Aeroecology: probing and modelling the aerosphere

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Synopsis Aeroecology is a discipline that embraces and integrates the domains of atmospheric science, ecology, earth science, geography, computer science, computational biology, and engineering. The unifying concept that underlies this emerging discipline is its focus on the planetary boundary layer, or aerosphere, and the myriad of organisms that, in large part, depend upon this environment for their existence. The aerosphere influences both daily and seasonal movements of organisms, and its effects have both short- and long-term consequences for species that use this environment. The biotic interactions and physical conditions in the aerosphere represent important selection pressures that influence traits such as size and shape of organisms, which in turn facilitate both passive and active displacements. The aerosphere also influences the evolution of behavioral, sensory, metabolic, and respiratory functions of organisms in a myriad of ways. In contrast to organisms that depend strictly on terrestrial or aquatic existence, those that routinely use the aerosphere are almost immediately influenced by changing atmospheric conditions (e.g., winds, air density, precipitation, air temperature), sunlight, polarized light, moon light, and geomagnetic and gravitational forces. The aerosphere has direct and indirect effects on organisms, which often are more strongly influenced than those that spend significant amounts of time on land or in water. Future advances in aeroecology will be made when research conducted by biologists is more fully integrated across temporal and spatial scales in concert with advances made by atmospheric scientists and mathematical modelers. Ultimately, understanding how organisms such as arthropods, birds, and bats aloft are influenced by a dynamic aerosphere will be of importance for assessing, and maintaining ecosystem health, human health, and biodiversity.

Introduction

The biosphere has been traditionally viewed as being composed of the lithosphere, hydrosphere and atmosphere, each of which interact dynamically with the other. In an ecological context, the Earth’s lower atmosphere or troposphere has long been considered an important functional component of the biosphere through the exchange of nutrients, water, and gases in the form of local, regional, and global climate variation and biogeochemical cycles. However, to our knowledge, the aerosphere—the relatively thin sub-stratum of the troposphere closest to the Earth’s surface that supports life—has rarely been considered beyond studies of meteorological conditions and functional ecosystem relationships, such as nutrient cycling and gas exchanges in the atmosphere (Oke 1987, Sorbjan 1989, National Research Council 1997). Until quite recently, ecologists with interests in organisms that depend on the aerosphere as a fluid medium for movement (e.g., dispersal, foraging, and migration), a source of food and nutrients, and ever-changing physical conditions (e.g., weather and air pollution), have worked more or less independently of atmospheric scientists. Research goals of organismal biologists who study airborne organisms have mostly focused on the behavior, ecology, and evolution of specific taxonomic groups (e.g., microbes, arthropods,
birds, and bats), or specific physiological or behavioral functions such as thermoregulation, water balance, respiration, or flight. In contrast, research goals of atmospheric scientists and engineers have largely emphasized how severe weather and climate can affect human well-being, and thus have focused on the efficacy and efficiency of human developments, including building construction (e.g., skyscrapers), modes of transportation (e.g., sail boats, aircraft, spacecraft), design and installation of communication infrastructure (e.g., tall towers and transmission lines), and power generation (e.g., utility and residential scale wind energy facilities). Achieving these two sets of goals in large measure depends upon understanding the dynamic properties of wind and associated meteorological conditions at local, regional, or global scales, and understanding how these conditions affect movements of organisms.

To our knowledge, no organism spends its entire life in the aerosphere, yet many species spend a significant portion of their lives in this environment (Wilcove 2008). Species that spend significant amounts of time in terrestrial and aquatic ecosystems also may depend on the aerosphere for daily and seasonal locomotion, and sometimes for courtship and mating. Important selection pressures accordingly influence the biology of flight, including the size and shape of structures that comprise the flight apparatus, and sensory modalities that provide information about the aerosphere, and the active and passive systems that control locomotor movements.

