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Partly Cloudy with a Chance of Migration: Weather, Radars, and Aeroecology

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ABSTRACT

Aeroecology is an emerging scientific discipline that integrates atmospheric science, earth science, geography, ecology, computer science, computational biology, and engineering to further understanding of biological patterns and processes. The unifying concept underlying this new transdisciplinary field of study is a focus on the planetary boundary layer and lower free atmosphere (i.e. the aerosphere), and the diversity of airborne organisms that inhabit and depend upon the aerosphere for their existence. Here we focus on the role of radars and radar networks in aeroecological studies. Radar systems scanning the atmosphere are primarily used to monitor weather conditions and track the location and movements of aircraft. However, radar echoes regularly contain signals from other sources, such as airborne birds, bats, and arthropods. We briefly discuss how radar observations can be and have been used to study a variety of airborne organisms and examine some of the many potential benefits likely to arise from radar aeroecology for meteorological and biological research over a wide range of spatial and temporal scales. Radar systems are becoming increasingly sophisticated with the advent of innovative signal processing and dual-polarimetric capabilities. These capabilities should be better harnessed to both promote meteorological and aeroecological research and explore the interface between these two broad disciplines. We strongly encourage close collaboration among meteorologists, radar scientists, biologists, and others towards developing radar products that will contribute to a better understanding of airborne fauna.

Capsule Statement: Radar observations provide a valuable means of investigating questions about ecology, abundance, and airborne movement of animals over large spatial and temporal domains, and play an important role in the transdisciplinary field of aeroecology.

An initial surge in developing radar technology occurred before and during World War II in response to the need for an improved method of detecting and tracking positions of enemy aircraft (Buderi 1998). It was rapidly discovered that radar systems offered a wide range of applications beyond air defense. For example, while engaged in the early testing of military radar, researchers began to observe backscattered signals associated with regions of precipitation (Doviak and Zrni´c 1993). Moreover, there was a noticeable correlation between the power of the backscatter to the intensity and type of precipitation. Today radars play a vital role in meteorology and weather forecasting.

It was also during the early phases of radar development that scientists reported that some radio-wave scatter could be attributed to the presence of airborne animals such as birds, bats, and arthropods. Here, we refer to this broad category of radio-wave scatter as "biological scatter" or bioscatter. The earliest account in the open scientific literature of radar being used to observe bioscatter is found in Lack and Varley (1945). Thus, it has been known for over 60 years that radar can be used to study the behavior of flying, or volant, animals in the planetary boundary layer and lower free atmosphere (i.e., the aerosphere). A brief historical account can be found in Gauthreaux (2006). Radar has been thoroughly integrated into research and operational meteorology; however, the same cannot be said for biology. That is not to say that radar has not been incorporated into biological research. There have been significant advancements in ornithology and entomology as a result of radar observations (e.g., Vaughn 1985; Reynolds 1988; Bruderer 1997a,b; Gauthreaux and Belser 2003; Diehl and Larkin 2005; Larkin 2005) and exciting discoveries continue to be made. Furthermore, radar observations have contributed extensively to entomology of economically-important pest and beneficial insects in North America, Europe, Africa, Australia and Asia (Chapman et al. 2011). And operational radar has been used for flight safety warnings during periods of heavy bird migration (van Belle et al. 2007; Shamoun-Baranes et al. 2008). However, when one considers the vast networks of radars currently in operation around the world, it can be argued that this technology has been underutilized for ecological research.

Using radar to detect and characterize the presence and movements of bioscatter is an example of the emerging scientific discipline of aeroecology. The objective of aeroecology is to broaden understanding about ecological patterns and processes that result from the behavior of organisms in the aerosphere. These patterns and processes are best investigated by integrating disciplines, such as atmospheric science, earth science, geography, ecology, computer science, computational biology, and engineering (Kunz et al. 2008). Monitoring and tracking airborne fauna successfully with radar requires expertise from many scientific disciplines, but especially from atmospheric science, computer science, and ecology. The convergence of these disciplines with a focus on “radar aeroecology” has significant potential for furthering scientific investigations on diverse research topics including daily and nightly dispersal, migratory patterns, foraging behavior, distribution and quantification of aerial biomass, aerial biodiversity, phenological patterns related to climatic variability, and conservation biology.

Here, we explore the benefits and challenges of developing a cohesive radar aeroecology program within the U.S. targeted at observations of volant organisms over a variety of spatial and temporal scales. In particular, we focus on data collected using the network of U.S. National Weather Service (NWS) weather surveillance Doppler radars (WSR-88D) collectively known as NEXRAD (Serafin and Wilson 2000). The NEXRAD network is already being used by some for biological research (e.g., Gauthreaux and Belser 1998; Russell et al. 1998; Diehl et al. 2003; Kunz and Horn 2008; Bonter et al. 2009; O’Neal et al. 2010) and radar tutorials are available for biologists (Gauthreaux and Belser 2003; Diehl and Larkin 2005; Larkin 2005; Mead et al. 2010). Moreover, progress is being made in the deployment and use of operational weather radars for biological studies in other countries (e.g., Dokter et al. 2010).

Although the focus of the present discussion is on NEXRAD, other radar networks may also have valuable potential for biological research. For example, the U.S. maintains and operates terminal Doppler weather radars, airport surveillance radars, and air route surveillance radars (Weber et al. 2007). These could be integrated into biological research (e.g., Leshem and Yom-Tov 1996, 1998). A comprehensive radar aeroecology program would be able to take advantage of existing infrastructure while leveraging the rich body of experience in radar technology. In fact, we contend that the collective body of NEXRAD observations stored as raw and processed data at the National Climatic Data Center already represents one of the largest biological data archives in the world. Here, we present some of the applications of radar to aeroecology, discuss some of the challenges associated with applying radar to studying biological targets, and propose the development of a cohesive radar aeroecology program within the U.S., targeted at understanding the movements of volant organisms over a range of spatial and temporal scales.

SIGNIFICANCE OF RADAR AEROECOLOGY. As one specific example of how NEXRAD is being used to assist biologists, consider the observation of purple martins (*Progne subis*) reported in Russell et al. (1998). Purple martins are insectivorous birds that feed in flight during the day. They often congregate in large roosting colonies prior to and during migration. Using NEXRAD data, Russell et al. (1998) identified the locations of several martin roost sites, observed the daily behavior of these birds, and conducted a detailed investigation of daily movement patterns of martins from one particular roost in South Carolina. As martins disperse from their roosting site and begin foraging for food early in the morning, they produce a distinctive ring shaped region of enhanced radar reflectivity when visualized on a plan position indicator display. An example of roost locations and daily dispersal of purple martins is depicted in Figure 1. These data were collected using the WSR-88D, KINX in Oklahoma. The most prominent “roost ring” is located about 40 km to the west of the radar, near Tulsa, Oklahoma. It has been estimated that this particular roost site attracts 100,000 to 250,000 purple martins annually. Flight patterns of the martins and other roosting species produce a distinct divergent flow field as seen in the Doppler velocity data shown in the lower panel of Figure 1.

This example illustrates that an important biological application of NEXRAD is, perhaps ironically, what it tells us about the ecology and behavior of animals on the ground. In circumstances where animals are concentrated or unevenly distributed in the landscape prior to initiating flight en mass, weather radars operating at low elevation angles can map these locations by capturing patterns aloft as animals enter the airspace (Diehl et al. 2003). Using radar for identifying spatial distributions and use of terrestrial habitats of volant animals promises to inform conservation and management of such species as bats, migratory birds, and emergent insects. Radar observations have further potential for assessing the use of aerial habitats and quantifying how animals use both aerial and terrestrial landscapes. Research advances in radar technology and data mining to quantify how flying animals use both terrestrial and aerial habitats will be informative for both basic and applied ecological research (Kunz and Horn 2008; Buler and Diehl 2009).

Because many species of flying animals perform ecological services that aid human society (e.g., Abramovitz 1998; Cleveland et al. 2006; Losey and Vaughan 2006; Sekercioglu 2006; Banyon and Jenkins 2010; Kunz et al. 2011), there are considerable economic consequences to our ability to enumerate how these animals use both the airscape and the landscape. Radar has been used to detect the movements of agricultural pest species directly (Leskinen et al. 2011) as well as capture their spatial encounters with foraging bats (Westbrook 2008). Indeed, the potential to quantify aerial densities of bats using radar may directly inform on the efficacy of bats as natural biological predators of agricultural pest insects. For example, the economic benefits of Brazilian free-tailed bats to cotton growers in the Winter Garden area of Texas was estimated at roughly 15% of the total cotton harvest (Cleveland et al. 2006). Radar-based monitoring of waterfowl populations may guide management decision in relation to hunting regulations and is already being explored as a method of quantifying the effects of waterfowl habitat restoration (J. Buler, pers, comm.). Although there will always be a need for on-the-ground monitoring in species management and conservation, radar shows promise as an effective remote sensing tool for identifying daily and migratory behavioral patterns. Efforts to use radar in lieu of other more labor intensive monitoring techniques may help relieve pressure on strained state and federal natural resource budgets.

