West Nile virus on the Yellow-Billed Magpie (*Pica nuttalli*). *Auk* 125:542–50
- Crowl TA, Crist TO, Parmenter RR, Belovsky G, Lugo AE. 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. *Front. Ecol. Environ.* 6:238–46
- Darwall W, Dulvy N. 1996. An evaluation of the suitability of nonspecialist volunteer researchers for coral reef fish surveys, Mafia Island, Tanzania—a case study. *Biol. Conserv.* 78:223–31
- Delaney DG, Sperling CD, Adams CS, Leung B. 2008. Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biol. Invasions* 10:117–28
- de Solla SR, Shirose LJ, Fernie KJ, Barrett GC, Brousseau CS, Bishop CA. 2005. Effect of sampling effort and species detectability on volunteer based anuran monitoring programs. *Biol. Conserv.* 121:585–94
- Dhondt AA, Tessaglia DL, Slothower R. 1998. Epidemic mycoplasmal conjunctivitis in House Finches from eastern North America. *J. Wildl. Dis.* 34:265–80
- Duncan J, Humphreys G. 1989. Visual search and stimulus similarity. *Psychol. Rev.* 96:433–58
- Dunn AM, Weston MA. 2008. A review of terrestrial bird atlases of the world and their application. *Emu* 108:42–67
- Eraud C, Boutin J-M, Roux D, Faivre B. 2007. Spatial dynamics of an invasive bird species assessed using robust design occupancy analysis: the case of the Eurasian collared dove (*Streptopelia decaocto*) in France. *J. Biogeogr.* 34:1077–86
- Fiedler W, Bairlein F, Koppen U. 2004. Using large-scale data from ringed birds for the investigation of effects of climate change on migrating birds: pitfalls and prospects. *Birds Climate Change* 35:49–67
- Field D, Voss P, Kuczenski T, Hammer R, Radeloff V. 2010. Reaffirming social landscape analysis in landscape ecology: a conceptual framework. *Soc. Nat. Resour.* 16:349–61
- Fink D, Hochachka WM, Zuckerberg B, Winkler DW, Shaby B, et al. 2010. Spatiotemporal exploratory models for broad-scale survey data. *Ecol. Appl.* In press
- Fitzpatrick M, Preisser E, Ellison A, Elkinton J. 2009. Observer bias and the detection of low-density populations. *Ecol. Appl.* 19:1673–79