On both temporal and spatial scales, the aerosphere is more variable and dynamic than the lithosphere or hydrosphere. Relative to strictly terrestrial and aquatic organisms, species that regularly occupy the aerosphere are almost immediately influenced by changing atmospheric conditions (e.g., pressure, wind, air density, precipitation, temperature), and other physical factors (e.g., solar radiation, polarized light, moon light, and geomagnetic and gravitational forces). Organisms that use the aerosphere for foraging, dispersal, and seasonal movements have evolved unique body forms and shapes, but also specific physiological traits (e.g., increased production of hemoglobin at high altitudes), thermoregulatory and respiratory responses, and the like, in response to different selection pressures. The aerosphere and the organisms that compose it not only are strongly influenced by predictable atmospheric conditions, but also by a myriad of anthropogenic conditions (e.g., lighted towns and cities, skyscrapers, air pollution, aircraft, radio and television towers, and more recently from the proliferation of wind turbines and communication towers) that increasingly have adverse effects on such essential activities such as feeding, dispersal, migration, and courtship (Kunz et al. 2007a, 2007b; National Research Council 2007; Arnett et al. 2008; Horn et al. 2008; Fig. 1). Similarly, human-altered landscapes (e.g., forest fragmentation, agriculture, and urbanization) are rapidly and irreversibly transforming the quantity and quality of available habitats for organisms that use the aerosphere, conditions that also can affect the structure and function of terrestrial and aquatic ecosystems and the assemblages of organisms therein. Prevailing climate change and its expected effects on global circulation of the atmosphere and resultant changes on local, regional, and weather conditions may have profound effects on the historic migratory patterns of animals that use the aerosphere (Wilcove 2008).

Challenges of probing and modeling the aerosphere

Ecologists who study species that use the aerosphere face three important challenges: (1) to discover how best to detect the presence, taxonomic identity, diversity, and activity of organisms that use this space, (2) to identify ways to quantify relevant environmental variables at different temporal and spatial scales, and (3) to determine how best to understand and interpret responses of organisms in the context of complex meteorological events and patterns within both natural and anthropogenically altered environments. Efforts to address these challenges require the collaboration of scientists from diverse disciplines who have expertise and instruments needed to probe the aerosphere whether by day or night, in arid and humid conditions, at low and high altitudes, in strong and weak magnetic fields, in cold and warm climates, and during calm and windy conditions. Increasingly available tools, some originally designed for military purposes, space exploration, climate modelling, and security applications, include remote sensing and imaging devices such as radar, lidar, aircraft surveillance, weather satellites, night vision, and thermal infrared imaging cameras. Other instruments designed specifically for the study of animal movements, include radio-telemetry networks of ground-based stations and satellites, devices that detect audible and ultrasounds of birds and bats, stable isotope and DNA markers for assessing migration, which can be particularly valuable when used in combination with remotely sensed atmospheric, oceanic, and landscape conditions. Availability of these tools and methods provides rich opportunities for addressing emerging questions in ecology and environmental sciences with an emphasis on the aerosphere.
Fig. 1 The aerosphere is influenced by both natural phenomena and anthropogenic factors. (A) Aerospheric view of a volcanic eruption on the island of Montserrat (news.nationalgeographic.com); (B) Counter-clockwise swirl of clouds as a cyclone passed over Iraq, and dust being transported within the warm sector of the system (ucsu.colorado.edu/~drewsc/sandstorm); (C) Aerial view of the North American landscape at night, showing lighted cities and towns (www.usgcrp.gov/usgcrp/images/ocp2003/8.1b-HCR); (D) Aerospheric view of skyscrapers New York City (www.justinlagace.com); (E) Aerial view of an agricultural landscape, showing the influence of center pivot irrigation in an arid region of Colorado (www.discoverlife.org/IM/EL_DP/0010/mx); (F) Aerospheric view of land-based communication towers (hawkins.pair.com/voadelano/voa_delano03.jpg); (G) Aerospheric view of a modern U.S. Air Force F-16 Fighting Falcon aircraft (galleries.fototagger.com/image/f-16_fighting_); (H) Aerospheric view of a modern, utility-scale wind energy facility in Palm Springs, California (www.planetscience.org/revisiontime/wind2.jpg).
The appropriate integration of diverse tools, technologies, and multiple databases promises to inform important ecological concerns and concepts, ranging from spread of invasive species, changes in biodiversity, and local- and global-scale animal movements in response to altered terrestrial, aquatic, and aerial environments. To date, ecologists have been hampered by a lack of technological awareness, inconsistent vocabularies, and challenges of working across different disciplinary platforms, including the complexities of establishing meaningful collaborations with atmospheric and computer scientists. Similarly, ecologists interested in proximate and evolutionary responses of airborne fauna to climate change and other anthropogenic perturbations have yet to optimally use the rich databases on landscapes assembled by earth scientists and geographers using remote sensing tools [e.g., American MODIS (Moderate Resolution Imaging Spectroradiometer), the European MERIS (Medium Resolution Imaging Spectrometer), and the Indian IRS-P6 (Indian Remote Sensing Satellite)].