RADAR AEROECOLOGY AND SCALE ANALYSIS. The concept of aeroecology promotes a broad and integrative approach when investigating the aerosphere and the myriad airborne organisms it supports. The same applies to radar aeroecology, which not only encompasses observations of bioscatter using radio waves, but also focuses on spatial and temporal activity of organisms that broadly correlate with meteorological events over a wide range of temporal and spatial extents. Movements of organisms in the aerosphere are also likely influenced by innate biological factors as well as a variety of meteorological conditions, including wind (Walls et al. 2005; Liechti 2006) and weather fronts (Shamoun- Baranes et al. 2010). The extent to which meteorological factors influence volant animals (the degree of causality) can also be related to scale, as shown in Figure 2. Although studies have examined the role of scale on causal relationships between weather and climate and biological systems (e.g., Clark 1985; Alerstam 1996; Berthold 1998; Peterson et al. 1998; Shamoun-Baranes et al. 2010), additional work is needed and would be facilitated within the framework of radar aeroecology.

It is common practice in meteorology to categorize certain phenomena according to discrete spatial scales such as micro-scale (0 - 2 km), meso-scale (2 km - 2,000 km), and macro- scale (2,000 km and larger) (Orlanski 1975). These categories can be further sub-divided into even smaller domains related not only to meteorological but also biological phenomena (Westbrook and Isard 1999), including predator-prey interactions and other types of foraging behaviors with different dimensions depending upon species of interest (Figure 2). For example, a single bat may forage over many kilometers on a given night hunting for aerial insects, but a single predatory event may last only a second. Macro-scale meteorological events such as storms likely influence seasonal and daily movements of both prey and predators that use the aerosphere, whereas micro-scale meteorological events such as turbulent eddies in the planetary boundary layer could influence the frequency and successes of local predatory behavior. At intermediate and larger scales, many species engage in nomadic wandering and daily and nightly dispersal behaviors. Because of the challenges associated with following movements of individuals (particularly volant animals), daily, nightly, and seasonal dispersal events are among the least well-studied life history phases of many species (Andreassen et al. 2002).

Annual migratory behaviors involve seasonal movements from warm subtropical or temperate regions to cool temperate regions in the spring to avoid limited food resources, followed by return migration in the fall to avoid mortality due to cold temperature and lack of food resources (Alerstam 1990; Fleming and Eby 2003; Newton 2008; Cryan and Diehl 2009; Bowlin et al. 2010; Faaborg et al. 2010; Robinson et al.

2010). Seasonal migration to avoid reduced food resources in winter is emblematic of the connectedness among meteorological and ecological phenomena at seasonal temporal and spatial scales. Migratory animals are also influenced by daily meteorological conditions. The effects of the spatial and temporal variability of daily, weekly, and monthly weather on migration demonstrate the multi-scale complexity of the connections between weather, climate and migratory behavior of volant animals (Richardson 1978; Sparks et al. 2002).

Adaptation, geography and climate underlie evolutionary, ecological, and meteorological phenomena to the extent that meteorological conditions influence heritable aspects of survival and reproduction (fitness) of individuals. Although conceptually the multi-scale linkages among climate, weather and animal movement behaviors are easy to grasp (Clark 1985), there has been a limited ability to empirically test hypotheses about the influence of daily and seasonal meteorological conditions on animal movements in the aerosphere due to the technological and logistical challenges of collecting data at the appropriate spatial and temporal scales (Bowlin et al. 2010). The use of national and international networks of radars and a radar aeroecology program promises to obtain greater understanding of movements and behaviors of volant organisms using radar observations over different spatial and temporal scales coupled with ancillary data such as meteorological conditions and local biological sampling.

VALIDATION OF RADAR SIGNAL ORIGINS. Understanding the behavior of volant animals at local scales is key to understanding their broad patterns of movement in the aerosphere. The effective use of radar as a means of monitoring such movements requires fundamental knowledge of how radio waves interact with bioscatterers. That is, one must carefully explore the theoretical and experimental assumptions applied to radar observations in the process of weather forecasting and the extraction of bioscatter.

Before one can effectively study bioscatter over large domains and consider how it is revealed through NEXRAD, careful investigations are needed to determine how bioscatterers are revealed using single radar platforms and over small spatial domains. Detailed studies at small spatial scales will also lead to better classification of bioscatter and estimates of numerical densities, which then can be used in basic ecological research (e.g., mosaic bioscatter maps), conservation planning (e.g., stopover habitat assessments) and assessing anthropogenic mortality factors (e.g., collisions of birds with aircraft and interactions of birds and bats with wind turbines and other tall structures).

As discussed in Bruderer (2003) and Larkin (2005), radar systems for biological research can be grouped into broad categories based on beam geometry. Fan-beam radars include airport surveillance radars, air traffic control radars, and ship navigation or marine radars. The formed beam pattern generally spans about 2◦ or less horizontally and 10◦ to 35◦ vertically. Such radars are relatively inexpensive and therefore often used in the field to observe bioscatterers. The radar is placed on a trailer or truck with the antenna allowed to rotate about a vertical axis at a fixed elevation angle. Although the broad vertical beam is unsatisfactory for obtaining information on height, some radar systems can be configured such that the antenna can be rotated about a horizontal axis as well, providing height data (Mabee et al. 2006)

In contrast to wide fan-beam systems, pencil-beam radars include weather radars, tracking radars, and wind profilers. These systems project a narrow conical beam. Antennas for pencil-beam radars are typically mounted on a pedestal that allows the radar antenna to be fixed in position or scan in azimuth and elevation. Fixed-beam radars, for example, may point vertically to observe bioscatterers as they pass overhead through the sampling volume.

Single radar installations offer a quantitative means of regularly observing the many types of periodic movements of volant animals in the vicinity of the radar such as insect eruptions (Reynolds et al. 2008), nightly foraging activity of bats emerging from roosts (Kunz and Horn 2008), pre-migration staging of purple martins (Russell and Gauthreaux 1999), and winter roosts of tree swallows (Winkler 2006). Routine monitoring of daily and seasonal movement patterns permits robust testing of hypotheses about potential deviations from natural variability due to perturbations from climatic variability, natural disasters, land use, urbanization, and other anthropogenic factors.

A major challenge in using radar as a biological research tool is determining the origin of received signals. Radar signals can result from backscatter caused by precipitation, various forms of aerosols, turbulence-induced gradients in the refractive index, biological organisms, buildings, trees, and so forth (Larkin 2005). They can also be produced by radio-wave interference from a host of terrestrial to intergalactic sources. Discriminating bioscatter from other sources of radar signals as well as among biological taxa is crucial for maximizing the utility of radar for biological research. Some methods for signal discrimination include using the temporal and spatial characteristics of the region associated with the received radar signal (Lakshmanan et al. 2010), a signal's velocity and polarimetric attributes when available (Bachmann and Zrnić 2007), and in the case of bioscatter — the wing-beat characteristics of the flying birds, bats and insects (Zaugg et al. 2008) and the natural history of their movements (Diehl and Larkin 2005; O'Neal et al. 2011).

Researchers have used several methods of "ground truth" to identify animals observed on radar, including observing birds migrating at night by watching the disc of the moon (Lowery and Newman 1955), passive thermal imaging (Gauthreaux and Livingston 2006), night-vision equipment (Mabee et al. 2006), acoustic monitoring of calls made in flight (Larkin et al. 2002; Farnsworth et al. 2004), and combinations of such methods (Liechti et al. 1995). Additional methods of identifying bioscatter in radar data have been proposed (Gauthreaux and Belser 1998; Zrnić and Ryzhkov 1998; Bachmann and Zrnić 2007; Schmaljohan et al. 2008; Mead et al. 2010). Here we only consider two of these radar techniques: wing-beat frequency and radar polarimetry.

The rate at which a particular volant animal flaps its wings is determined by a variety of parameters related to characteristics of the air through which it is flying and the animal itself (e.g., Pennycuick 2001; Bullen and McKenzie 2002; Hedenström 2008). Among those pertaining to the animal are body size, body mass, wing span, wing area, and so forth. As birds, bats, and insects engage in flight, changes in their body shape resulting from wing beating produce corresponding changes in the amount of their body surfaces exposed to probing radio waves. These changes appear on radar as periodic fluctuations in backscattered radio wave signals (Bruderer et al. 2010). Radar-measured wing-beat patterns differ considerably between major taxonomic groups of flying animals, particularly between insects and vertebrates such as birds and bats. Algorithms operating on these data can discriminate between wing-beat patterns and classify individual bioscatterers into broad taxonomic categories (Vaughn 1985; Zaugg et al. 2008).

In Figure 3 we present an example of how wing-beat patterns in radar data differ between flying animals that vary considerably in size and shape. Shown are time-series of received signals corresponding to three different flying animals taken with an X-band radar during a study of fall-migrating ducks in Illinois (O’Neal et al. 2010). The wing beats of the insect shown in the upper time-series are rapid and shallow, presumably related to its mass and flight kinematics. Songbirds can interrupt flapping with occasional coasting (middle time- series), flap continuously, or rapidly alternate between flapping and coasting. The lower time-series shows the wing-beat pattern of a single dabbling duck, probably a Mallard (*Anas platyrhynchos*). The time series of traces from flying birds show considerable detail in beat- to-beat consistency, and such fine structure is commonly observed with radar but this fine structure does not persist when birds are illuminated from different orientations.

