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Research

The grand challenges of migration ecology that radar aeroecology can help answer

Silke Bauer, Judy Shamoun-Baranes, Cecilia Nilsson, Andrew Farnsworth, Jeffrey F. Kelly, Don R. Reynolds, Adriaan M. Dokter, Jennifer F. Krauel, Lars B. Petterson, Kyle G. Horton and Jason W. Chapman

S. Bauer (https://orcid.org/0000-0002-0844-164X) (silke.s.bauer@gmail.com), Swiss Ornithological Inst., Sempach, Switzerland. – J. Shamoun-Baranes and A. M. Dokter, Inst. for Biodiversity and Ecosystem Dynamics, Univ. of Amsterdam. – AMD, C. Nilsson, A. Farnsworth and K. G. Horton, Cornell Lab of Ornithology, Ithaca, NY, USA. – J. F. Kelly, Corix Plains Inst., Univ. of Oklahoma, Norman, OK, USA. – D. R. Reynolds, Natural Resources Inst., Univ. of Greenwich, Chatham, Kent, UK and Rothamsted Research, Harpenden, Hertfordshire, UK. – J. F. Krauel, Ecology and Evolutionary Biology, Univ. of Tennessee, Knoxville, TN, USA. – L. B. Petterson, Biodiversity Unit, Dept of Biology, Lund Univ., Sweden. – J. W. Chapman, Centre for Ecology and Conservation, and Environment and Sustainability Inst., Univ. of Exeter, Penryn, Cornwall, UK and College of Plant Protection, Nanjing Agricultural Univ., Nanjing, P. R. China.

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Many migratory species have experienced substantial declines that resulted from rapid and massive expansions of human structures and activities, habitat alterations and climate change. Migrants are also recognized as an integral component of biodiversity and provide a multitude of services and disservices that are relevant to human agriculture, economy and health. The plethora of recently published studies reflects the need for better fundamental knowledge on migrations and for better management of their ecological and human-relevant effects. Yet, where are we in providing answers to fundamental questions and societal challenges?

Engaging a broad network of researchers worldwide, we used a horizon-scan approach to identify the most important challenges which need to be overcome in order to gain a fuller understanding of migration ecology, and which could be addressed using radar aeroecological and macroecological approaches. The top challenges include both long-standing and novel topics, ranging from fundamental information on migration routes and phenology, orientation and navigation strategies, and the multitude of effects migrants may have on resident communities, to societal challenges, such as protecting or preventing migrant services and disservices, and the conservation of migrants in the face of environmental changes. We outline these challenges, identify the urgency of addressing them and the primary stakeholders – researchers, policy makers and practitioners, or funders of research.

Keywords: migration routes, phenology, migrant services and disservices

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Introduction

Over the past decades, many migratory populations have faced substantial declines, and these have mainly been a consequence of rapid and massive expansions of human structures and activities, habitat alterations and climate change. Migratory animals might be particularly affected as they rely on multiple, distant sites throughout their annual or lifecycles (Runge et al. 2014, 2015) and changes in any of those sites are fitness-relevant and may carry over to demographic rates and trends in their populations. There are also several evolutionarily novel factors such as artificial light at night (ALAN), electromagnetic noise, or wind energy installations, which have enormously expanded in recent years and now represent significant and ubiquitous distortions particularly to aerial migrations (Engels et al. 2014, Fijn et al. 2015, McLaren et al. 2018).

At the same time, migrants are an integral component of biodiversity and through their roles in community structure and dynamics, migrants shape the diversity in otherwise separated ecosystems (Bauer and Hoye 2014). Migrants also provide a multitude of services and disservices that are relevant to human agriculture, economy and health (Bauer et al. 2017). For instance, the predation of insect pests by migratory birds, bats and predatory insects, and the pollination of plants by migratory insects and bats are highly desired and economically rewarding services (Kunz et al. 2011, Frick et al. 2017a, Reynolds et al. 2017). Conversely, disservices needing mitigation include the transport of zoonotic or agricultural parasites, or the consumption of crops by pests. Making better use of migrant services and reducing their disservices could save money and lives but we are still only at the beginning of getting a better understanding of migrant interactions with (resident) communities and their role in shaping ecosystem functions (Bauer et al. 2017).

The plethora of studies published recently within the realm of migration ecology reflects the need for better fundamental knowledge on migrants and migrations but also the need for better management of their ecological and human-relevant effects. Yet, what are the research priorities and where are we in providing answers to fundamental questions and societal challenges? Although important advances in answering these questions have been made with individual bio-logging devices (Kays et al. 2015, Wilmers et al. 2015), they can usually only be applied to relatively small numbers of individuals. However, if we are concerned with large-scale patterns typical of migrations and their long-term trends, a complementary, macroecology approach might be better suited (Kelly and Horton 2016). For aerial migrants, networks of radars can provide such an approach as they survey the airspace over large regions and entire continents and allow comprehensive assessment and quantification of the biomass transport across, into and out of large geographic regions. Due to their much coarser taxonomic resolution, the scientific value of radar methods has often been questioned. Yet, the installation of new sensors and, more importantly, the compilation of data across entire networks of radars have led to a renaissance of radar aeroecology and increasing application within migration ecology (Kelly and Horton 2016, Chilson et al. 2017, Shamoun-Baranes et al. 2017).