**Goals of the aerocology symposium**

The papers presented in this symposium address some of the limitations and challenges highlighted above, and highlight opportunities for gaining new insights that could arise from overcoming these challenges. To accomplish these goals, each of the authors considered several ecological questions that require analyses that embrace ecological and environmental sciences relevant to the aerosphere. Specifically, questions relate to animal displacements, and atmospheric and biological factors that may affect daily and seasonal patterns of prey density, foraging behavior, and migration. In addition to developing and promoting new tools and technologies to support research in aerocology, it is important to integrate knowledge from different disciplines by encouraging the participation of scientists from varied backgrounds to develop a broader understanding of complex processes and the responses of organisms to a dynamic aerosphere. To achieve these goals, the authors share ideas with respect to novel tools, emphasize tangible and specific scientific questions, and adopt novel research paradigms. To this end, we have identified instrumentation and software tools, and discuss their applications to improve our collective understanding of the aerosphere and the interactions of airborne organisms with the hydrosphere and lithosphere. Several research areas were not included in this symposium because time was limited. Notwithstanding, we include brief comment on these and other emerging disciplines relevant to understanding the ecology of organisms that use the aerosphere.

**Historical and current research on aerocology**

Weather radar historically has been used for detecting groups of migrating birds (Able 1970; Bruderer and Steidinger 1972). Since the early 1990s, weather surveillance, NEXRAD (NEXt Generation RADar) Doppler radar has been used at various temporal scales to quantify movements of birds (Diehl et al. 2003; Diehl and Larkin 2005; Larkin 2005; Gauthreaux and Belser 2003, 2005; Gauthreaux et al. 2003, 2006; Kunz 2004), although it has become increasingly clear that many targets also include bats and insects (Westbrook et al. 1998; Kunz 2004; Cleveland et al. 2006; Cryan and Diehl in press). Similarly, tracking radar is being used to investigate foraging, dispersal, and migratory movements of flying arthropods, birds, and bats (Bruderer and Boldt 2001; Bruderer and Popa-Lisseanu 2005; Larkin 2005). Additionally, use of vertical profiler radar promises to provide new insight into the distribution and movement of air masses, and of arthropods, birds, and bats in the aerosphere (Smith et al. 1993; Eaton et al. 1995; McLaughlin 2003; Kunz et al. 2007b; T.A. Kelly, personal communication).

Advances in radio-telemetry (e.g., miniature radio transmitters for insects, small birds and bats, and satellite tracking with GPS for larger species), have advanced our knowledge of movements at smaller spatial and temporal scales than can be provided by radar. Recent developments of integrated arrays of receiving antennae and satellite tracking of small birds and bats (Cochran and Wikelski 2005; Smith et al. 2005; Wikelski et al. 2007), in addition to advanced canopy-netting techniques (Hodgkinson et al. 2002), are beginning to yield new insights on animal movements, pollination of flowers by nectarivores, and dispersal of seeds by frugivores (Hodgkinson et al. 2003; Thies and Kalko 2004; Croxall et al. 2005; Nathan et al. 2005; Thies et al. 2006)—research that also is relevant to the conservation of biodiversity (Trakhtenbrot et al. 2005) and for understanding the transmission and mitigation of emerging diseases (Chivian 2003; Epstein et al. 2003).

Radio transmitters, together with other visualization methods, also are enabling researchers to quantify energy expenditure, wingbeat patterns, respiration, and flight altitudes of small, free-ranging animals (e.g., Lord et al. 1962; Dudley 2000; Altshuler et al. 2004; Bowlin et al. 2005). Use of wind tunnels
and computer-aided visualization techniques (Srygley and Thomas 2002; Altshuler and Dudley 2003; Pivkin et al. 2005; Swartz et al. 2006; Hedenström et al. 2007; Henningsson et al. 2008; Muijres et al. 2008) also are helping to inform field ecologists in how flow dynamics and atmospheric conditions influence flight behavior of bats, birds, and insects (e.g., Dillon et al. 2006).

