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POLICY PERSPECTIVE

Aeroconservation for the Fragmented Skies

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Abstract

From birds to bacteria, airborne organisms face substantial anthropogenic impacts. The airspace provides essential habitat for thousands of species, some of which spend most of their lives airborne. Despite recent calls to protect the airspace, it continues to be treated as secondary to terrestrial and aquatic habitats in policy and research. Aeroconservation integrates recent advances in aeroecology and habitat connectivity, and recognizes aerial habitats and threats as analogous to their terrestrial and aquatic counterparts. Aerial habitats are poorly represented in the ecological literature and are largely absent from environmental policy, hindering protection of aerial biodiversity. Here, we provide a framework for defining aerial habitats to advance the study of aeroconservation and the protection of the airspace in environmental policy. We illustrate how current habitat definitions explicitly disadvantage aerial species relative to non-aerial species, and review key areas of conflict between aeroconservation and human use of the airspace. Finally, we identify opportunities for research to fill critical knowledge gaps for aeroconservation. For example, aerial habitat fragmentation may impact biodiversity and ecosystem function similarly to terrestrial habitat fragmentation, and we illustrate how this can be investigated by extending existing methods and paradigms from terrestrial conservation biology up into the airspace.

Introduction

The airspace provides essential habitat for an enormous array of biodiversity including microorganisms, wind-dispersed seeds, fungal spores, arthropods, bats, and birds (Kunz *et al.* 2008; Womack *et al.* 2010; Diehl 2013). Migratory aerial species rely on a clear path through the airspace to move between summer and winter habitats, while aerial insectivores rely on the airspace to forage. Insects such as the Ephemeroptera (mayflies) rely on aerial swarms for mating (Brodskiy 1973), and the Alpine Swift (*Tachymarptis melba*) can remain airborne for months, foraging, sleeping, and mating in the air (Liechti *et al.* 2013). At higher altitudes, aerial microorganisms exhibit strategies, such as increased UV resistance, which allow them to survive in the high reaches of the atmosphere (Yang *et al.* 2008; Womack *et al.* 2010).

Aerial species represent a substantial portion of global biodiversity. Twenty-eight percent of vertebrate species assessed by the International Union for the Conservation of Nature (IUCN) fly or glide, and rely to some extent on the airspace (Figure 1). This proportion may be much higher for insects, spiders, and plants that produce wind-dispersed seeds.

Unfortunately, a growing number of anthropogenic threats are intruding into the "crowded airspace" (Lambertucci *et al.* 2015; Table 1). Collisions with human infrastructure and aircraft result in billions of wildlife deaths each year (Longcore & Rich 2004; Womack *et al.* 2010; Diehl 2013; Baxter-Gilbert *et al.* 2015; Lambertucci *et al.* 2015; Arnett *et al.* 2016; Figure 2). Moving vehicles kill billions of flying insects (Baxter-Gilbert *et al.* 2015), wind turbines kill millions of bats (Arnett *et al.* 2016), and aircrafts kill thousands of birds (Dolbeer *et al.* 2015). In Canada alone, an estimated 44.6 million adult birds die each year from collisions with buildings, wind farms, communication towers, and other sources of aerial fragmentation (Calvert *et al.* 2013). Global use of unmanned