- Flather CH, Sauer JR. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology* 77:28–35
- Freckleton RP, Gill JA, Noble D, Watkinson AR. 2005. Large-scale population dynamics, abundance-occupancy relationships and the scaling from local to regional population size. *J. Anim. Ecol.* 74:353–64
- Freckleton RP, Noble D, Webb TJ. 2006. Distributions of habitat suitability and the abundance-occupancy relationship. *Am. Nat.* 167:260–75
- Freeman SN, Noble DG, Newson SE, Baillie SR. 2007. Modelling population changes using data from different surveys: the common birds census and the breeding bird survey. *Bird Study* 54:61–72
- Galloway A, Tudor M, Vander Haegen W. 2006. The reliability of citizen science: a case study of Oregon White Oak stand surveys. *Wildl. Soc. Bull.* 34:1425–29
- Gaston KJ, Blackburn TM. 2000. *Pattern and Process in Macroecology*. Oxford: Blackwell Sci. xii, 377 pp.
- Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH. 2000. Abundance-occupancy relationships. *J. Appl. Ecol.* 37:39–59
- Gaston KJ, Blackburn TM, Gregory RD, Greenwood JJD. 1998. The anatomy of the interspecific abundance-range size relationship for the British avifauna: I. Spatial patterns. *Ecol. Lett.* 1:38–46
- Gaston KJ, Curnutt JL. 1998. The dynamics of abundance-range size relationships. *Oikos* 81:38–44
- Genet KS, Sargent LG. 2003. Evaluation of methods and data quality from a volunteer-based amphibian call survey. *Wildl. Soc. Bull.* 31:703–14
- Gibbons DW, Donald PF, Bauer HG, Fornasari L, Dawson IK. 2007. Mapping avian distributions: the evolution of bird atlases. *Bird Study* 54:324–34
- Greenwood JJD. 2007. Citizens, science and bird conservation. *J. Ornithol.* 148:S77–124
- Hames R, Rosenberg K, Lowe J, Barker S, Dhondt A. 2002. Adverse effects of acid rain on the distribution of the Wood Thrush *Hylocichla mustelina* in North America. *Proc. Natl. Acad. Sci. USA* 99:11235–40
- Hanowski JAM, Niemi GJ. 1995. A comparison of on- and off-road bird counts: Do you need to go off road to count birds accurately? *J. Field Ornithol.* 66:469–83
- Harris JBC, Haskell DG. 2007. Land cover sampling biases associated with roadside bird surveys. *Avian Conserv. Ecol.* 2(2):12. Available at <http://www.ace-eco.org/vol2/iss2/art12/>
- Hartup BK, Dhondt AA, Sydenstricker KV, Hochachka WM, Kollias GV. 2001. Host range and dynamics of mycoplasmal conjunctivitis among birds in North America. *J. Wildl. Dis.* 37:72–81
- Hartup BK, Mohammed HO, Kollias GV, Dhondt AA. 1998. Risk factors associated with mycoplasmal conjunctivitis in House Finches. *J. Wildl. Dis.* 34:281–88
- Hepper FN. 2003. Phenological records of English garden plants in Leeds (Yorkshire) and Richmond (Surrey) from 1946 to 2002. An analysis related to global warming. *Biodivers. Conserv.* 12:2503–20
- Hickling R, Roy DB, Hill JK, Fox R, Thomas CD. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Change Biol.* 12:450–55
- Hitch AT, Leberg PL. 2006. Breeding distributions of North American bird species moving north as a result of climate change. *Conserv. Biol.* 21:534–39
- Hochachka WM, Dhondt AA. 2000. Density-dependent decline of host abundance resulting from a new infectious disease. *Proc. Natl. Acad. Sci. USA* 97:5303–6
- Hochachka WM, Dhondt AA. 2006. House Finch (*Carpodacus mexicanus*) population- and group-level responses to a bacterial disease. *Ornithol. Monogr.* 60:30–43
- Hochachka WM, Dhondt AA, McGowan KJ, Kramer LD. 2004. Impact of West Nile virus on American crows in the northeastern United States, and its relevance to existing monitoring programs. *EcoHealth* 1:60–68
- Howe J. 2006. The rise of crowsourcing. *Wired* 14.06
- Hüppop O, Hüppop K. 2003. North Atlantic Oscillation and the timing of spring migration in birds. *Proc. R. Soc. Lond. Ser. B* 270:233–40
- Irwin A. 2001. Constructing the scientific citizen: Science and democracy in the biosciences. *Public Underst. Sci.* 10:1–18
- James F, McCulloch C, Wiedenfeld D. 1996. New approaches to the analysis of population trends in land birds. *Ecology* 77:13–27
- Jenni L, Kery M. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proc. R. Soc. Lond. Ser. B* 270:1467–71

Establishes a density-dependent pattern in the transmission of a novel disease in wild birds.