To identify the significant medium- to long-term challenges that might not be well recognized or investigated, or have great relevance for many societal issues, we used a 'horizon scan-approach' (Hays et al. 2016) and focused on challenges that can be addressed with a macrosystem-level approach using radar technology. Our aims were to identify basic research priorities for scientists, to inform policy makers, and to increase awareness of neglected or emerging issues.

To this end, we compiled a list of migration ecology challenges which can be tackled by radar during an international workshop with 50+ participants with professional backgrounds ranging from fundamental movement research to applied conservation and management (Luzern, Switzerland, Feb 2014). This list was subsequently circulated among 135 leading migration and movement ecologists worldwide, who were asked to identify the most relevant issues and score them according to priority. Approximately 1/3 of these questionnaires were returned, and we used the overall scores to select the highest-ranked questions and classified them post-hoc into broader themes: 1) migration characteristics; 2) mechanisms of movement and environmental influences; 3) effects of migrants; 4) human influences on migration; and 5) technical and methodological challenges (Fig. 1). In the following, we briefly outline these challenges and highlight the developments within radar aeroecology that will facilitate the identified research or operational priorities. Additionally, the authors assessed the novelty of the challenges and the urgency of their answers post-hoc for the three major taxa of aerial migrants (birds, bats and insects) (Fig 2), identified their typical spatial and temporal scales, and the most relevant stakeholders (Fig 3).

We would like to emphasize that we do not aim at providing a comprehensive review of the challenges within migration ecology in general. Instead, we focus on the subset of challenges that can meaningfully be addressed with a macroecology approach using radar. Similarly we do not review the rich history of radar aeroecology as this has been done elsewhere (Drake and Reynolds 2012, Chilson et al. 2017), but focus on advances that have been made in the last decade or so.

1. Migration characteristics

a. What are the migration routes and important sites, and how can we produce continental-scale maps of flyways and migratory networks?

Most of our present understanding of bird migration routes originates from individual tracking or observation data (Thorup et al. 2014), based on which major avian flyways and important non-breeding sites have been suggested.