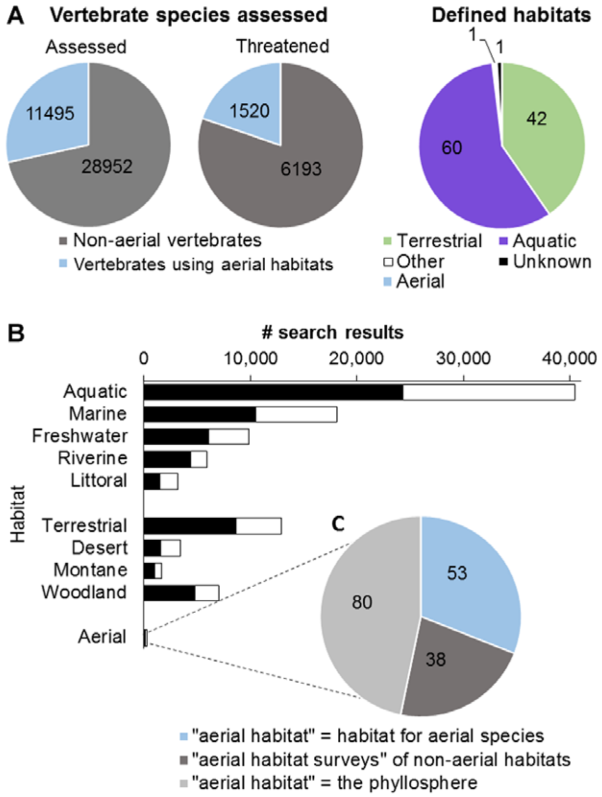

Figure 1 Despite many threatened species relying on aerial habitats, assessments of species' conservation status and research on habitats and habitat conservation focus heavily on terrestrial and aquatic habitats. (A) Proportion of vertebrates assessed and listed as threatened by the IUCN that use aerial and nonaerial habitats. (B) Disproportionate representation of select habitat types in the scientific literature, based on Google Scholar search results (September 6, 2015). Bars show the number of hits that reference each search term; black subsections represent the results that also reference "conservation." (C) "Aerial habitat" actually refers to habitats other than the airspace in most of the 248 unique documents referencing this term.

aerial vehicles (UAVs) by law enforcement, researchers, hobbyists, and military organizations is increasing, and commercial UAV-based delivery services are in development in some countries. Substantial overlap between the flight altitudes of UAVs and aerial species (Figure 2) suggests that growing UAV activity will increase UAV-wildlife collisions. The three-dimensional nature of aerial habitats creates the illusion that flying, soaring, or gliding organisms can simply circumnavigate anthropogenic structures, aircraft or UAVs. Yet, empirical data clearly demonstrate that this is often not the case.

Here, we identify a critical gap in conservation ecology and policy that sits at the intersection of four key, current topics (Figure 3). The growing field of aeroecology (Kunz *et al.* 2008) is revealing how flying animals use the airspace. The airspace was recently defined as habitat (Diehl 2013), complete with heterogeneous resource distribution and the potential for anthropogenic activities to create impacts analogous to those documented in fragmented terrestrial habitats. Alongside compelling evidence that terrestrial habitat fragmentation significantly reduces biodiversity (Haddad *et al.* 2015), it has become increasingly clear that anthropogenic structures and transportation are a major source of mortality for flying wildlife (Calvert *et al.* 2013; Lambertucci *et al.* 2015; Arnett *et al.* 2016). The intersection of these policy issues and research areas represent a major conservation gap: targeted conservation of aerial species and habitats. We propose a new field, "aeroconservation," to integrate these important research areas and develop effective conservation tools for aerial habitats and biodiversity.

The skies are not simply "crowded" by human activities (Lambertucci *et al.* 2015) – they represent critical but undefined habitats that have little policy support. Long-distance migrants must fly a gauntlet of threats (Movie S1) through habitats that are not effectively protected, in part because these habitats are not clearly defined. Substantial effort has been made to conserve wildlife corridors and mitigate the barrier effects of infrastructure in terrestrial habitats. It is time to consider similar mitigations for aerial habitats. To meet the challenge of aeroconservation, we propose: (1) defining aerial habitat types clearly in international policy, (2) articulating responsibility for aerial habitat conservation in environmental legislation, and (3) targeting conservation research to support the urgent needs of threatened aerial species and habitats.

Explicit definitions for aerial habitat

Habitat definitions vary among jurisdictions, but are often based on those used by the IUCN. We therefore use the IUCN's current Habitat Classification scheme here, to illustrate our concern. The IUCN scheme recognizes only terrestrial and aquatic habitats (Figure 1B). A flexible third category, "Other," could be applied to aerial habitat but typically is not (e.g., 0.2% of 1,150 IUCN assessments of bat species list "Other" habitat, but do not refer to airspace). The IUCN assessment of the Globe Skimmer dragonfly (*Pantala flavescens*) considers 14 terrestrial habitat types, but does not list the airspace used for dispersal or intercontinental migrations (Hobson *et al.* 2012; IUCN 2015).Thus, status assessments based on the current habitat classifications consider only terrestrial and aquatic habitat types, incorrectly implying that aerial species rely only on their nonaerial habitats such as migratory stopovers, roosts, or nests for survival.