- Jiguet F. 2009. Method learning caused a first-time observer effect in a newly started breeding bird survey. *Bird Study* 56:253–58
- Jones C, Ostfeld R, Richard M, Schaubert E, Wolff J. 1998. Chain reactions linking acorns to gypsy moth outbreaks and lyme disease risk. *Science* 279:1023–26
- Jordan R, Singer F, Vaughan J, Berkowitz A. 2009. What should every citizen know about ecology? *Front. Ecol. Environ.* 7:495–500
- Keller GS, Yahner RH. 2007. Seasonal forest-patch use by birds in fragmented landscapes of south-central Pennsylvania. *Wilson J. Ornithol.* 119:410–18
- Kelling S, Hochachka W, Fink D, Riedewald M, Caruana R, et al. 2009. Data-intensive science: a new paradigm for biodiversity studies. *BioScience* 59:613–20
- Kendall WL, Peterjohn BG, Sauer JR. 1996. First-time observer effects in the North American Breeding Bird Survey. *Auk* 113:823–29
- Koenig WD. 2003. European Starlings and their effect on native cavity-nesting birds. *Conserv. Biol.* 17:1134–40
- Koenig WD, Knops JMH, Dickinson JL, Zuckerberg B. 2009. Latitudinal decrease in acorn size in bur oak (*Quercus macrocarpa*) is due to environmental constraints, not avian dispersal. *Botany* 87:349–56
- Kueppers LM, Torn MS, Harte J. 2007. *Quantifying Ecosystem Feedbacks to Climate Change: Observational Needs and Priorities*. Rep. Off. Biol. Environ. Res., Off. Sci., U.S. Dept. Energy. Berkeley: Lawrence Berkeley Natl. Lab.
- Kuhn I, Böhning-Gaese K, Cramer W, Klotz S. 2008. Macroecology meets global climate change research. *Global Ecol. Biogeogr.* 17:3–4
- La Sorte FA, Lee TM, Wilman H, Jetz W. 2009. Disparities between observed and predicted impacts of climate change on winter bird assemblages. *Proc. R. Soc. B* 276:3167–74
- La Sorte FA, Thompson FR. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88:1803–12
- Lawler JJ, O'Connor RJ. 2004. How well do consistently monitored breeding bird survey routes represent the environments of the conterminous United States? *Condor* 106:801–14
- Lemoine N, Schaefer H-C, Böhning-Gaese K. 2007. Species richness of migratory birds is influenced by global climate change. *Glob. Ecol. Biogeogr.* 16:55–64
- Lepczyk CA, Boyle OD, Vargo TL, Gould P, Jordan R, et al. 2009. Citizen science in ecology: the intersection of research and education. *Bull. Ecol. Soc. Am.* 2009:308–17
- Link WA, Sauer JR. 1999. Controlling for varying effort in count surveys—an analysis of Christmas Bird Count data. *J. Agric. Biol. Environ. Stat.* 4:116–25
- Link WA, Sauer JR. 2007. Seasonal components of avian population change: joint analysis of two large-scale monitoring programs. *Ecology* 88:49–55
- Link WA, Sauer JR, Niven DK. 2008. Combining breeding bird survey and Christmas Bird Count data to evaluate seasonal components of population change in northern bobwhite. *J. Wildl. Manag.* 72:44–51
- Lotz A, Allen CR. 2007. Observer bias in anuran call surveys. *J. Wildl. Manag.* 71:675–79
- Lowman M, D'Avanzo C, Brewer C. 2009. A national ecological network for research and education. *Science* 323:1172–74
- Machlis G, Force J, Burch WJ. 1997. The human ecosystem part I: the human ecosystem as an organizing concept in ecosystem management. *Soc. Nat. Resour.* 10:347–67
- MacKenzie DI. 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species*. Burlington, MA: Elsevier
- Maclean IMD, Austin GE, Rehfish MM, Blew J, Crowe O, et al. 2008. Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Glob. Change Biol.* 14:2489–500
- Macmynowski DP, Root TL, Ballard G, Geupel G. 2007. Changes in spring arrival of Nearctic-Neotropical migrants attributed to multiscalar climate. *Glob. Change Biol.* 13:2239–51
- Marra PP, Francis CM, Mulvihill RS, Moore FR. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142:307–15
- McCaffrey R. 2005. Using citizen science in urban bird studies. *Urban Habitats* 3:1–86
- McGowan KJ, Zuckerberg B. 2008. Summary of results. In *The Second Atlas of Breeding Birds in New York State*, ed. KJ McGowan, K Corwin, pp. 15–42. Ithaca, NY: Cornell Univ. Press

- Meyerson LA, Mooney HA. 2007. Invasive alien species in an era of globalization. *Front. Ecol. Environ.* 5:199–208
- Newman C, Buesching C, MacDonald D. 2003. Validating mammal monitoring methods and assessing the performance of volunteers in wildlife conservation—“Sed quis custodiet ipsos custodiet?” *Biol. Conserv.* 113:189–97
- Nichols JD, Williams BK. 2006. Monitoring for conservation. *Trends Ecol. Evol.* 21:668–73
- Niemuth ND, Dahl AL, Estey ME, Loesch CR. 2007. Representation of landcover along breeding bird survey routes in the northern plains. *J. Wildl. Manag.* 71:2258–65
- Pabian S, Brittingham M. 2007. Terrestrial liming benefits birds in an acidified forest in the Northeast. *Ecol. Appl.* 17:2184–94
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Penrose D, Call S. 1995. Volunteer monitoring of benthic macroinvertebrates: regulatory biologists’ perspectives. *J. North Am. Benthol. Soc.* 14:203–9
- Petrie SA, Francis CM. 2003. Rapid increase in the lower Great Lakes population of feral mute swans: a review and a recommendation. *Wildl. Soc. Bull.* 31:407–16
- Pierce BA, Gutzwiller KJ. 2007. Interobserver variation in frog call surveys. *J. Herpetol.* 41:424–29
- Ratcliff J. 2008. *The Transit of Venus Enterprise in Victorian Britain*. London: Pickering & Chatto
- Repasky RR. 1991. Temperature and the northern distributions of wintering birds. *Ecology* 72:2274–85
- Robbins C, Sauer J, Greenberg R, Droege S. 1989. Population declines in North American birds that migrate to the Neotropics. *Proc. Natl. Acad. Sci. USA* 86:7658–62**
- Rocha-Camarero G, DeTrucios SJH. 2002. The spread of the Collared Dove *Streptopelia decaocto* in Europe: colonization patterns in the west of the Iberian Peninsula. *Bird Study* 49:11–16
- Root TL. 1988. Environmental factors associated with avian distributional boundaries. *J. Biogeogr.* 15:489–505
- Royle JA, Kéry M, Gautier R, Schmid H. 2007. Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecol. Monogr.* 77:465–81**
- Royle JA, Nichols JD, Kéry M. 2005. Modelling occurrence and abundance of species when detection is imperfect. *Oikos* 110:353–59
- Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–74
- Sauer JR, Peterjohn BG, Link WA. 1994. Observer differences in the North-American breeding bird survey. *Auk* 111:50–62**
- Schmeller DS, Henry PY, Julliard R, Gruber B, Clobert J, et al. 2009. Advantages of volunteer-based biodiversity monitoring in Europe. *Conserv. Biol.* 23:307–16
- Simons T, Alldredge M, Pollock K. 2007. Experimental analysis of the auditory detection process on avian point counts. *Auk* 124:986–99
- Stohlgren TJ, Barnett D, Flather C, Fuller P, Peterjohn B, et al. 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biol. Invasions* 8:427–47
- Stoleson SH, Beissinger SR. 1997. Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. *Ecol. Monogr.* 67:131–54
- Stutchbury B. 2007. *Silence of the Songbirds*. New York: Walker
- Thomas CD, Lennon JJ. 1999. Birds extend their ranges northwards. *Nature* 399:213
- Torn MS, Harte J. 2006. Missing feedbacks, asymmetric uncertainties, and the underestimation of future warming. *Geophys. Res. Lett.* 33:L10703
- Vallecillo S, Brotons L, Thuiller W. 2009. Dangers of predicting bird species distributions in response to land-cover changes. *Ecol. Appl.* 19:538–49
- Venier LA, Pearce J, McKee JE, McKenney DW, Niemi GJ. 2004. Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. *J. Biogeogr.* 31:315–31
- Villard M-A, Maurer B. 1996. Geostatistics as a tool for examining hypothesized declines in migratory songbirds. *Ecology* 77:59–68
- Villard M-A, Trzcinski MK, Merriam G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv. Biol.* 13:774–83