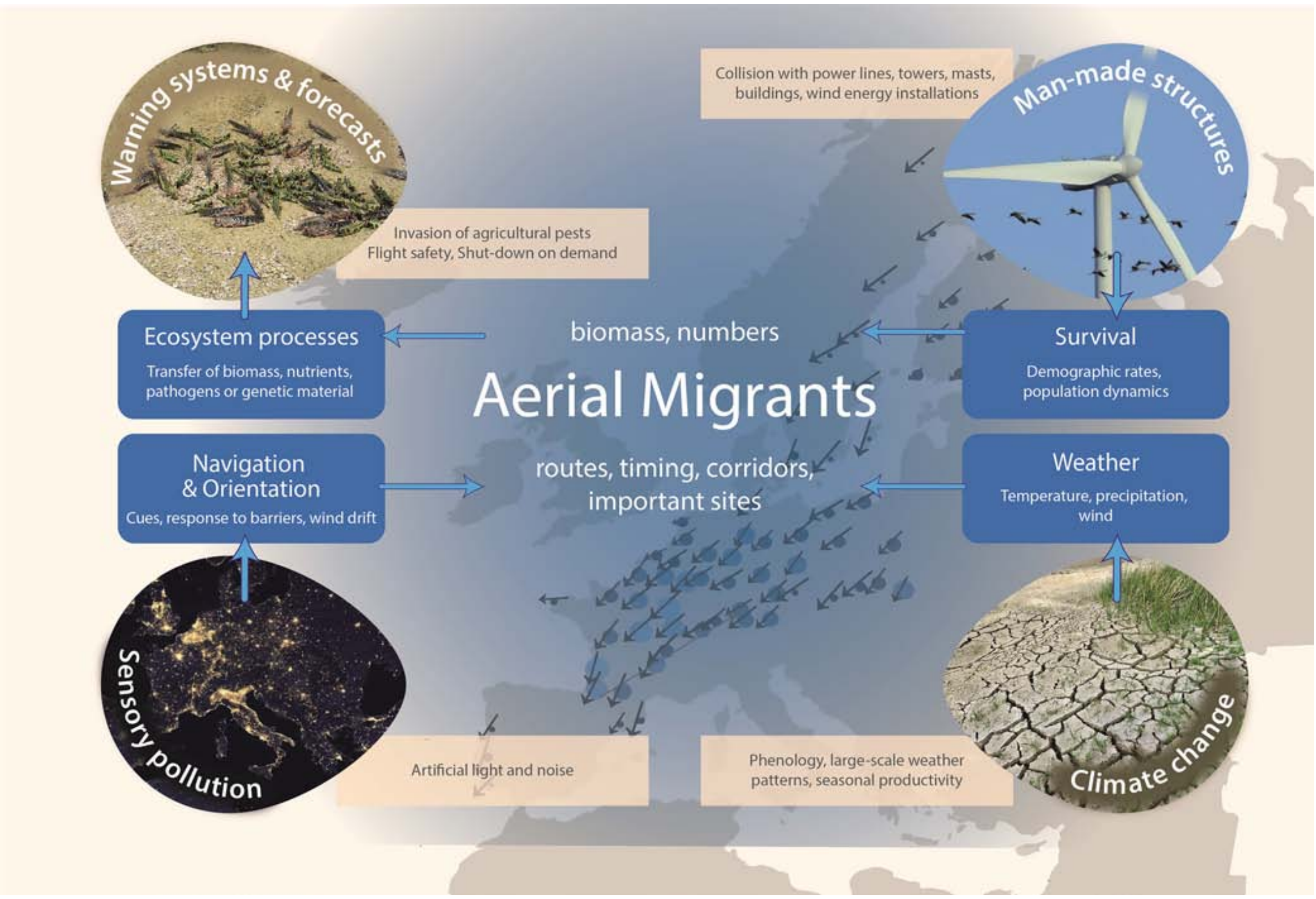


Figure 1. The major challenges identified in migration ecology cover long-standing and novel questions. Obviously, characterizing migration routes and timing and quantifying migrant numbers is fundamental to all other questions (central area). Understanding navigation and orientation as well as the influence of weather and climate on migrants and migrations is also fundamental to understanding how migrations are shaped and which consequences these have for (the abundance of) migrant populations (blue boxes). The identified challenges also included those that highlight the direct and indirect influences of human structures and actions on aerial migrants as well as mitigation of human-wildlife conflicts or migrant disservices. For instance, sensory pollution through artificial light and noise can impact navigation and orientation and global climate changes can change the timing of migration. Background image modified after Nilsson et al. 2019.

However, it is still unclear how general these suggested flyways are and where the majority of migratory animals are during the different phases of their migration; this applies particularly to nocturnal, non-iconic and/or small migrants such as bats and insects.

Continuous large-scale surveillance with radar networks can generate maps of where large numbers of migrants pass and thereby identify migration corridors and their typical (topographical) characteristics (Nilsson et al. 2019). Such efforts will not only provide fundamental insights into migratory processes and their large-scale patterns, but also identify bottlenecks, crucial stopover areas and sensitive times. An important step towards identifying important areas for migrants has been made by Buler and Dawson (2014), who used weather radar data from the eastern US to identify areas and habitats of high conservation value for large numbers of avian migrants. Radar data have also been combined with large scale citizen science data in the USA (eBird) for a detailed view of the bird migration strategies at the flyway level (Horton et al. 2018) or with systematic entomological surveys in investigations of the migration circuit of the painted lady butterfly *Vanessa cardui* in the Western Palaearctic (Stefanescu et al. 2013).

b. How can we quantify migrant biomass and numbers and their geographical variation?

Monitoring migrating animals over large spatial scales can estimate the abundances of their populations and show trends that indicate the vitality of the full migratory avifauna, or insect species assemblies at an ecosystem level. The biomass of aerial migrants that seasonally enter and leave a particular region could unravel patterns in recruitment (biomass gain) and mortality (biomass loss) (Chapman et al. 2012, Hu et al. 2016) and be linked to environmental variables that drive the variability in long-term trends. Such information is critical for the early detection of population declines (Dokter et al. 2018), and for installing timely remedial measures.

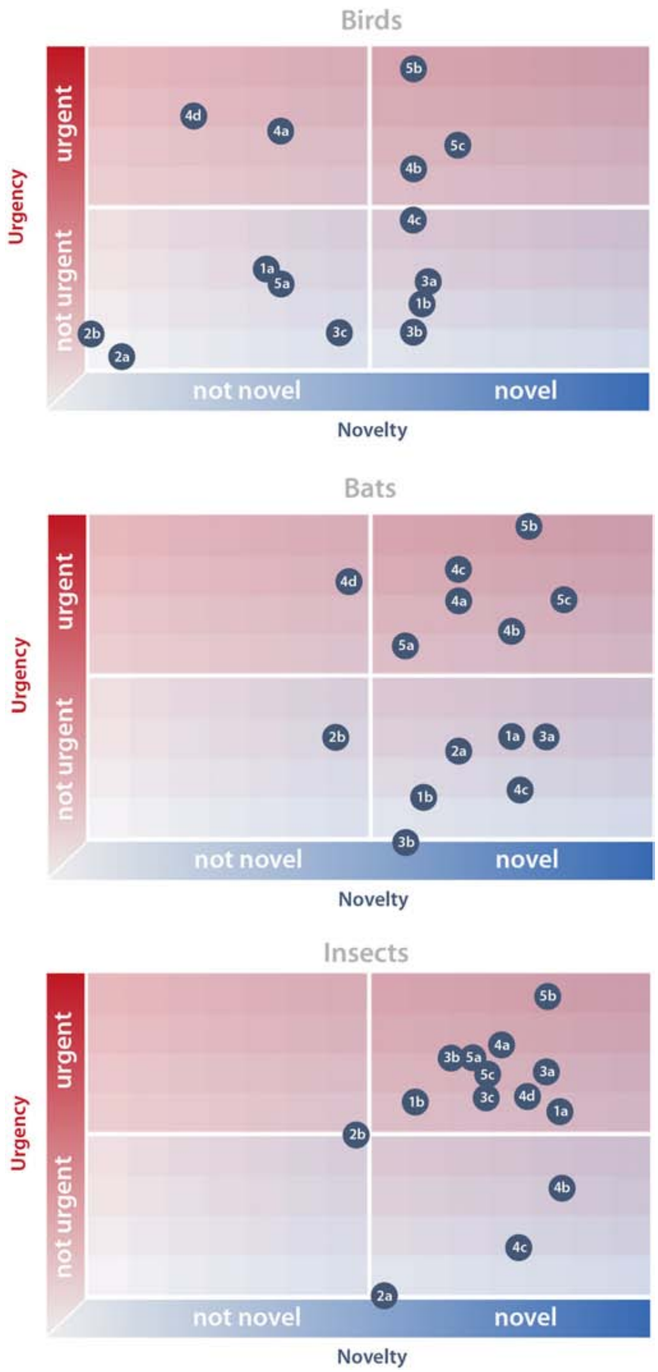


Figure 2. The challenges in migration ecology along gradients of novelty and urgency – separately for birds, bats, and insects. Circled numbers refer to the challenges identified (and the corresponding sections in the main text).