In contrast, many assessments of nonaerial species include habitats connecting nonbreeding and breeding

Table 1 Aerial threat typology and potential effects associated with anthropogenic impacts on aerial habitats

Threat type		Examples	Potential effects
Direct collisions	With stationary structures	Buildings, transmission lines, solar panels, fences	Increased mortality; injury
	With moving structures	Cars, trains, ships, moving turbine blades, aircraft	Increased mortality; injury Range expansions of microorganisms or seeds dispersed by aircraft.
Physical barriers	From stationary or moving structures	Buildings, vehicles, fences, aircraft	Physical fragmentation of aerial habitat Effective habitat fragmentation through barrier effects (e.g., through individuals avoiding high-traffic aerial routes) Modified airflow affecting dispersal of microorganisms, wind-dispersed seeds, ballooning spiders, etc.
Pollution	Chemical pollution	Emissions from manufacturing or mining operations	Increased UV radiation through ozone depletion, particularly for high-altitude microorganisms
		Smoke billows from wildfires	Reduced visibility from particulate suspended in the air, leading to increased collision risk and disrupting celestial navigation
		Emissions from transportation	Physiological impacts on organisms exposed to toxic doses.
	Heat pollution	Solar flare at solar power installations	Increased mortality
		Urban heat islands	Modified local climate
		Heat plumes from cooling towers or wildfires	Modified airflow patterns, affecting dispersal of microorganisms, wind-dispersed seeds, ballooning spiders, etc.
	Light pollution	Airport and urban lighting	Disrupted celestial navigation through reduction of visible starlight or through attraction toward artificial light Increased risk of collisions (i.e., for night-flying insects).
	Noise pollution	Vehicle and aircraft traffic, manufacturing activities, natural resource extraction	Disrupted acoustic communication (insects, birds, bats) Disrupted acoustic navigation (e.g., echolocating bats).

areas (IUCN 2015). As an illustration, the IUCN assessments of the European and American Eel (*Anguilla anguilla; A. rostrata)* both include habitat types used for "passage" from breeding to nonbreeding areas, analogous to the airspace used by migrating or dispersing aerial species. This approach acknowledges that boundaries among habitat types are ecologically permeable, and that most species rely on the protection of multiple habitat types for survival (Burke & Gibbons 1995; IUCN 2015).

The absence of aerial habitat recognition extends to international policy. For example, the Convention on the Conservation of Migratory Wild Species of Animals defines a species' range as "the areas of land or water that a migratory species inhabits, stays in temporarily, crosses or overflies at any time on its normal migration route." Aerial habitats are excluded despite an explicit acknowledgment in the text that some species fly. Thus billions of birds, bats, insects, and other organisms rely on undefined and therefore unprotected aerial habitat to complete critical life processes.

To facilitate the incorporation of aerial habitats into habitat classification schemes, we propose habitat subdivisions for the troposphere (0–15 km altitude; Table S1, Figure 2). Adopting these habitat definitions would allow more complete assessments of the habitat requirements of aerial organisms. We have based the proposed scheme loosely on the existing definitions of marine pelagic habitats, which are also three-dimensional and therefore challenging to define. Pelagic habitats are defined in part by the amount of light penetrating from the surface, and whether it is sufficient for photosynthesis. For aerial habitats, we defined biologically meaningful categories based on temperature and oxygen levels in the airspace.

Basoaerial habitat includes the airspace extending from the top of the adjacent terrestrial habitat, upward to an absolute altitude of 1 km, at which the temperature has dropped 10°C below that of the air directly above the adjacent terrestrial or aquatic habitat. Thus, movement within the basoaerial layer requires relatively little physiological adjustment to tolerate the increased altitude. The basoaerial layer will be thicker above grasslands or water bodies, and thinner above high forest canopies. Threats to organisms in basoaerial habitat include collisions with vehicles, aircraft, wind turbines and buildings (Baxter-Gilbert *et al.* 2015; Dai *et al.* 2015; Lambertucci *et al.* 2015), and light pollution (Longcore & Rich 2004). Mesoaerial