Stands out as a seminal paper using Breeding Bird Survey data to quantify large-scale trends in bird populations.

Provides a hierarchical spatial model for estimating abundance and occurrence when detection is imperfect.

Is one of the first papers to detect and quantify first-year observer effects in Breeding Bird Survey participants.

Stands out as the first paper to demonstrate advancing laying dates continent-wide in a North American migratory bird.

- Visser ME, Perdeck AC, van Balen JH, Both C. 2009. Climate change leads to decreasing bird migration distances. *Glob. Change Biol.* 15:1859–65
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–95
- Webb TJ, Noble D, Freckleton RP. 2007. Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *J. Anim. Ecol.* 76:123–34
- Weir LA, Royle JA, Nanjappa P, Jung RE. 2005. Modeling anuran detection and site occupancy on North American Amphibian Monitoring Program (NAAMP) routes in Maryland. *J. Herpetol.* 39:627–39
- Winkler D, Dunn P, McCulloch C. 2002. Predicting the effects of climate change on avian life history traits. *Proc. Natl. Acad. Sci. USA* 99:13595–99**
- Wootton JT. 1987. Interspecific competition between introduced house finch populations and two associated passerine species. *Oecologia* 71:325–31
- Yoccoz NG, Nichols JD, Boulinier T. 2001. Monitoring of biological diversity in space and time. *Trends Ecol. Evol.* 16:446–53
- Zuckerberg B, Porter WF. 2010. Thresholds in the long-term responses of breeding birds to forest cover and fragmentation. *Biol. Conserv.* 143:952–62
- Zuckerberg B, Porter WF, Corwin K. 2009a. The consistency and stability of abundance-occupancy relationships in large-scale population dynamics. *J. Anim. Ecol.* 78:172–81
- Zuckerberg B, Woods AM, Porter WF. 2009b. Poleward shifts in breeding bird distributions in New York State. *Glob. Change Biol.* 15:1866–83

RELATED RESOURCES

- Bhattacharjee Y. 2005. Citizen Scientists supplement work of Cornell researchers. *Science* 308:1402–3
- Cohen J. 2008. Citizen Science: Can volunteers do real research? *BioScience* 58:192–97
- Irwin A. 1995. *Citizen Science: A Study of People, Expertise, and Sustainable Development*. New York: Routledge
- Karasti H, Baker KS. 2008. Digital data practices and the long-term ecological research program growing global. *Int. J. Digit. Curation* 3:42–58
- Silvertown J. 2009. A new dawn for citizen science. *Trends Ecol. Evol.* 1118:1–5
- Visser ME, van Noordwijk A, Tinbergen J, Lessells C. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. B* 265:1867–70



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