Quantification of migrant abundances, their biomass and nutrient transport into and out of regions can be first proxies for the influence of migrants on the structure and dynamics of resident communities, and ecosystem function (Bauer and Hoye 2014, Hu et al. 2016). A key challenge for the quantification of migrant abundances and biomass across continents is that the 'biological' data resulting from radar networks should be comparable, across radar systems and countries (Dokter et al. 2011, Nilsson et al. 2019). Meteorological and ecological research communities should therefore intensify their efforts towards standardization and calibration of radar systems.

2. Migration – mechanisms and environmental influences

a. How do free-flying migrants detect and respond to winds, and deal with ecological barriers?

The compass mechanisms used to set a suitable direction have been identified for many migrants (Mouritsen 2018), but much of our knowledge comes from experiments performed in highly artificial situations, such as birds constrained in Emlen funnels, or insects tethered in flight simulators, and in the absence of natural wind currents. By comparison, we know less about 1) how migrants use their compasses to maintain beneficial directions under natural conditions, where they are exposed to varying currents; and 2) how migrants detect currents (Chapman et al. 2011).

The ability to compensate for wind drift throughout migratory journeys has been extensively demonstrated by radar studies of nocturnal songbird migrants (Alerstam et al. 2011, Chapman et al. 2016), which appear to follow a cost-effective strategy of 'drift when they can, but compensate when they must' (Horton et al. 2016b). Songbirds indirectly assess current speed and direction by visually assessing their wind-induced displacement relative to ground features (Chapman et al. 2015) and thus, will be influenced by ambient light levels from natural and anthropogenic light sources (see below). Coordinated radar studies of songbirds' abilities to compensate for varying flows under different levels of natural light and ALAN will make a valuable contribution to our knowledge of how birds measure and deal with wind drift.

Radar studies have also demonstrated that high-flying insect migrants are extremely efficient at selecting favourably-directed flows (Chapman et al. 2010); they also partially compensate for drift, albeit to a lesser degree than songbirds (Chapman et al. 2016). Nocturnal insect migrants directly assess the flow (Chapman et al. 2015), potentially via detection of wind-related micro-turbulence (Reynolds et al. 2016) – although so far this has only been tested in one locality (the UK). Comparative radar measurements of insect headings in relation to wind at multiple locations are required to discover how insects assess the flow vector.

Extensive areas of unsuitable habitats (e.g. deserts and seas) or topographical barriers (mountain ranges) pose significant problems for migratory animals. Individual tracking studies of large migrants, particularly soaring birds, suggest that they have evolved migratory routes to avoid barriers (Strandberg et al. 2010). The situation is less clear for smaller migrants (songbirds and insects), which are thought to migrate on a broad front. However, continental-scale

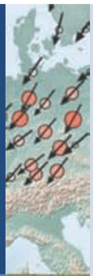
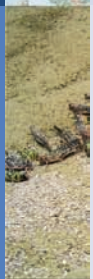
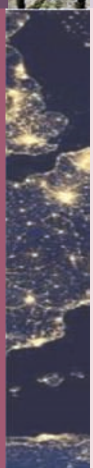
Challenge		Topic	Stakeholder	Information
Description		Migration routes, sites	**Nature conservation, National and interna-tional legislation and policy makers**	Habitat association of migrants throughout the annual cycle Identification of crucial places for international treaties and management plans
		Biomass, numbers		Population trends, demographics of migrants for early detection of conservation concerns
Mechanisms		Orientation, navigation	**Ecologists, Sensory biologists**	Fundamental knowledge on migrant strategies, behavioural rules and response to cues
		Weather	**Scientists, legislation and policy makers**	Weather effects on spatial and temporal migration patterns
Services and disservices		Transport effects	**Nature conservation, Ecologists**	Connectivity of disparate habitats, Ecosystem functioning
		Warnings, forecasts	**Agricultural managers, farmers, agronomists, health agencies,**	Warning systems for invasion of agricultural pests, dispersal of parasites with zoonotic potential, preven-tion of outbreaks
			Airport operators, wind energy sector	Birdstrike prevention, shutdown-on-demand protocols
Human influences		Climate change	**International and national legislation and policy makers**	Specific aspects of climatic change that are problematic for migrants
		Sensory pollution	**City planners, legislation, conservation**	Attraction and concentration of migrants, reduction of light and noise emissions
		Man-made structures	**Architects, policy makers, wind energy sector,**	Identification of problematic areas, installation of collision-reducing materials, Advise on location of wind parks
		Conser-vation	**Nature conservation, policy makers**	Protection of crucial sites and times, their habitat quality and land use, developing efficient management plans
Technical challenges		Classifi-cation	**Meteorologists, ecologists**	Improving meteorological services and products via better exclusion of biological targets
		Data infra-structure	**Data scientists, general public**	Sustainable data infrastructure, long-term storage and open access for radar products
		Integration other data	**General public, ecolo-gists, remote sensing**	Validation of methods, integration with other methods for species composition

Figure 3. For each challenge identified, we listed the most important stakeholder as well as the information that would be most beneficial to their work and products.

radar studies are providing evidence that, at least for nocturnal songbirds, this is not the case. For example, in western Europe, the main passerine migration largely avoids the Alps and long oversea crossings (Nilsson et al. 2019). Future studies using radar networks will allow researchers to characterise migration routes of a wide range of migrants and assess the frequency of routes which avoid barriers and long sea crossings.

b. What is the influence of (seasonally changing) weather conditions on (initiation, duration, termination of) migration and ultimately on survival and population dynamics?