Measuring physiological traits of foraging and migrating animals, under different atmospheric conditions (Greenstone 1990, 1991), also has begun to advance our knowledge of how animals respond to different aerospheric conditions. Moreover, novel efforts are being made to understand how insects, birds, and bats navigate during migration (Holland et al. 2006a, 2006b). Experimental manipulations have included alteration of magnetic fields to understand how animals navigate over long distances (e.g., Cochran et al. 2004; Srygley et al. 2006; Holland et al. 2006b; Wang et al. 2007). A recent initiative to employ radio technology on a near-earth satellite to track small animals around the globe holds considerable promise for understanding migratory movements of free-ranging animals (Wikelski et al. 2007). A recent global initiative, known as the International Cooperation for Animal Research Using Space (ICARUS; www.icarusinitiative.org), also has been formed to help achieve this goal. Other initiatives, including NEON (National Ecological Observatory Network [http://www.neoninc.org/]), and related Research Coordination Networks, such as MIGRATE (Migration Interest Group: Research Applied toward Education [www.migrate.ou.edu]), both funded by the National Science Foundation, have been formed to help answer important questions such as the influence behavioral plasticity of migrants, drivers of population dynamics of migratory animals, determinants of individual fitness, and impacts of environmental change on migratory life-histories (JF Kelly, personal communication).

Recent developments in audible and ultrasonic acoustic detection and analysis, coupled to high-speed infrared and thermal images now make it possible to quantify three-dimensional flight trajectories of bats as they pursue airborne arthropods (Schnitzler and Kalko 2001; Holderied et al. 2005; Holderied and Jones in press; Hristov et al. 2008), and to unambiguously identify the mix of free-ranging bat species in both temperate and tropical assemblages (Parsons and Jones 2000; Brigham et al. 2004; Szewczak 2004; Parsons and Szewczak in press). This technology now makes it possible to characterize species richness and activity patterns that previously been difficult to quantify or record species have gone completely undetected, such as many aerial insectivorous bats, especially in tropical regions (Jung et al. 2007). Night vision devices and thermal infrared cameras have become increasingly used to observe birds, bats, and insects aloft, not only for assessing foraging behaviors (Simmons 2005; Betke et al. 2007; Horn et al. 2008; Hristov et al. 2008), but also for censusing animals during nightly emergence flights (Sabol and Hudson 1995; Frank et al. 2003; Betke et al. 2007, 2008; Hristov et al. 2008). When used simultaneously with tracking radar, night vision devices and thermal infrared cameras also make it possible to distinguish between birds and bats as they respond to anthropogenic structures such as wind turbines (Gauthreaux and Livingston 2006; Kunz et al. 2007a; 2007b).

Many important aspects of the behavior of flying organisms in the aerosphere occur in groups, sometimes of immense sizes. Many collective behaviors are influenced by the three-dimensional geometry of the environment, and by the cognitive abilities of animals that interact with prevailing atmospheric conditions. Understanding the behavior of individuals in isolation does not necessarily provide information about the properties of individuals within groups (Couzin and Krause 2003). Increased focus on empirical studies, self-organization theory, and mathematical modelling of group and collective behavior of insects, birds, and other organisms promises to help advance knowledge about daily flocking behavior at the population level and group dynamics during migration (Couzin 2006a, 2006b).

Use of stable isotopes of carbon and nitrogen as dietary tracers also can provide valuable insights into trophic relationships of airborne predators and their prey (Ibáñez et al. 2001; Sullivan et al. 2006; Popa-Lisseanu et al. 2007), and isotopes of hydrogen can additionally be used for discerning geographic origins of nocturnal migrants (Hobson and Wassenaar 2001; Cryan et al. 2004; Kelly et al. 2002; 2005, Hobson et al. 2006).

Collaborations of biologists with atmospheric scientists and aerospace engineers are needed to help advance understanding of animal behavior in the aerosphere. In turn, these collaborations can help advance the technical design and function of small, unmanned aerial vehicles, as inspired by the ecology, behavior, physiology, and biomechanics of real organisms (Watts et al. 2001; Pivkin et al. 2005; Swartz et al. 2006).

The symposium

To the extent possible, each contribution from this symposium has posed several important questions
and has reviewed existing and upcoming applications that inform new answers. Interdisciplinary approaches are emphasized, particularly those designed to optimally exploit the expertise of domain scientists in behavior, ecology, biomechanics, meteorology, computer science, and geography—approaches that are central to developing meaningful cross-disciplinary collaborations.