Radar polarimetry techniques provide another means of discriminating between different observed species. For a dual-polarimetric radar, horizontally and vertically polarized radio waves are transmitted and received either simultaneously or alternatingly (Doviak et al. 2000). The amount of received backscattered power for the two different polarizations not only depends on the size and composition of a scatterer but also its shape and orientation. For example, a large raindrop having an oblate spheroidal shape will produce more backscatter in the horizontal polarization than in the vertical polarization. The differential reflectivity (ZDR), which is the ratio of radar reflectivity (Z) computed from the horizontal and vertical polarizations, is used as a measure of aspect from radar scatter. Some of the earliest uses of ZDR for the study of airborne fauna involved explorations into the role of insects as the source of “clear air” echoes in weather radar (Mueller and Larkin 1985; Achtemeier 1991). Additional dual-polarimetric parameters, which we will not discuss here, have also been used for discriminating biological scatter from atmospheric scatter (Zrni´c and Ryzhkov 1998; Bachmann and Zrni´c 2007; Melnikov et al. 2010; Moisseev et al. 2010).

We recently completed a series of radar observations using the NOAA mobile X-band (3-cm wavelength) dual-polarized weather radar (NOXP) to observe Brazilian free-tailed bats (*Tadarida brasiliensis*) in Texas during the summer of 2010. Using the NOXP, which has a beam width of approximately 1◦, we were able to make detailed observations of multiple colonies of bats as they emerged from their roosts and departed on nightly foraging bouts. Figure 4 shows data collected when the radar was positioned about 11 km south of the location of Frio Cave, near Uvalde, Texas. This and other caves in south-central Texas are known to host large maternity colonies of Brazilian free-tailed bats that aggregate during the spring and summer to give birth and raise young (Kunz and Robson 1995). The NOXP measurements shown in Figure 4 correspond to an elevation angle of 3◦ and the NEXRAD data represent composite values from the NSSL mosaic radar product, NMQ (see below).

Dual-polarization products such as ZDR can be used to discriminate between insects and bats because they are sensitive to the shape of the scattering target. For the most part, large (≈ 5 dB) values of ZDR shown in the figure correspond to insects. After the bats dispersed and began feeding on insects, they exhibite strongly negative ZDR values (around -6 dB; not shown). The cause for these values has been the subject of investigation and could be related to resonant scatter (Zrni´c and Ryzhkov 1998). Availability of such dual- polarimetric parameters will make it possible to better understand the foraging behaviors of bats in response to the location and distribution of insects.

The NEXRAD network in the U.S. is currently undergoing a dual-polarimetric upgrade (Doviak et al. 2000), which should be completed by 2012. Dual-polarimetric radars provide a powerful means of discriminating between biological and non-biological scatter and among different biological taxa. Similar to hydrometeor classifications based on dual-polarization characteristics that are currently in use (Straka et al. 2000), several biological classification algorithms are being developed (Moisseev et al. 2010). Access to data from these radars at S-band (frequency used by NEXRAD), C-band (frequency used at many airports) and X-band (frequency used for smaller radar networks and many mobile radars) for overlapping spatial and temporal domains promises to provide signal-processing tools for a wide range of novel meteorological and biological applications.

ANIMAL DENSITIES FROM RADAR DATA. Some biological questions can be explored simply by observing changes in the spatio-temporal patterns present in bioscatter data, whereas other investigations require a more quantitative form of analysis. There are numerous examples in the literature demonstrating how radar can be used to record backscatter from individual or groups of birds, bats, and insects in flight (Liechti et al. 1995; Gauthreaux and Belser 1998; Gauthreaux et al. 2008; Schmaljohan et al. 2008; Dokter et al. 2010). Ground-truth and validation data collected using modeling exercises or through radar experiments conducted in the laboratory or in the field are necessary to empirically resolve scaling issues that impact the translation of radar data into biologically meaningful units, such as number densities of organisms, which can be used for basic ecological research and conservation planning. Such estimates will contain both process and sampling errors resulting in varying levels of uncertainty, and thus validation studies are needed to determine the extent of these uncertainties and to assess the accuracy and utility of these methods.

The smallest spatial grain of biological scatter that can be observed by radar corresponds to the physical dimensions of the organism itself. For example, under the right conditions, the intensity of bioscatter can be related to the number density of the airborne individuals sampled by the radar. For such an analysis, the scattering properties of the animal (e.g., size, shape, aspect, and composition) must be known. These properties can be observed in the laboratory under controlled conditions and applied to bioscatter data in the field or measured directly in the field (Edwards and Houghton 1959; Vaughn 1985).

Using the laboratory facilities at the University of Oklahoma some of us have recently made radar cross section (RCS) measurements of a live Brazilian free-tailed bat at X-band (Figure 5). The bat was tethered using nylon line that allowed motion of its wings and to simulate flight while its body was held stationary inside an anechoic chamber. A 12-inch metal sphere was used to calibrate the equipment. Using these data, the backscattered power corresponding to the sphere and the bat were calculated. From such RCS measurements, it is possible to convert measured values of radar reflectivity into counts or number densities of bats observed at the same radar wavelength.

If the observing radar has been properly calibrated, the retrieved RCS can be used to estimate individual body size of a given organism (Riley 1985; Wolf et al. 1993). Backscatter from animals whose size is similar to that of the wavelength falls into the complicated Mie (resonant) region, so that greater RCS values do not necessarily relate linearly to larger body sizes (Vaughn 1985). Additionally, animals have irregular shapes that may further complicate such measurements. As an approximation of the RCS of a particular bioscatterer (i.e., animal), an alternate approach is to consider a spherical volume of water of the same mass (Eastwood 1967; Vaughn 1985; Martin and Shapiro 2007).

As an alternative to laboratory or theoretical calculations, one can also estimate the RCS value for a particular species with a well calibrated radar in conjunction with visual surveys (Larkin 1991; Schmaljohan et al. 2008; O'Neal et al. 2010). This is typically performed using a pencil-beam radar to estimate numbers and visual surveys to verify the species being observed. Two radars can be used when quantifying numbers or number densities of bioscatterers, such that a smaller, mobile radar is used for validation at small scales and a larger, stationary radar (e.g., WSR-88D) is used for extended spatial coverage of bioscatter patterns (Diehl et al. 2003; Schmaljohan et al. 2008; Dokter et al. 2010; O'Neal et al. 2010).

The accuracy of quantitative predictions based on radar data will depend on the spatial distribution of the animals in the aerosphere. For example, the equivalent radar reflectivity (Z_e) reported for NEXRAD WSR-88D radars is calculated under the assumption that the power returned from any volume of the atmosphere results from a uniform distribution of scatterers within that volume. While this assumption may be well founded for broad front songbird migrations (Nebuloni et al. 2008), it is less clear how well it applies when targets/scatterers fill only a portion of the radar beam or when the distribution of foragers or migrants is clumped. Although beam-blockage or attenuation will almost always be negligible with biological backscatter, nonlinear additivity and the exact shape of the beam are nevertheless important to consider. Detailed studies at small spatial scales are needed, which can lead to better classification of bioscatter and accurate estimates of densities of airborne organisms.

USING NEXRAD TO MONITOR THE AEROSPHERE. In meteorology, multiple instrument platforms are incorporated to investigate the atmosphere. Similar approaches have also been adopted to learn about the dynamics of aerial organisms in large aggregations (e.g., Lowery and Newman 1955; Liechti et al. 1995; Larkin et al. 2002; Gauthreaux and Livingston 2006; Mabee et al. 2006). Small portable radars, adapted for biological research, are powerful tools for investigating the behavior of individual or small groups of animals in the aerosphere, but they typically have a limited sampling domain. Larger radar installations such as the NEXRAD network provide extended coverage, but at the expense of spatial and temporal resolution. The spatial domain of behavioral processes of biological aggregations, such as bat and bird colonies typically falls within the coverage of a single WSR-88D and can be used, for example, to investigate nightly and daily emergence and foraging behavior of insectivorous bats (Kunz and Horn 2008).

Focusing our attention on the macro-scale phenomena depicted in Figure 2, it is clear that an integrative approach involving a network of radars is needed to optimally monitor and interpret bioscatter at regional to continental scales. The NEXRAD network consists of multiple WSR-88D installations, with 156 of these distributed across the U.S. The extent of horizontal coverage provided by NEXRAD depends on altitude and the area of interest, but most of the eastern half of the continental U.S. can be observed at an altitude of 3 km (Maddox et al. 2002). Coverage at this altitude is considerably reduced along the Rocky Mountains and to the west (Maddox et al. 2002). This situation improves; however, if we are able to add other networked operational radars such as terminal Doppler weather radars, airport surveillance radars, and air route surveillance radars (Weber et al. 2007). Furthermore, a network of small X-band radars could significantly improve coverage near the surface and in mountainous regions (McLaughlin et al. 2009).

A concerted effort has been made to make current and archived NEXRAD data available to the public via the Internet (Kelleher et al. 2007). Data from individual WSR-88D installations along with visualization software can be requested for free from the National Climatic Data Center. So-called Level II radar products are available as reflectivity, radial velocity, and spectrum width presented in a spherical coordinate system centered at the radar site. In addition to the Level II data, several derived and estimated Level III meteorological products are also available as discussed below. In addition to meteorologists and atmospheric scientists, some biological research groups have begun incorporating NEXRAD data into their research programs (see for example the provided references to the work done by Gauthreaux and colleagures); however, the task of integrating the data across radar sites can be challenging.