A primary challenge for migratory animals is adjusting to temporally and spatially unpredictable weather phenomena en route, and the capacity to respond to them is a driving force behind the fitness of individual migrants. Beyond the individual, there is evidence that survival during the migratory phase of the annual cycle limits populations of migrant birds (Finch et al. 2014) although this might not be the case for most insects (Chapman et al. 2012) due to their high intrinsic rates of reproduction. It is also possible that the inherent dangers of migration, including weather, place biogeographic limits on species distributions (Toews 2017). Understanding how migrants cope with weather en route is central to predicting the future of migrants in an era of global change.

For birds, there is ample evidence that individual migrants are highly attuned to key physical environmental variables such as wind speed and direction, air pressure, temperature, and precipitation (Richardson 1990). Generally, wind conditions and precipitation are the largest factors determining migration conditions (La Sorte et al. 2014a, Kranstauber et al. 2015, Shamoun-Baranes et al. 2017). Migrants can assess favourable migration conditions ahead as is evident in predictable mass movements of migrants, e.g. autumn migrants departed over the Gulf of Mexico with the passage of strong cold fronts (Cohen et al. 2017).

Migratory birds also adjust to atmospheric conditions aloft while in flight (Horton et al. 2016a). If weather conditions deteriorate, migrants ‘fall-out’ in high densities particularly near large geographic barriers (Moore et al. 1990). While these behaviours appear to provide fitness benefits, it is not uncommon for migrants to die ‘en route’ as a result of extreme or persistent unfavourable weather. While ‘en route’ weather clearly impacts the population dynamics of migrants (Newton 2007), there remain few studies in which these seasonal carry-over effects have been clearly demonstrated (Senner et al. 2015).

The capacity to integrate information from weather radars on system level patterns with data from sensors carried by individual migrants is already possible – though rarely employed. This approach would benefit research even on taxa not otherwise suited to weather radar study, for example bats flying in low densities. Advanced biologging efforts promise to revolutionize our understanding of how individual migrants cope with changing weather in real time. The key role of weather radar data in this integration will be to provide a context around whether individual behaviours were typical or unusual relative to the mass flow of migrants in flight.

3. Effects of migrants

a. What is the effect of migrant-mediated transfer of biomass, nutrients, pathogens or genetic material on ecosystem processes?

It is increasingly recognized that migratory animals can alter the structure and dynamics of communities and ecosystem functions through a variety of transport and trophic effects (Bauer and Hoye 2014). These effects often also represent important services and disservices relevant for human agriculture, economy and health. For instance, bats pollinate fruit plants or consume insect pests; birds disperse plant seeds and invertebrates; and insects consume crops, transport crop and livestock diseases, and pollinate crops. In some cases, migrants may represent several effects, for example migratory noctuid moths are serious agricultural pests but also an important food resource for migratory bats in Texas (Krauel et al. 2015, Frick et al. 2017a).

However, an understanding of the role of migrants in community dynamics and ecosystem function is as yet limited to a few iconic examples and hardly known for the majority of migrants. Radar monitoring of aerial migrants can provide fundamental information on migration routes and times (see 1a and 1b above), which is also a prerequisite for identifying the role of migrants in ecosystem processes. A first step could be to estimate the nutrient and energy transfer by migrants from seasonal patterns of mortality and recruitment (Hu et al. 2016). For the effect of migrants on other ecosystem processes, we need to complement radar monitoring with a range of studies, e.g. epidemiological screening for the parasite load of migrants, or local studies for the consequences of nutrient and biomass transfer to local communities, etc.

b. How can radar assist in the development of warning systems for the invasions of migratory pests of crop, livestock, humans?

Warning systems for the invasion of migratory pests of crops, livestock or humans exist only to a limited degree, mainly for massive outbreaks of insect pests of agriculture. Special-purpose entomological radars have been used for 50 years in programmes of applied research, which have contributed greatly to our understanding of the migration of many serious insect pests (Drake and Reynolds 2012). Additionally, inputs from monitoring radars are, or might be, useful for operational warning systems, e.g. pest aphids such as bird cherry-oat aphid *Rhopalosiphum padi* and diamondback moth *Plutella xylostella* (Nieminen et al. 2000, Leskinen et al.

2011), migrating corn earworm *Helicoverpa zea* and beet armyworm *Spodoptera exigua* moths in southern USA (Westbrook et al. 2014), and the exodus flights of spruce budworm *Choristoneura fumiferana* moths in eastern Canada (Boulanger et al. 2017).

Radar-derived variables alone can rarely identify migrants unambiguously – but the following criteria will assist recognition. First, if pest insects have distinctive characteristics of size, body shape and/or wing-beat characteristics, perhaps combined with a seasonal occurrence, this tends to limit the likelihood of confusion with non-focal species. An example for this are Australian plague locusts *Chortoicetes terminifera*, for which entomological monitoring radars have provided inputs into the Australian Plague Locust Commission's operational monitoring and forecasting system (Drake and Reynolds 2012, Drake and Wang 2013). Second, if insects of interest predominate in the airspace over a region, at least during certain seasons or years, it can reasonably be assumed that they are the major component of the biological scatterers detected by radars. The putative radar-observed migrations need to be confirmed by insect trapping or surveys. Situations where a single or few species dominate the aerial fauna more likely occur in faunistically-simple regions, e.g. at high latitudes or in arid regions, or during major insect outbreaks.