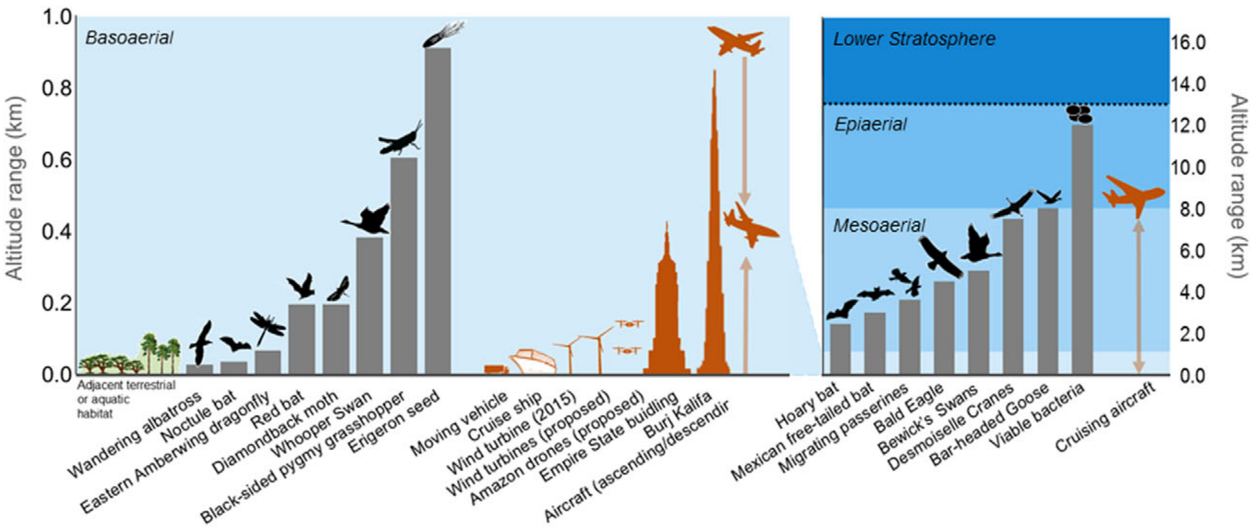

Figure 2 Aerial species fly a gauntlet of threats as they navigate fragmented aerial habitats. Gray bars in the left panel show flight altitudes reached by selected aerial species in the basoaerial; altitudes of selected threats in each aerial habitat type are shown in red. The indicated (dashed line) altitude of the tropopause (upper limit of the troposphere) is approximate because the height of the troposphere varies according to latitude. The troposphere encapsulates the basoaerial, mesoaerial, and epiaerial layers (blue shading).

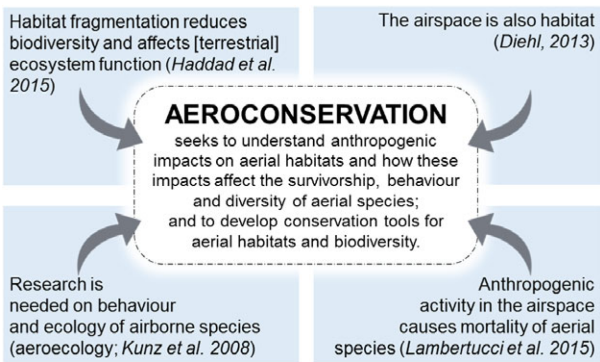

Figure 3 Aeroconservation integrates four key research areas related to habitat and species conservation, illustrated in this schematic by a major contribution from each area.

habitat (1–8 km altitude) is characterized by steadily decreasing temperatures (-10°C/km) and decreasing oxygen levels as altitude increases. At approximately 8 km in altitude, there is insufficient oxygen for typical human survival (the so-called "death zone" described by high-altitude climbers; Krakauer 1997). Birds flying near or above the upper limits of mesoaerial habitats exhibit physiological adaptations to these extreme conditions (Scott 2011). Anthropogenic threats in mesoaerial habitats (1–8 km) include light pollution and collisions with aircraft. Finally, temperatures in epiaerial habitat plunge toward -56°C at the tropopause. The altitude of the tropopause, which defines the upper limit of epiaerial habitat, varies with latitude. Thus, epiaerial habitat begins at 8 m in altitude and rises to between 9 and approximately 17 km in altitude, depending on latitude. Threats to species in epiaerial habitat include cruising aircraft and light pollution. Epiaerial microorganisms exhibit adaptations to high altitude (Yang *et al.* 2008), but their biology and diversity are not well understood (Womack *et al.* 2010).