The NOAA National Severe Storms Laboratory (NSSL), in collaboration with the Federal Aviation Administration (FAA), has instituted a highly effective means of fusing data from these radar systems along with observations from other instruments into one collective data product. Within the framework of the National Mosaic and multi-sensor QPE (Quantitative Precipitation Estimation) system (NMQ), base Level II NEXRAD data are ingested, controlled for quality, and combined to form a 3-D reflectivity map projected onto a Cartesian grid (Zhang et al. 2004, 2011). The horizontal resolution of the NMQ output is 1-km with 31 vertical levels and a temporal resolution of 5 minutes. A weighting function is employed in those regions corresponding to overlapping radar coverage (Zhang et al. 2005).

The NMQ project provides a host of severe weather and QPE products, which are provided to governmental agencies and academic institutions in quasi-real time. Many of these data products can be retrieved from a publicly accessible web portal (http://nmq.ou.edu/). Such a resource will be useful for researching bioscatter because biologists who are interested in the collective behavior of airborne organisms on a daily and seasonal basis and at multiple spatial scales can observe phenomena seldom detectable with other existing technologies. The recent observational and analytical capability of NMQ will stimulate new hypotheses about animal movements and interactions in the aerosphere and provide a framework for testing such hypotheses through data mining and quantitative analyses and visualizations of archived and real-time data.

A display from the NMQ web portal corresponding to composite reflectivity for 17 May 2010 at 03:00 UT is depicted in Figure 6. The upper image shows the merged reflectivity data before applying algorithms for quality control (QC), which attempt to remove non- meteorological effects (Lakshmanan et al. 2010). We refer to these as non-QC data. In addition to the weather signal, these non-QC reflectivity values contain contributions from bioscatterers, sun spikes, anomalous propagation, and radio interference. Bioscatter corresponding to the northward nocturnal spring migration of birds in the eastern U.S., along with echoes from bats emerging from large cave roosts, comprise the dominant contribution to signals. Because most birds and all bats migrate at night, radar provides an excellent tool for monitoring mass migratory movements. The lower image has been subjected to the NMQ quality control as discussed in Zhang et al. (2011) and references therein. Both the quality controlled and non-QC data are currently available from the NMQ web portal, with the latter serving as a base reference when examining weather outputs.

Having access to gridded fields of reflectivity data produced through NMQ not only enables the study of macro-scale biological processes involving organisms that use the aerosphere, but also facilitates comparison with other continental-scale data sets such as those containing meteorological quantities. Consider for example the radar data from NMQ shown in Figure 7, corresponding to the emergence and subsequent dispersal of Brazilian free-tailed bats from their day roosts in south-central Texas during July 2010. Often the bats initially disperse in all directions, resulting in a signature ring shape (Figure 7), which is similar to that associated with the departure of the purple martins (Figure 1). The reflectivity and velocity data shown in Figure 1 correspond to a single WSR-88D site (KINX), but the results shown in Figure 6 have been merged from several WSR-88D sites. Four of these WSR-88D sites (KSJT, KGRK, KDFX, and KEWX) are depicted in Figure 7. Also shown are the locations of four roost sites (Rucker Cave, Frio Cave, Ney Cave, and Bracken Cave). Regions of enhanced reflectivity in the vicinity of the roost sites resulting from the emerging bats are clearly evident. After emerging from their roosts, birds and bats may orient in one or more preferred directions based on the prevailing meteorological conditions and availability of food resources. For the case of emerging bats shown in Figure 7, the location and abundance of the food source (insects) is likewise affected by both current and seasonal weather conditions.

When investigated over the span of several years, NMQ data can be used to look for shifts in patterns of emergence. Further, the NMQ data can be used to test hypotheses about causes of these shifts, and whether group behavior at bat or bird colonies can be observed and explained in terms of both biotic and non-biotic influences. For example, in Figure 8, we show time series of NMQ output calculated over a 24-hour period corresponding to the locations of the roost sites depicted in Figure 7. Data streams of radar data, surface observations, satellite measurements and other parameters can be visualized directly using the NMQ web site (upper panel) or downloaded and then processed and displayed using a variety of software packages (lower panel). The values shown in the upper panel of Figure 8 were computed using data corresponding to the NMQ grid cell (1-km2 grain size) nearest to the cave location. For the time series plotted in the lower panel, the maximum value of Z over a 3 × 3 grid on NMQ cells surrounding the cave locations were used.

The evening emergences of bats can be seen in the reflectivity data for each of the sites as peaks occurring at dusk between 00:00 and 02:00 UTC (19:00 and 21:00 CDT). This is followed by elevated values of reflectivity until they return from foraging at sunrise. Enhancements in the reflectivity between 12:00 and 14:00 UTC (07:00 and 09:00 CDT) indicate the return of the bats. For the case of Bracken Cave, a double fly-out pattern can be seen in the time-series data of Z. One occurs just after 00:00 UTC and other at around 01:25 UTC (corresponding to Figure 7. The roost ring from the initial emergence as well as the beginning of the second can be seen in Figure 7 as the bats return from their first nightly feeding bout (Kunz et al. 1995).

NATIONAL BIOSCATTER DATABASE. Any investigation of the effects of changes in land cover and climate on ecological patterns and processes requires a sufficient time series at a continental scale. Few time-series data sets have been collected in a consistent and uniform manner that can be used to scale from a grain size of 1 km to a continental domain. Networks of radar installations such as NEXRAD could be used to provide information needed to test hypotheses regarding the timing, distribution and abundance of active migration and foraging events in unprecedented ways. However, monitoring and interpreting time series of bioscatter at a continental scale that lends itself to aeroecological studies will require a workflow that not only integrates the national network of radars into a uniform data set but also one that has biological significance, including ground truth verifying of the identity of volant animals. The next step in promoting the utility of radar aeroecological research is to develop and create derived products analogous to those available within the Level III NEXRAD data but with a diverse user community in mind. That is, we need Level III products geared for uses beyond atmospheric science per se.

In Figure 9 we present an illustration of how NEXRAD data could be used to create Level III products geared to both meteorologists and ecologists and potential cross-disciplinary research outputs. The NEXRAD Level III meteorological data products are already heavily used by many government agencies and private sector enterprises. We expect that the proposed NEXRAD Level III biological products will also have a significant impact if they are made readily available for the entire continental U.S. They will not only foster many areas of biological research but also promote cross-over studies between meteorology and biology as illustrated in Figure 9. For example, this type of cross-over research between biology and meteorology is expected to benefit investigations into the potential impacts of climatic variability.

Radar biological data will continue to be gathered within constraints imposed by meteorological conditions. Therefore, before attempting to create a database of Level III biological products, we should carefully consider the nature of the data that actually go into constructing the NMQ national mosaic. Depending on meteorological conditions, each of the WSR-88Ds is operated in one of several scanning modes or volume coverage patterns (VCP), which sets the radar’s rotation rate, sampling period, number of elevation angles, and so forth. Each VCP has been designed to meet certain agency specifications. For example, the reported average return power and radial velocity should be accurate to within 1 dB and 1 m s^{-1}, respectively. Since the VCPs have been optimized for meteorological rather than biological conditions, the sensitivity of the radar to bioscatter will vary depending on the type of VCP being used. For example, a radar operating in a VCP mode designed for observations of clear air would be more appropriate for observations of migrating songbirds than the same radar running a VCP designed for observations of precipitation.

Moreover, one must factor in the separation between a particular region of bioscatter and the next nearest WSR-88D as the distance between bioscatterers and radar installation will affect the lowest altitude that can be sampled. For example, the disk-shaped patches of enhanced reflectivity depicted in the upper panel of Figure 6 are centered on individual radar sites. The combined effects of the Earth's curvature and the fact that the lowest elevation angle sampled by NEXRAD is seldom less than 0.5◦ means that airborne fauna located at moderate heights can only be detected if they occur in airspace near a radar site. Fortunately, the effects of geometry (location of the radar sites with respect to the biological scatterers) and scanning parameters (the type of VCP being used) are known and can considered when interpreting data (Buler and Diehl 2009).

Bearing in mind that caution should be exercised when interpreting radar data in terms of bioscatter, we feel that Level III biological products should be created both for archived and real-time data. Maps depicting these products will be particularly powerful when coupled with climate, land cover and phenological data that match both the temporal and spatial scale of the radar archive. For example, most volant animals are too small to carry energy reserves for more than a few days; thus, they often respond rapidly to their local environment (Bowlin et al. 2010; Robinson et al. 2010). By comparing changes in land cover and climate with the timing and rate of changes in foraging, migratory, and stop-over behaviors, we can test hypotheses about the magnitude of these local effects on animal behaviors and spatiotemporal scaling of different species. Improving our ability to track aerial movements of birds, bats, and arthropods, however, remains a primary challenge in biology (Wilcove and Wikelski 2008; Holland and Wikelski 2009; Bowlin et al. 2010).