Pest warning systems using non-biological radars are currently rather dependent on operator experience to distinguish between insect, birds and precipitation, although algorithms for distinguishing insect targets (particularly those appearing on dual-polarization weather radars) are being devised (Chilson et al. 2017).

c. How can we utilize radar studies and radar data for generating and disseminating real-time radar-based analysis and forecast products to serve the human community?

To reduce the risk of bird-aircraft collisions, radar is being used in an operational capacity by military aviation in several countries for (near) real-time monitoring of avian migration, and to develop migration forecast models used operationally (Shamoun-Baranes et al. 2018, Van Gasteren et al. 2019). Both are used to alter flight planning under high collision risk, saving money and lives. Although the benefits of radar-based monitoring and forecasting for flight safety are obvious, to date such systems are operational only in a few regions (<www.flysafe-birdtam.eu>, Van Gasteren et al. 2019). Upscaling to larger geographical ranges and developing improved forecast models at continental scales (Van Doren and Horton 2018) or across national borders could constitute an enormous societal benefit.

Another rapidly growing application of radar products and migration forecasts is the wind energy sector – in particular, to assess, and possibly mitigate, their impact on aerial migrants (Fijn et al. 2015, Köpel 2017). Real-time information from radars can be used to initiate temporary shutdown procedures, inform models to assess collision risk in a given area (Liechti et al. 2013a) and/or to develop other mitigation measures. Forecast models can be extremely valuable in reducing the economic impact of curtailment on the energy grid, by enabling market adjustments in advance (e.g. 48 hours in advance). However, operational systems and baseline information needed for the development of reliable forecast models are still lacking for many areas, especially offshore. While wind energy also represents a significant threat to migratory bats (Hein and Schirmacher 2016), radar has been overlooked as a potential conservation tool.

Near-real time data on migration fluxes and forecast models can also be enjoyed and utilized by nature enthusiasts. While not systematically documented, birders are known to regularly explore the military forecast system to get information on migration (H van Gasteren, personal communication). Social media outlets such as twitter as well as projects like BirdCast (http://birdcast.info) provide an exciting new outlet for sharing radar observations of migration beyond the scientific community.

4. Human influences on migrants and migrations

a. How does climate change affect migration?

Among myriad ecological phenomena, migration is a particularly insightful proxy for climate-change effects because it is tightly coupled with Earth's system dynamics (Helm et al. 2013). There is good evidence that the timing of avian migrations is changing in response to climate change (James and Abbott 2014, Gilroy et al. 2016). These changes may disrupt ecosystem functions if they result in broad mismatches between migration timing and the timing of seasonal productivity (Jones and Cresswell 2010). A more complete understanding of how migrants respond to environmental change would be useful for predicting impacts of climate change on migration systems, and how these may carry over to communities and ecosystems. Many studies have documented changes in migration phenology associated with climate change (Carey 2009, La Sorte et al. 2014b), yet large gaps remain in our understanding of migration phenology and its relationship to climate (Cohen et al. 2018).

Substantial research effort has been invested in attempts to scale-up organism-focused research approaches to answer these questions. These attempts have used numerous methods such as massive bird banding efforts, broad-scale stable isotope and genetic sampling, and individual tracking studies (Hobson 2008, Thorup et al. 2014). Particularly the latter often reveal spectacular migratory behaviours (Liechti et al. 2013b). Although valuable in their own context, all of these approaches fail to sample broadly and densely enough to support coherent system-level inferences about continental-scale migration systems.

It would be desirable to have a measure of migration phenology that enables comparisons with existing phenology network data and individual migrant tracking data. Linking phenology across levels of biological organization from individuals to ecosystems through time and space would help us understand the scaling of biological impacts of climate change (Kelly and Horton 2016). A data-science research program centred on use of the weather surveillance radar archive could provide this inference. This approach offers key advantages, such as nearly continuous, continent-scale sampling, that make it capable of addressing the challenge of advancing our understanding of migration at the system-level (Kelly and Horton 2016). Automated workflows mine NEXRAD and other data archives to produce robust metrics for quantifying migration systems, which are scalable across time and space (Van Doren and Horton 2018). A key innovation is to capture the complexity of migration systems analysis while focusing on easily interpreted and universal metrics of migration systems: migratory intensity and migratory trajectory. Most of the diverse methods employed by organismal ecologists to study migration are motivated by efforts to measure these two parameters. Progress in this direction is occurring rapidly and it is likely that we will achieve this vision in North America by 2020.

b. What is the effect of sensory pollution on migration?