Crowded skies: conflicting priorities in management of aerial habitats

Aerial species cross a range of altitudes (Scott 2011; Figure 2) and jurisdictional boundaries. Thus, aeroconservation will require interagency coordination within a jurisdiction, and transboundary cooperation among jurisdictions. This poses a challenge because ensuring human safety and economic growth can conflict with protection of aerial biodiversity. For example, the International Civil Aviation Organization encourages elimination of birds and bird habitat from airports because these species pose a threat to aircraft safety (Kelly & Allan 2006). The U.S. Federal Aviation Administration further recommends exclusion of habitat for "hazardous wildlife" within an 8 km radius of each airport's air operations area. With over 13,000 airports in the United States, this area of exclusion not only impacts more than 2.6 million km^2 of terrestrial habitat – twice the total of all protected areas in the United States – but also more than 2.6 million km^3 of basoaerial habitat through which planes ascend and descend, creating a network of high-risk areas for aerial organisms.

We also face novel conflicts between our desire to protect biodiversity in the Anthropocene, our need to mitigate climate change (in part to protect biodiversity), and our current, insatiable demand for energy. Renewable energy technologies developed to provide sustainable alternatives to fossil fuels can have substantial impacts on basoaerial habitats. Wind energy installations increase mortality of local and migratory birds and bats, and solar energy installations that include solar power towers can incinerate flying birds or arthropods that cross the "solar flux" (Dai *et al.* 2015; Walston *et al.* 2016). Although the impact of each individual installation on threatened aerial species is likely negligible, the long-term, cumulative impacts of the growing number of installations may not be. Thus, decreasing the impacts of renewable energy on aerial wildlife represents a major challenge in aeroconservation. An associated challenge is the conversion of estimated mortality rates from these threats to projected, population-level impacts. Currently, such impacts are unclear because mortality estimates are highly variable among studies (Calvert *et al.* 2013; Arnett *et al.* 2016) and baseline data on population trends are unavailable for many aerial taxa (Baxter-Gilbert *et al.* 2015; Arnett *et al.* 2016).

The final ecological frontier?

The airspace also remains poorly represented in ecological and conservation research, despite recent interest in aeroecology (Kunz *et al.* 2008; Womack *et al.* 2010). To illustrate this on a broad scale, we conducted a Google Scholar search for the terms "aquatic habitat" and "terrestrial habitat," which returned ~40,000 and ~13,000 records, respectively. In contrast, our search for the term "aerial habitat" returned 171 records, and only 31% of these used the term to describe habitat for aerial taxa (Figure 1C). We are not suggesting that there is no interest in the airspace among ecologists, or that it has never been considered. Instead, we hope to catalyze progress in aeroconservation by highlighting: (1) a critical, persistent gap in conservation biology and (2) an opportunity to extend paradigms and research methods from terrestrial ecology upward into the airspace. We explore one example below: the fragmentation of aerial habitat.

Fragmented skies – applying paradigms from terrestrial ecology to the airspace

Diehl (2013) proposed that aerial habitat could also be "fragmented," but the implications of aerial habitat fragmentation have not yet been studied. Fahrig (2003) defined habitat fragmentation as the "breaking apart of habitat," a process that can cause chronic changes in species diversity and ecosystem function (Andren 1994; Lindenmayr & Fischer 2013; Haddad *et al.* 2015). Describing the airspace as "fragmented" may be counterintuitive to ecologists accustomed to visualizing this process in two-dimensional, terrestrial landscapes. Nevertheless, we propose that anthropogenic intrusions into aerial habitats can create barriers to movement, functionally dividing basoaerial habitat into isolated fragments.

The multidimensionality of the airspace can complicate our perception of its connectivity. In discussing aerial habitat fragmentation and aeroconservation with colleagues, we have repeatedly heard the argument that flying wildlife can surely avoid obstacles as large as buildings. For organisms such as ballooning spiders or aerial microorganisms that do not control their aerial trajectory (Womack *et al.* 2010; Blandenier *et al.* 2014), obstacle avoidance may simply be impossible. However, we acknowledge that many obstacles encountered by aerial species appear easily surmountable from our perspective. For example, transmission lines are not *that* high – surely birds can simply fly over them? In many cases they do, but expecting aerial species to consistently increase flight altitude in response to habitat fragmentation discounts the constraints of the altitudinal niches to which they are adapted (Scott 2011, Finn *et al.* 2012), and may raise the potential energetic and fitness costs of flight. Exposure to aerial predators and energetic costs of flight may increase with flight altitude, especially for species that are not adapted to high-altitude gliding (Niskanen *et al.* 2014), while increased altitude also increases the length of the total flight path. The challenges of obstacle avoidance in the airspace are clearly illustrated by the millions of aerial vertebrates and arthropods that collide with anthropogenic features every year.