Using Doppler weather surveillance radar, Gauthreaux et al. (2008) discuss major challenges in understanding daily and seasonal movements of airborne fauna. Reflectivity data contain information on the quantity of organisms aloft, and data on velocity and winds aloft are needed to determine the different types of organisms that use the aerosphere. The latter is accomplished by examination of statistical distributions of the maximum ground speeds of airborne fauna in the aerosphere. Because migrating birds and bats have mean velocities greater than most insects and randomly foraging birds and bats in a sample volume of the atmosphere, these data can often be used to detect and discriminate specific targets aloft.

Horn and Kunz (2008) used NEXRAD databases to explore how Brazilian free-tailed bats disperse nightly into the aerosphere, and how this information can provide insight into local population dynamics. NEXRAD radar images are georeferenced and compiled in a GIS along with colony locations and landscape features. In temporal sequences of NEXRAD images, identification of individual bat colonies is accomplished by assessing reflectivity from bats aloft using computer vision algorithms. These measurements are used to compute relative colony size and mean direction of travel and to compare variation in emergence behavior both within and among colonies. Analyses using circular statistics suggest that multiple factors play a role in the nightly flight and dispersal behavior of bats, and demonstrate that NEXRAD data can be a valuable resource for monitoring the nightly behavior of large bat colonies, and larger-scale seasonal and interannual changes in abundance of local populations.

Larkin and Szafoni (2008) discuss how tracking radar data can be used to investigate nocturnal aggregations of birds. Statistical analyses of detailed flight paths support the hypothesis that individual birds that fly together (closer than 200–300 m) move in the same direction and at the same speed more often than those that are widely dispersed. Evidence from tracking radar suggests that birds flying together also may have similar wing beat frequencies than can be expected by chance.

Hristov et al. (2008) provide an overview of recent applications of thermal infrared imaging in ecological research and discuss how this technology has revolutionized our ability to observe and document the behavior of free-ranging organisms in the dark. Unlike traditional imaging that requires visible light, thermal infrared imaging relies on the emission of heat energy from objects in the environment. Temperature-sensitive cameras and computer vision algorithms are used to detect differences in thermal values in their fields of view and to depict information visually as different brightness (temperature) values. As noted in this article, successful applications of thermal infrared imaging from ongoing studies of bat ecology and behavior also are relevant for the study other organisms.

Kalko et al. (2008) present results based on recordings and analysis of echolocation calls of Neotropical bats that, for the first time, permit explicit species identification as well as assessment of foraging activity in these species-rich tropical assemblages. Use of miniature radio transmitters also makes it possible to assess foraging strategies, range size, and differential habitat use of species that previously have been otherwise difficult to study. Given the high impact of bats as seed dispersers, pollinators, and predators on arthropods, the fine resolution of movements afforded by radio-telemetry provides a better understanding of the links between spatial use and resource distribution and abundance. In turn, this provides novel information needed to understand temporal dynamics, to help quantify the ecosystem services provided by bats, and to predict how anthropogenic changes may affect the abundance and distribution of their prey.

Jones and Holderied (2008) discuss how echolocation is used by bats to detect, localize, and classify airborne targets at night. As obstacles or prey species are approached, it has become increasingly clear that the call structure of echolocating bats changes in predictable ways: calls become shorter to reduce overlap between pulse and echo, and calls change in shape so that localization errors in the detection of insect prey can be minimized. Echolocation behavior and flight performance of bats are closely synchronized by monitoring both features simultaneously using stereo photo- and videogrammetry, and by acoustic tracking of their flight paths. These approaches make it possible to quantify the intensity of signals used by free-ranging bats, and thus demonstrate systematic changes in signal design in relation to the proximity of obstacles (e.g., moving insect prey and stationary objects) in the aerosphere.
Westbrook (2008) discusses long-distance migration of important agricultural pests, such as adult corn earworm moths (*Helicoverpa zea*), also called cotton bollworm moths, and several other noctuid moth species upon which bats and birds sometimes feed. These seasonal geographic expansions of pest populations and the consequent increased infestations of agricultural crops are documented on a continental scale in North America. Observed patterns of migratory flight by these insect pests are largely associated with vertical profiles of temperature and wind direction and are concentrated in the atmospheric boundary layer. Collective patterns of moth migrations generally are related to wind direction, but often at significant angular deviations. Preliminary analyses suggest that moth distributions in the aeroosphere can be estimated from discrete moth counts using X-band radar and bulk reflectivity data from NEXRAD Doppler radar.