Recent advances in Doppler radar technology and networking can be correlated with detailed data on individual behaviors to work toward a mechanistic understanding of animal responses to land cover and climate. Tracking methods such as radio transmitters, geolocators, and tracking radar provide valuable data on individual animal movements usually at local to regional spatial scales. Generally, individual tracking methods are limited to short time spans (days, weeks or at most a year). In contrast, the NEXRAD archive provides a near continuous time series of the distribution and abundance of all airborne animals over the continental U.S. (Bowlin et al. 2010; Robinson et al. 2010). Data from tracking individual animals could be coupled with a nearly 20-year radar archive (1993-2011) of continental scale animal movement data to take advantage of strengths of both approaches. Whereas information on movements from individual animals could help us interpret radar observations, the NEXRAD data archive promises to provide critical insights into how the aerosphere-lithosphere dynamic is being impacted by local, regional, and continental patterns of changes in climate and land cover.

SUMMARY AND CONCLUSIONS. Airborne animals are highly responsive to environmental change in the terrestrial landscape (Herkert 1994; Murphy 2003) and aerosphere (Shamoun-Baranes et al. 2010), and depend heavily on the interface between the Earth’s surface and the aerosphere. In particular, migrating fauna must respond rapidly to their environment to find adequate refugia and acquire sufficient energy to endure diverse conditions they will likely encounter en route during migration. These animal movements represent convergent and sometimes co-evolved phenotypic traits shaped by natural selection to take advantage of predictable shifts in seasonal patterns (phenology) of ecosystem productivity (Pulido 2007; Kunz and Horn 2008; Hedenström 2008). Some of the most compelling evidence of biological responses to changes in climate and land cover comes from experiments and observations of migratory and aerial foraging behaviors at local scales compared with availability of food and climatic variability (Wilkinson and Fleming 1996; Buskirk et al. 2009; Bridge et al. 2010). Understanding individual behavioral responses to environmental changes is fundamental to a mechanistic understanding of aeroecological dynamics and will build a foundation for predicting consequences of future environmental change. The emerging discipline of aeroecology seeks to understand these important ecological mechanisms and the role of meteorological variability on aeroecological dynamics.

Since its inception, radar has proven to be a valuable tool for studying animals in the aerosphere. Numerous technological developments have had a significant impact on the field of radar aeroecology during the ensuing years. One of these has been the use of radar polarimetry, a technique used to better discriminate bioscatter from weather signals and to better distinguish between birds, bats, and insects (Mueller and Larkin 1985; Zrni´c and Ryzhkov 1998). Advancements in radar polarimetry for biological studies may have a significant impact on aeroecological research in light of the planned upgrade of NEXRAD to include such capabilities (Doviak et al. 2000). Moreover, continued advancements in computer and networking technology is making it progressively easier to process large volumes of data and to make them readily available to a wide community of users. The time has come for meteorologists, radar scientists, biologists, and others to work together more closely on developing radar products that will contribute to a better understanding of airborne fauna. These could be similar, for example, to the current Level III data and distributed frequently on a Cartesian coordinate system (as is done through the NMQ project). Such a database could be easily queried, mined, and related to other databases containing meteorological and geographic information system content to provide a powerful research tool for answering important transdisciplinary questions. Although much of this paper focused on radar aeroecology within the U.S. using operational networks and NEXRAD in particular, much of the discussion applies to single radar installations or other radar networks. The application of radars for biological research should also be considered as integral to new radar systems such as networked X-band radars (McLaughlin et al. 2009) and phased-array weather radars (Zrni´c et al. 2007).

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List of Figures

1 Reflectivity (upper panel) and Doppler velocity (lower panel) data collected on August 2, 2009 using the WSR-88D (KINX) located near Tulsa, Oklahoma. The location of KINX is indicated by the white circle. The departure of purple martins (*Progne subis*) from a roosting site resulted in the ring-shaped region of echo located just west of Tulsa. The Doppler velocity data indicate radial motion outward from the roost at the center of the ring.

2 Depiction of the spatial and temporal scales of common meteorological phenomena and movement patterns of organisms supported by the aerosphere, which can be observed by radar. Regions of overlap indicate those scales at which movements of airborne organisms could be influenced by prevailing meteorological conditions.

3 Wing beats of single animals on an X-band radar. The time series of received power (arbitrary scale) over a 1-s interval are sampled at the 2087 s^{-1} pulse rate of the radar as the animals fly through the narrow, stationary beam of the radar. The data were collected as "radar ground truth" in a study of fall- migrating ducks on WSR-88D, coming off wetland areas in Illinois (O'Neal et al. 2010).

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6 Displays of composite reflectivity obtained from the NMQ web portal for May 17, 2010 at 03:00 UT. The upper panel shows a reflectivity maps before applying quality control to remove non-meteorological effects. The date is near the peak of nocturnal spring migration of songbirds in the northern part of the U.S.; insects and probably bats also contribute to the radar return. The lower panel shows the same data after quality control. The underlaid grey shading denotes terrain elevation with lighter colors representing higher elevations.

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8 Time series data from NMQ corresponding to the four different bat roosts depicted in Figure 7. The upper panel shows data streams for Bracken Cave representing different observed quantities: reflectivity, rainfall rate (Q2), surface temperature, and surface dew point temperature. Here Q2 refers to data from tipping bucket rain gauges. Time series of reflectivity values for all four cave locations are presented in the lower panel. Both plots span the same 24-hour time period. The vertical red dashed line in the lower panel marks the time depicted in Figure 7.

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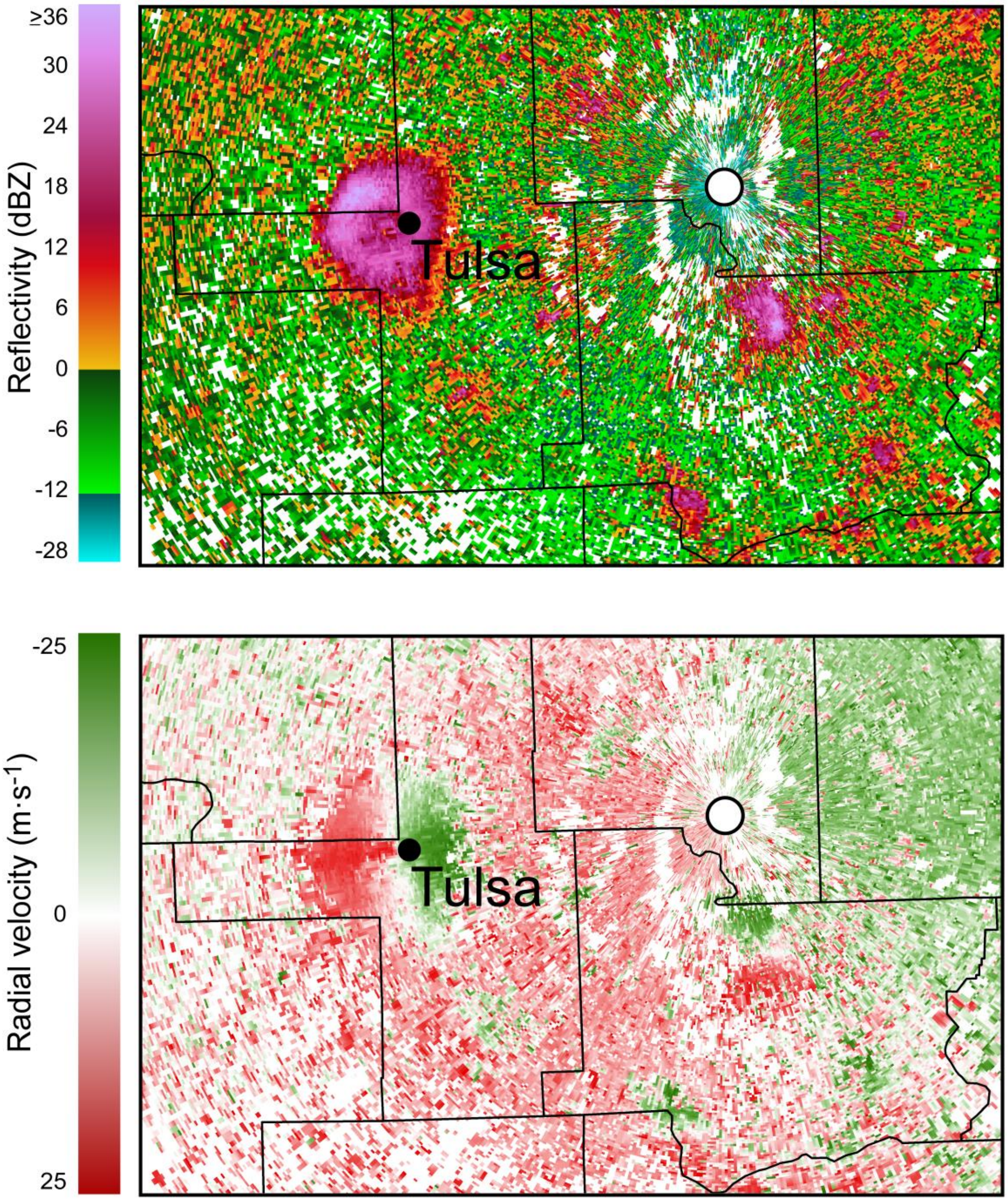