Globally, light pollution (ALAN) has increased dramatically during the 20th century (Falchi et al. 2016) and numerous aerial migrants from diverse taxa pass through photo-polluted skies annually (La Sorte et al. 2017, Cabrera-Cruz et al. 2018). ALAN represents a powerful stimulus, which could interfere with avian sensory systems such as the magnetic and celestial compasses, that can entrain attraction to and disorientation from light or avoidance of illuminated stopover habitat across diverse spatial scales (Van Doren et al. 2017, McLaren et al. 2018). While light pollution is not novel in the environment, it is still a relatively new stimulus from an evolutionary perspective. The possibility to measure light pollution globally using remote sensing enables scientists to study its relationships to behaviour and ecology from local to macroscales. ALAN's effects can be disruptive (Winkler et al. 2014) or even deadly (Jones and Francis 2003), ranging from significant alterations of body condition, disruptions of life histories or increased mortality through collisions with structures (Gaston et al. 2013), and may depend on proximate situations in which birds experience this. Less is known about the impact of ALAN on insect and bat migrations, but negative effects, such as reductions in moth feeding behaviours (van Langevelde et al. 2017, Grubisic et al. 2018) and bat species diversity in urban areas (Ancillotto 2015), appear likely. Future research should elucidate ALAN-effects at local to continental scales, during different phases of the annual cycle and with respect to vertical and horizontal lights, ground-based and aerial-based light, and combined effects of light intensity, spectra, location, and atmosphere.

Similar to artificial light, anthropogenic electromagnetic noise has reached unprecedented levels. Its effects on aerial migrants are largely unclear, although it has been demonstrated that, e.g. electromagnetic noise disrupts magnetic compass orientation in caged birds under laboratory conditions (Engels et al. 2014) and new research efforts are clearly needed.

Large-scale radar studies spanning a range of urbanised and rural habitats could therefore test the ideas that anthropogenic light and electromagnetic noise represent insidious new threats to the survival of nocturnal migrants, by comparative analyses of large-scale migration patterns, individual flight behaviour and orientation performance under a range of carefully measured ALAN and electromagnetic noise levels at local to continental spatial scales and nightly to decadal temporal scales.

c. What are the effect of man-made structures on migration routes and flight behaviour?

Collisions with man-made structures such as power lines, wind turbines, tall towers, masts and buildings kill large numbers of birds and bats annually, although there is great variation in estimates of fatalities and their ecological significance (Cryan et al. 2014, Lambertucci et al. 2014). However, for poorly-studied species such as migratory tree bats, mortality from wind turbines in North America appears to represent a substantial population-level threat (Frick et al. 2017b) and further research is urgently needed. Radar-based approaches have emerged as key tools to detect, monitor and counteract these effects (Fijn et al. 2015, May et al. 2015), and have been employed particularly in wind farms. Large-scale radar mapping of migration now allows careful spatial prioritization at the planning phase of wind turbine installations. Interestingly, when investigating effects of manmade structures, mobile radars can complement and extend results from larger radar networks by increasing resolution locally as has been shown in studies of foraging behaviour and fine-scale variation in habitat use of bats around wind turbines (Cryan et al. 2014). The influence of man-made structures on insect migration and flight behaviour has been considerably less explored. But like responses to natural topographic features, insects may follow man-made linear structures and can accumulate in streams of air flowing downwind from wind turbines, buildings and other tall structures. Indirect evidence for such concentrating effects at wind farms comes from the attraction of foraging insectivorous bats to these sites (Cryan et al. 2014, Foo et al. 2017). Additionally, tall buildings can influence insect flight behaviour through effects on microclimate and sunlight availability but responses of migratory insects to urbanisation may differ from those of non-migratory insects (Luder et al. 2018).

d. Conservation of migrants and migrations

The conservation of small, long-distance migrants such as songbirds, bats, and insects, and their migration systems, pose specific challenges (Runge et al. 2014, Hüppop et al. 2019). Migrants are dependent on multiple, potentially scattered or fragmented stopover sites (Fraser et al. 2012). Continental monitoring systems based on weather radar networks (Chilson et al. 2012b, Shamoun-Baranes et al. 2014) have emerged as one of the few techniques that can provide basic data on the use of specific habitats by large numbers of small passerine birds over very large spatial scales. For example, by examining spatial variation in dusk departure activity of nocturnal songbird migrants along the eastern seaboard of the USA (which reflects stopover decisions from the cessation of migration the previous night), Buler and Dawson (2014) demonstrated the huge importance of highly-localised floodplain hardwood forests for migratory passerines. Continuous, large-scale monitoring using weather radar also has a great potential in mapping key areas for some bat species (Chilson et al. 2012b) as well as sites and routes important for migrating moths and butterflies (Stefanescu et al. 2013, Krauel et al. 2015). Such information is invaluable for the prioritization of conservation measures in migratory systems, where actions in one location are likely to affect the situation at other locations along the route, especially across international borders (López-Hoffman et al. 2017). Establishing migratory patterns and the relative importance of paths and stopover sites emerges as more important than ever for conservation now that the connectedness of migratory populations becomes evident (Fraser et al. 2012). Migrants are likely to face difficulties adapting their migration strategies to keep up with a changing climate (Schmaljohann and Both 2017). Establishing the key stopover sites to ensure the long-term conservation of systems with migrating birds, bats, butterflies and moths is therefore a key challenge for radar aeroecology in years to come. However, securing the key sites on the ground may not be enough. The airspace connecting them is a central part of aerial migration systems and the concept of aerial protected areas, similar to marine protected areas, has recently emerged as a promising new tool to protect bird, bat and insect migration systems (Chilson et al. 2012a, Diehl 2013, Davy et al. 2017). Future efforts are therefore needed to explicitly add a vertical, airspace dimension to the conservation of long-distance migrants.

5. Technical and methodological challenges for improving the utility of radar data

a. Which classification and identification methods improve the taxonomic resolution of radar data?