As a thought experiment, imagine a population of passerine birds (or damselflies, or hemipterans). Picture a species that can meet its habitat requirements in an urban area, and that typically flies within a few meters of the ground to reduce energetic costs of flight (Finn *et al.* 2012), or to avoid predation. In urban areas, buildings that are taller than the preferred flight height of this species create functional barriers, analogous to those documented in terrestrial species that avoid roads that they are physically able to cross (D'Amico *et al.* 2016). Our hypothetical aerial species can fly around buildings where gaps exist, but this increases the distance of their journey from one point to another, potentially increasing predation risk and energetic costs, and further decreases the functional connectivity of their habitat.

Aeroconservation can benefit not only from the paradigms of terrestrial ecology, but also the tools. For example, connectivity analyses could identify critical

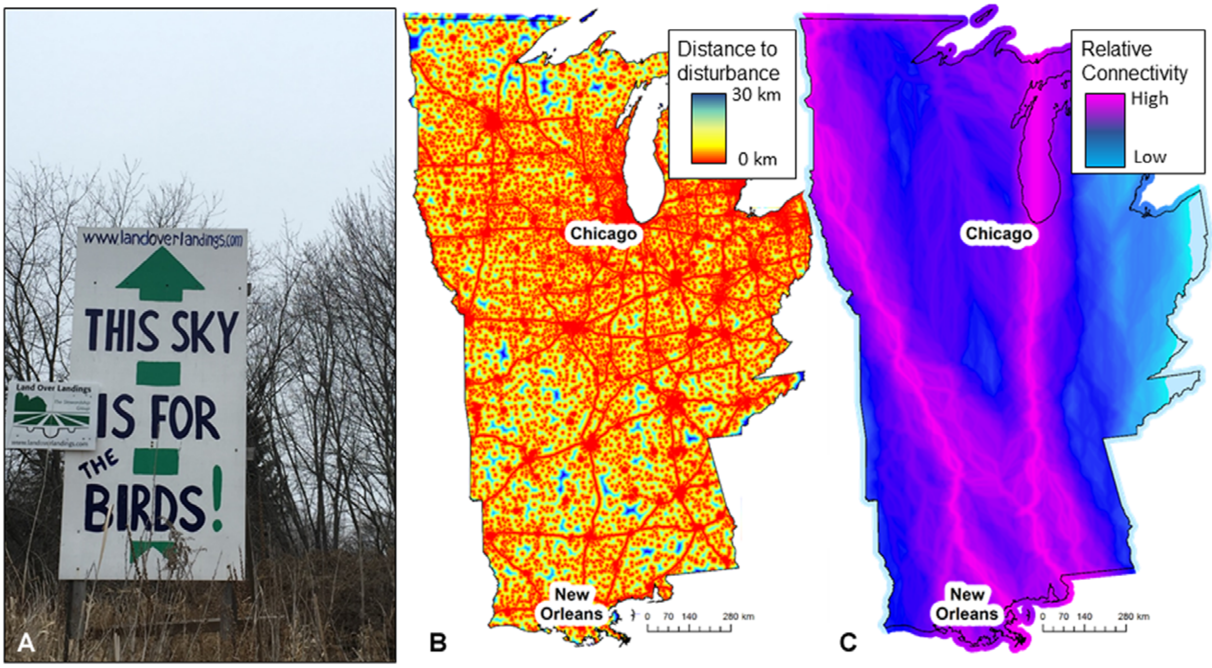

Figure 4 Conservation of aerial species requires protection of aerial habitats. There is growing awareness of the need to conserve airspace for wildlife, illustrated here by a sign in Ontario, Canada, that was posted in response to a proposed airport (A). Yet, conservation policy lags behind public awareness, limiting effective management of aerial habitats (Table 1). Tools used to quantify fragmentation of terrestrial habitats can also be used for the conservation of airspace, such as (B) linkage maps (Koen *et al.* 2014). Here, we quantify aerial movement corridors that have the lowest cumulative exposure to aerial habitat fragmentation in the Mississippi flyway. Most points in the eastern United States are <30 km from sources of fragmentation (B). As a result, basoaerial habitat connectivity is low, shown in (C). We define fragmentation as proximity to airports, cities, highways, wind farms, or communication towers, although we acknowledge that further sources of aerial habitat fragmentation also exist. Termini for the corridors are the Yucatan Peninsula (Mexico), Hudson's Bay (Canada), and Wood Buffalo National Park (Canada), approximating avian migration through the United States and Canada. See online supplemental material for further details of this analysis.

corridors for aerial habitat connectivity, an approach we illustrate in Figure 4. Such corridors could be overlaid with habitats essential to terrestrial or aquatic habitat connectivity, allowing identification of "connectivity hotspots."

In addition to anthropogenic impacts on aerial vertebrates and arthropods, potential human impacts on microorganisms adapted to aerial habitats provide rich research opportunities (Yang *et al.* 2008; Womack *et al.* 2010). Selective pressures on aerial microorganisms are likely altered by climate change, pollution, and human activity. Shifting temperature or precipitation patterns could affect survival of aerial microorganisms, potentially altering community structure. Altered wind patterns and aircraft movements could influence microorganism dispersal, modifying the biogeography of aerial microorganisms with unpredictable effects. Although we consider it unlikely that the facilitated movement of aerial microorganisms would cause a major ecological catastrophe, the rapid increase in emerging infectious diseases (Jones *et al.* 2008) serves as an illustration that invasive microorganisms can have unpredictable effects on naïve ecosystems.