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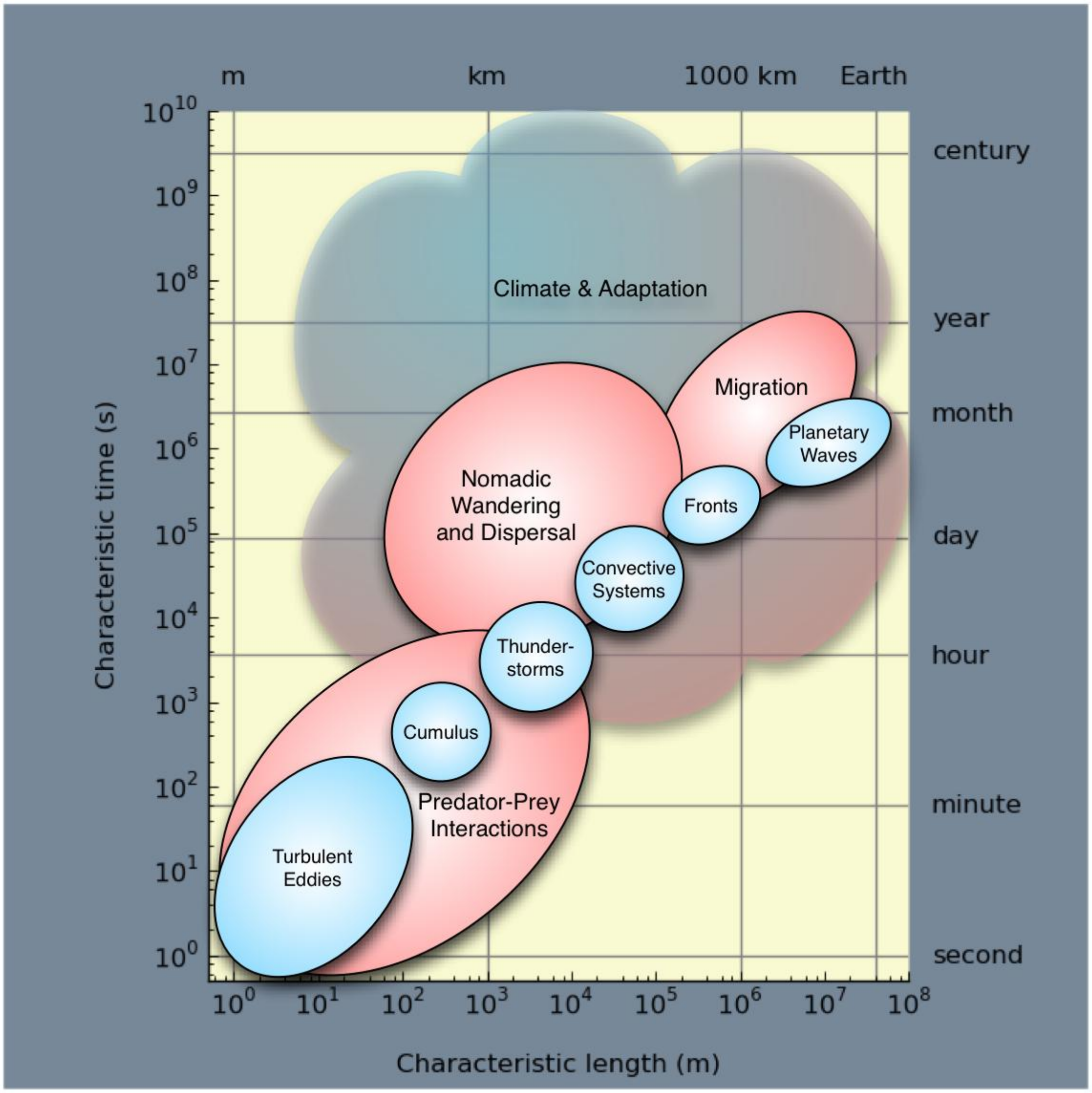

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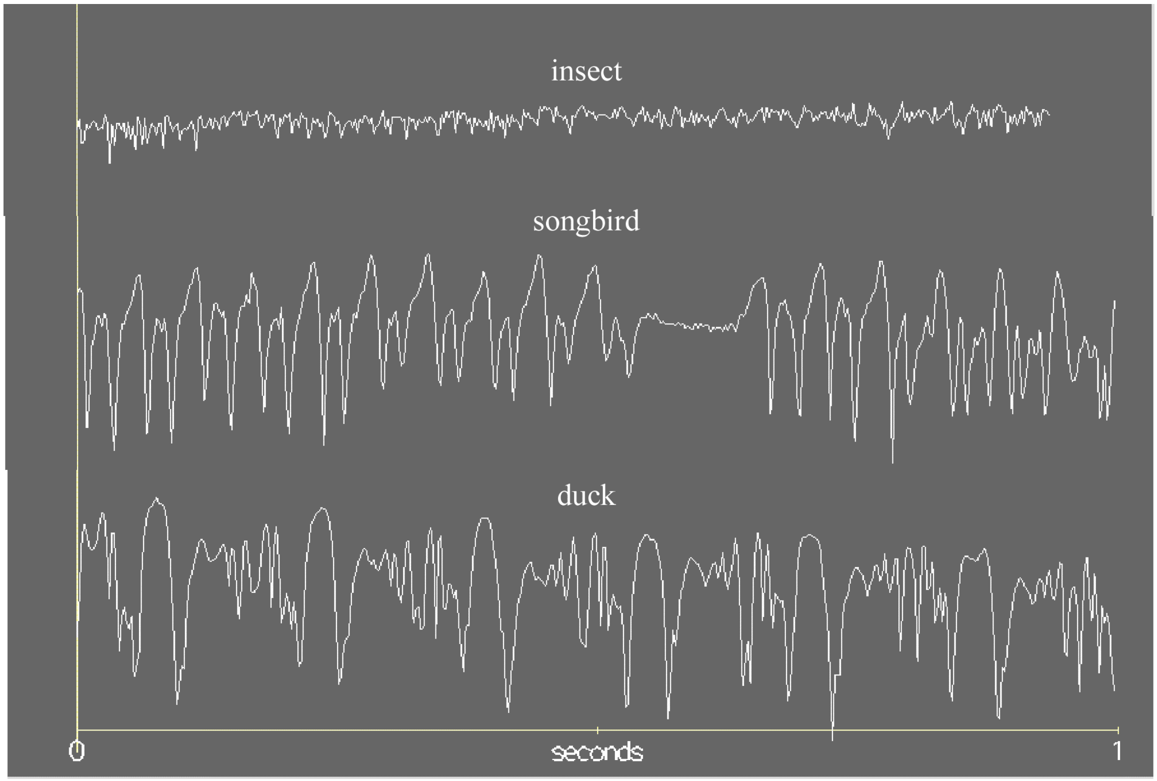

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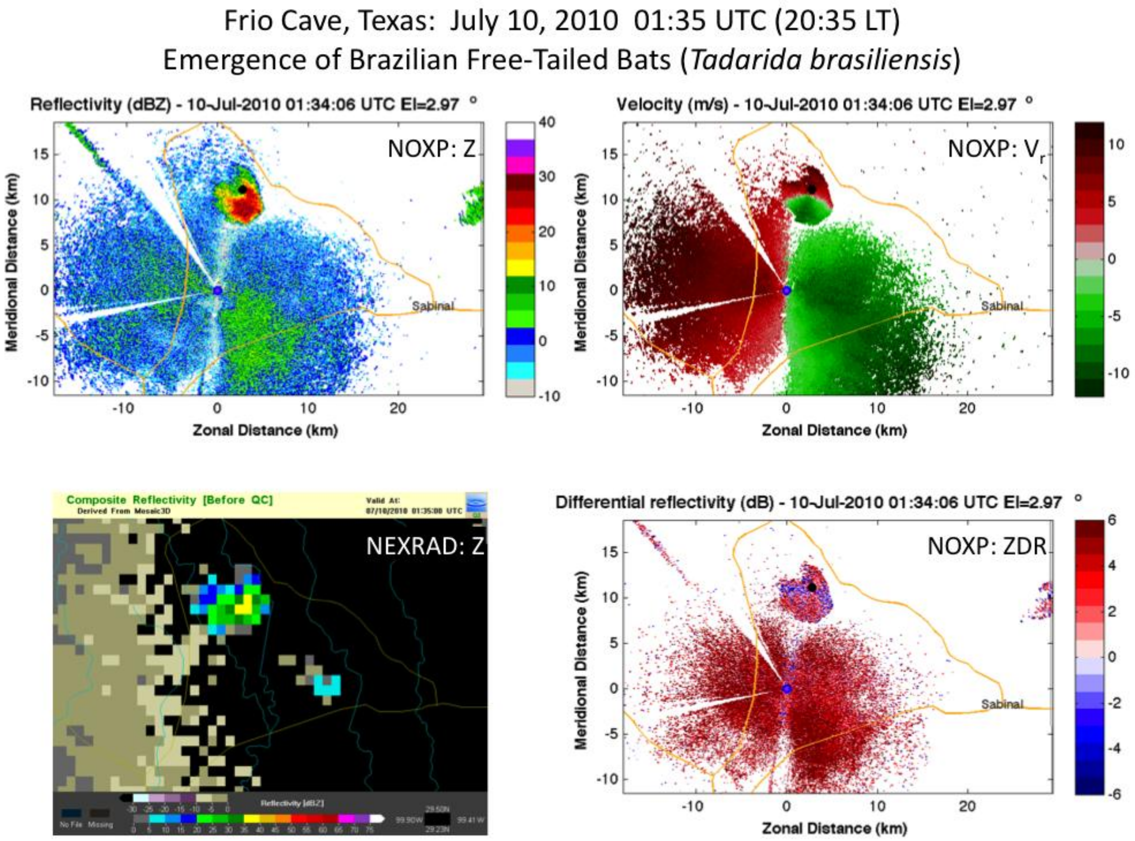