McCracken et al. (2008) discuss bat echolocation calls recorded using radio microphones suspended in the aeroosphere from kites and tethered helium balloons. These data mostly include calls of Brazilian free-tailed bats from ground-level up to 1118 m above ground level (AGL). Altitudinal profiles show significantly different levels of bat echolocation call activity at different levels AGL in the aeroosphere. Bat activity was greatest at ground level and 400–600 m AGL, coincident with the atmospheric boundary layer and the highest densities of moths as described in the paper by Westbrook (2008). Feeding buzzes, indicating attacks on aerial prey, were most abundant near ground level and at 400–600 m AGL, although some were detected at altitudes up to 1 km AGL.

Srygley and Dudley (2008) review data on insects in the atmospheric boundary layer by tracking individuals as they migrate across the Caribbean Sea and the Panama Canal. Data presented on dragonflies of the genus *Pantala* show that migration occurs in October and is associated with frontal systems. Butterflies and dragonflies are capable of directed movement toward a preferred compass direction in variable winds, whereas moths of the genus *Urania* migrate from Central to South America and drift with winds over water. Butterflies navigating in the aeroosphere appear to use both global and local cues. In support of optimal migration theory, butterflies and dragonflies appear to adjust their flight speeds to maximize migratory distance per unit energy, whereas moths do not.

Swartz et al. (2008) examine the biomechanics and physiology of flight of bats in the laboratory, and explore how this knowledge can help advance understanding of foraging, dispersal, and migration of free-ranging animals. Laboratory studies of animal flight in wind tunnels provide valuable information for improving and understanding of airflow dynamics. Emphasis is placed on flow characteristics of distinct aerial environments as a critical first step toward understanding the ecology of free-ranging animals aloft. The dynamics of natural airflow, characterized by air speeds, variability, intensity, and turbulence, will likely influence many aspects of an animal’s behavior in the aeroosphere. A combination of field- and laboratory-based research also is needed to delineate conditions under which flight mechanics and energetics are influenced by turbulence created by other animals.

Cochran et al. (2008) discuss the advanced use of miniaturized radio-transmitters that allow for the continuous monitoring of behavioral and physiological variables of small, free-ranging animals that use the aeroosphere. Monitoring of nocturnal migratory flights of three species of neotropical thrushes in the mid-western US has revealed variations in wing beat frequencies, flight speeds and body accelerations that may reflect ascending and descending movements of individuals during flights. Individual thrushes also pause (in wingbeat) more often than expected during their migratory flights, likely to save energy. The high variation in wingbeat frequencies also cautions against categorizing radar echoes as particular types of birds.

**Future directions**

To further advance the emerging discipline of aerocology, studies are needed that integrate the research discoveries of atmospheric scientists, engineers, and computer scientists with those of ecologists, physiologists, and functional morphologists, to more fully understand the activity and movements of organisms in the aeroosphere. Research that incorporates laboratory and field studies on biomechanics, physiology, behavior, and ecology also promises to provide new insights into how, where, when, and why organisms interact with anthropogenic features in the aeroosphere. To this end, studies are needed to assess: (1) physiological and behavioral responses of airborne organisms to climate change, (2) behavioral and ecological responses of organisms to structures that extend into the aeroosphere (e.g., communication towers, tall buildings, and wind turbines), (3) how landscape fragmentation and land use change affects movements, and (4) how the altered structure of aerocological communities, through the invasion of exotics, may affect species
distributions and abundance (Lindenmayer and Fischer 2006; National Research Council 2007; Kunz et al. 2007a; Lian 2007; Wilcove 2008). Use of stable isotopes to investigate trophic relationships between insects, birds, bats, and their prey also promises to yield valuable insight into how the myriad of organisms interact in the atmosphere. Ultimately, understanding the ecosystem services provided by arthropods, birds, and bats that use the atmosphere is important for maintaining ecosystem health, human health, and biodiversity on the planet (Daily et al. 1997; Cleveland et al. 2006; Chivian and Burnstein 2008).

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