Reaching for the sky

Effective aeroconservation requires effective solutions and tools for the conservation of aerial habitats and biodiversity. Substantial efforts are already underway, supported both by the development of new technologies, and the implementation of common-sense solutions. These include installation of new types of window glass that are less likely to cause bird collisions, and mandated temporary shut-downs of wind energy installations during peak bird or bat migration periods. However, these efforts are largely limited to local mitigation of collision-based impacts on particular taxa. The recognition of aerial habitats now needs to be translated into policy, qualifying the habitats themselves for legal protection where necessary.

Flying aircraft or UAVs at low altitudes is often prohibited over some protected areas, typically to protect terrestrial species from disturbance (e.g., Otto *et al.* 2003). Such rules could be extended to protect aggregations of aerial species, and dynamic aerial reserves have been proposed to protect aerial foraging or migratory habitat (Diehl 2013; Lambertucci *et al.* 2015). While we echo the call for protected aerial reserves, we argue that it is premature until aerial habitats are acknowledged in policy and legislation, and until the extent of legislative influence into aerial habitat is clarified (Lambertucci *et al.* 2015; Linchant *et al.* 2015). In many countries, legislation such as the U.S.A. Clean Air Act addresses the abiotic components of air quality. These types of legislation could serve as a platform to provide legal protection to aerial biodiversity. Similarly, legislation governing terrestrial and aquatic conservation (e.g., the Canadian Species at Risk Act) could be modified to include aerial habitats where required for species protection.

We acknowledge that there are substantial logistical challenges associated with aeroconservation, and we are hopeful that new technologies will emerge to meet them. For example, radar can detect mass migrations or significant ephemeral concentrations of prey for aerial insectivores (Farnsworth *et al.* 2015), enabling habitat protection when necessary and allowing human use at other times (dynamic aerial reserves). Stable isotope analyses and the increasing miniaturization of biologging tools allow identification of migratory and dispersal pathways for an increasing diversity of airborne organisms (Fraser *et al.* 2010; Stanley *et al.* 2015).

Building effective strategies for aeroconservation will not be simple or fast. It will require transboundary partnerships and creative collaborations among legislators and policy makers, conservation practitioners, researchers, and the public. We invite you to join us in lifting our conservation tools up off the ground, and developing effective protection for the thousands of species with which we share the skies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

The following supplementary material is available for this article:

Movie S1. This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1755–263X.2008.00002.x.

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