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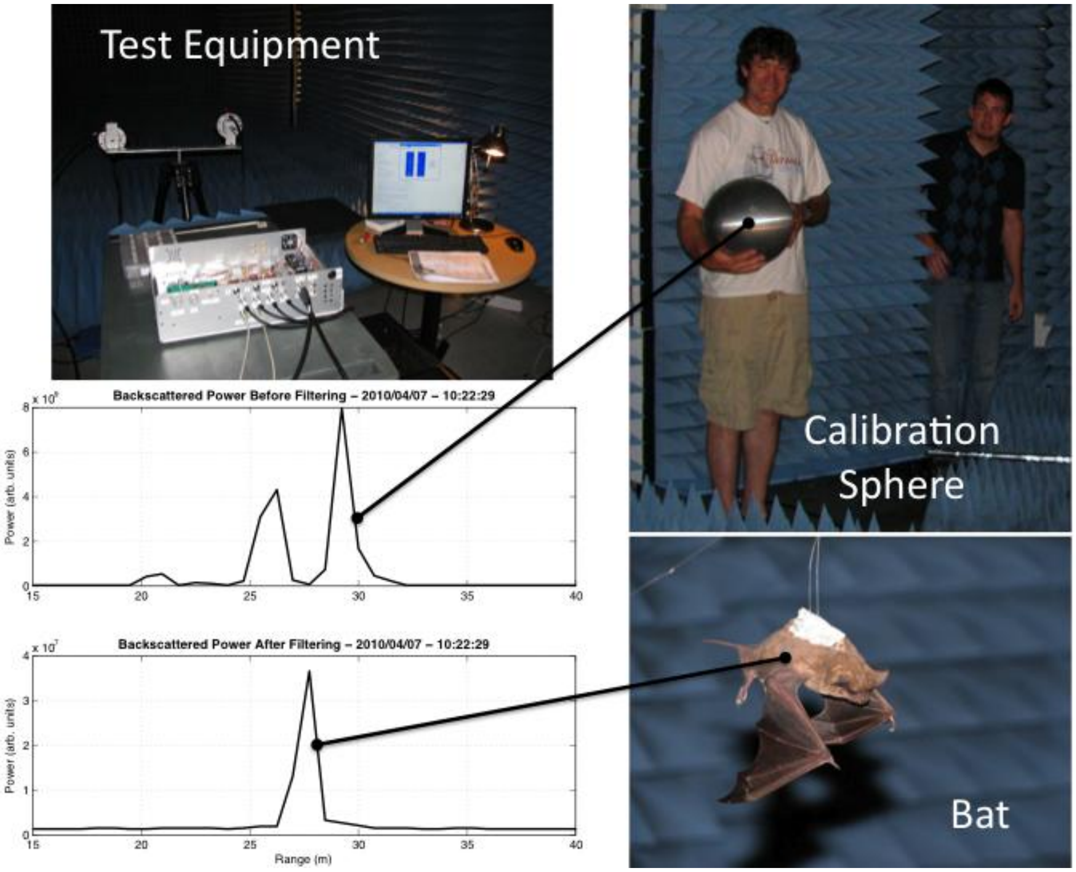

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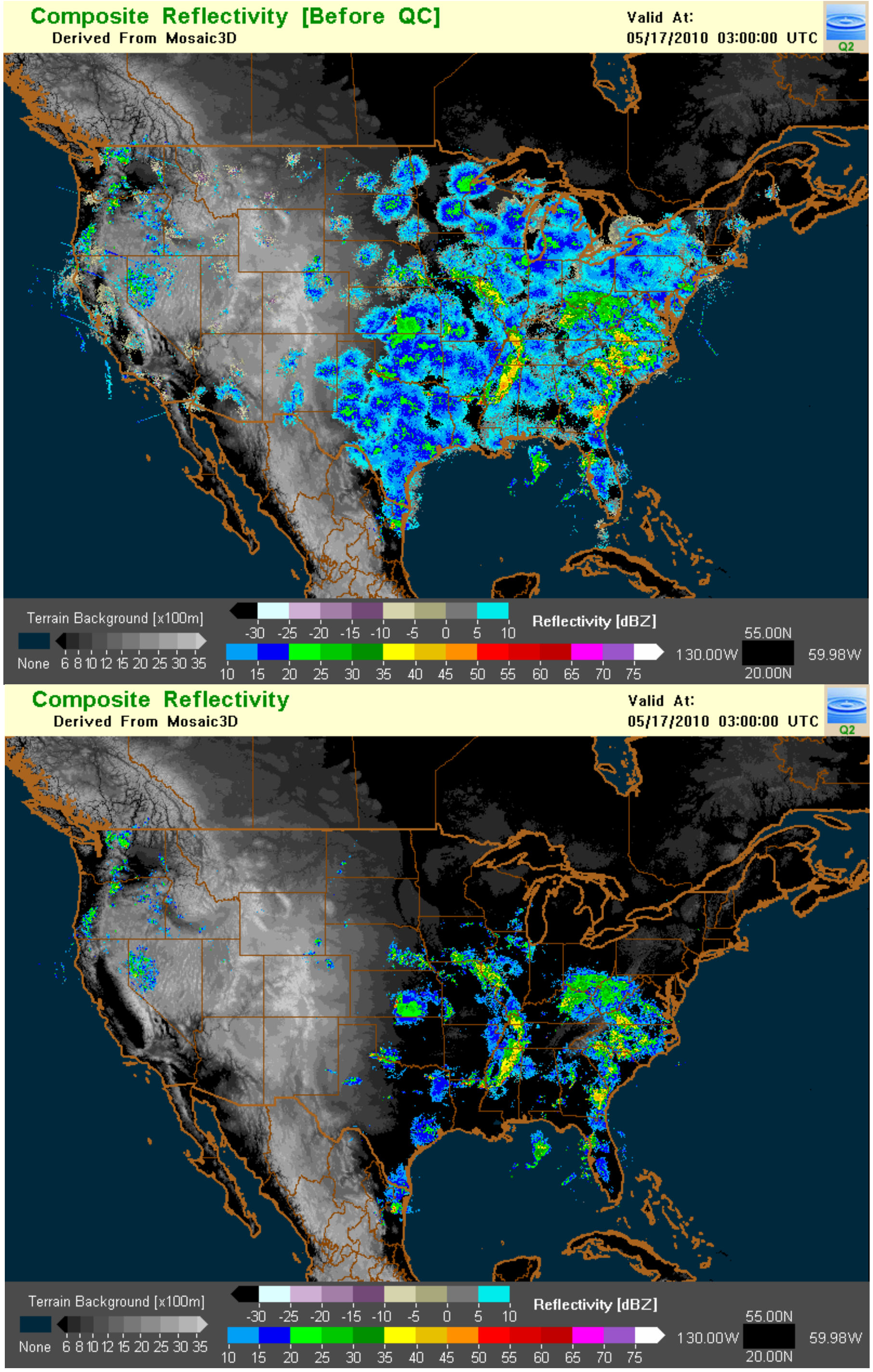

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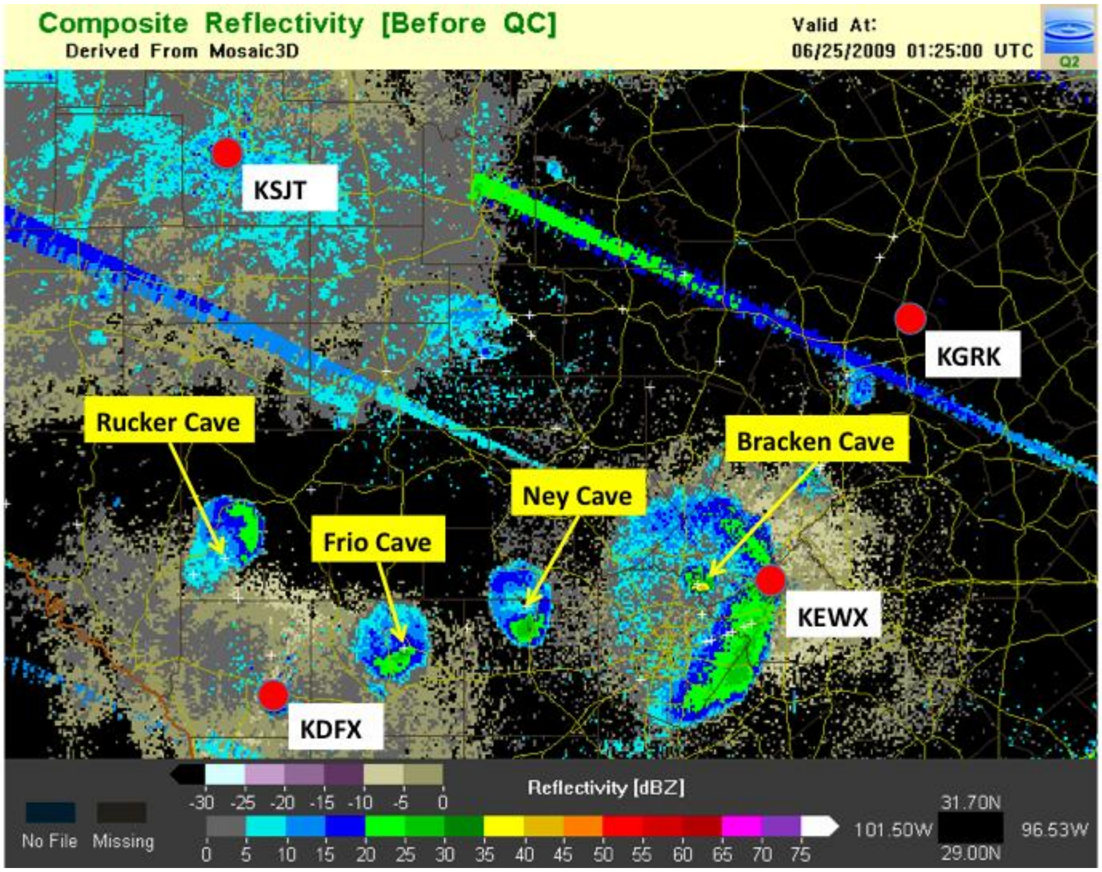

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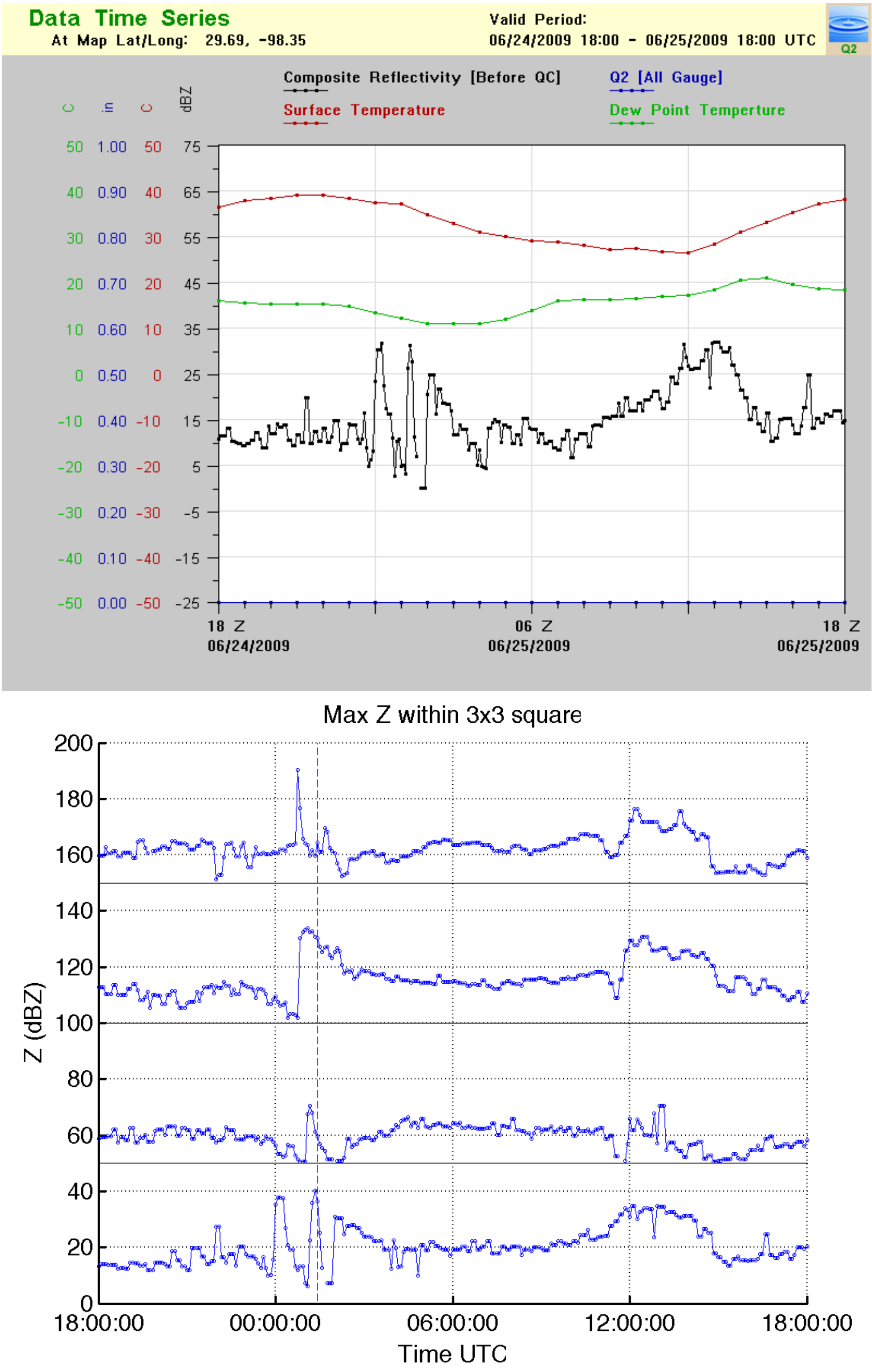

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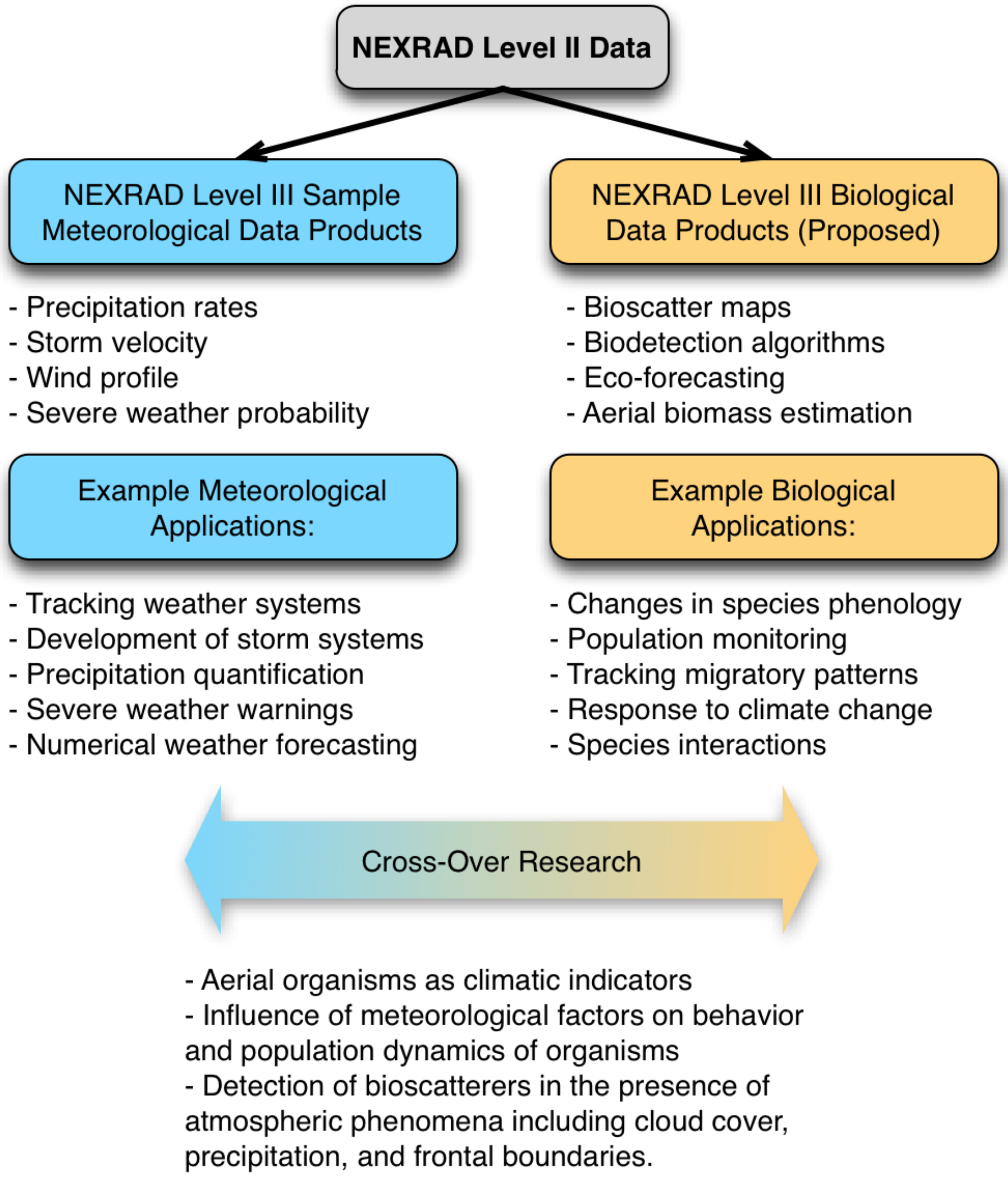

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