Distinguishing different biological targets, especially when they are mixed in the same observation remains a major challenge for radar aeroecology and is critical for improving the quality and quantity of biological information that can be extracted from radar signals. As dual polarization weather radars are replacing single polarization radars, i.e. they transmit radio waves in horizontal AND vertical polarizations and can thus determines target size and shape, new opportunities arise for improving target identification. Researchers have only started to explore the full potential of dual-polarization radars, utilizing the additional information provided by these radars and meteorological data products to improve target identification (Stepanian et al. 2016). Theoretical simulations can be used to predict, which polarimetric signals are expected for various combinations of species and size distributions of migrating animals (Mirkovic et al. 2016, 2018). Such predictions will be very helpful in interpreting observed polarimetric radar signals and may provide insight of how to pin down the identity of migrating animals aloft based on their polarimetric signature.

Although polarimetric techniques are not expected to refine identification of targets to the species level, there is great potential for identifying size distributions and species communities. Another challenge will be the harnessing of deep-learning techniques for radar studies, which have already revolutionized the field of general image recognition (LeCun et al. 2015). These techniques will be extremely valuable in identifying and extracting complex biological features in radar imagery. Currently a major hurdle to this breakthrough is amassing the extensive training datasets that power these algorithms. Supervised labelling of data by experts is essential to validate these techniques against canonical workflows. Machine learning also has great potential to improve taxonomic identification based on wing-beat patterns (Zaugg et al. 2008). Wing-beat pattern detection is still limited to dedicated bird and insect radar systems but could be implemented on a much wider range of sensors. For example, several modern dual-polarization weather radars already perform vertical looking scans, during which wing-beat detection could be implemented. Finally, cross-validation of data from co-located radars of different types as well as with other aerial sampling methods (Nilsson et al. 2018, Krauel et al. 2018b, Liechti et al. 2019, see also section 5c) will be crucial to ensure robust interpretation of results.

b. Long-term data storage, access, visualisations

The large volumes of radar data and their efficient storage, access, processing, analyses and visualization require appropriate e-science infrastructure. Such infrastructure is not only needed to support research but also for the development and dissemination of sustainable services for different stakeholders.

In recent years, one of the greatest advances for radar research is the possibility to access operational weather radar data. For the United States, a freely available archive of weather radar data going back to the 1990s exists on a cloud data storage platform (Ansari et al. 2018). In Europe, the harmonization of meteorological data across nations is in progress (Huuskonen et al. 2014). However, long-term data storage for biological applications is still a major challenge, including hardware and software solutions but also international agreements for the system's maintenance and access to data. In collaboration with the operational programme for the exchange of weather radar information (OPERA) a prototype data pipeline is operational, in which weather radar data are processed using an automated bird detection algorithm (Dokter et al. 2019) at a central meteorological data hub (Michelson et al. 2018), with bird migration data output stored in an online repository. Finally, visualizations can be powerful tools for disseminating information within and outside the research community. Open source tools have been developed to create novel flow visualizations of migration across large spatial scales and integrating data from multiple radar sites (Shamoun-Baranes et al. 2016, Nilsson et al. 2019).

The development of an e-science infrastructure for radar monitoring of bird movement is probably most feasible for similar radar systems (e.g. weather radar networks), however they would be highly valuable for integrating data from bird detection radars which are used for research and monitoring for risk assessment and mitigation in aviation safety and wind energy. Perhaps the greatest bottleneck at this time is acquiring seed funding to set up such a system and then developing a business model for sustainable services.

c. Integration of radar with other data

Radar aeroecological studies provide access to previously inaccessible aspects of migration ecology, in particular behaviours at night and aloft as well as behaviours and patterns across large spatial and temporal scales. Radar data at such scales and for such purposes rarely, if ever, include species-specific information, and robust interpretation of radar data requires integration with additional data sources. So, a fundamental concern for radar studies is the inability to characterize patterns and behaviours at the species-level. There is broad agreement that a general characterisation of (bird) movements across scales is highly valuable and provides important information complementary to individual- or species-level studies, but the integration of techniques is paramount to enhance such research toward a more complete understanding of aerial animal migration (Robinson et al. 2010) and addressing the new multi-scale and big data approaches. The rapid pace of data collection, across a multitude of platforms, including citizen science (Sullivan et al. 2014), tracking technologies (Kays et al. 2015), and molecular (Krauel et al. 2018a), affords a myriad of opportunities to relate system-based properties, as measured by radar, with individual or species-level observations (Dokter et al. 2013, Laughlin et al. 2013, La Sorte et al. 2015, Kelly and Horton 2016). Although avian studies that integrate radar data with other sources, such as acoustic (Farnsworth et al. 2004) and eBird (La Sorte et al. 2015, Kelly et al. 2016, Horton et al. 2018) data are becoming more common, there is still much room for improvement. Additionally, other data sources are and will continue to be useful for validation of radar data to study other biological taxa, including sampling of insects both directly and via fecal sampling from predators as well as acoustic recording of bats at specific altitudes (Krauel et al. 2018a, b). Finally, integration of radar data with diverse remote sensing data (e.g. weather, habitat) and individual tracking data (e.g. from Motus or ICARUS, Kays et al. 2015, Taylor et al. 2017) provides an opportunity to link broad-scale patterns of animal behaviour with similarly scaled environmental patterns and individual behaviours.

Synthesis and outlook

We have identified the most pertinent challenges within migration ecology that can be tackled with radar aeroecology. These challenges are a mix of long-standing and novel questions, indicative of a fast-moving field, and cover the range from fundamental to applied research (Fig. 1). Particularly the latter shows that various stakeholders become increasingly more important and reflects the societal responsibility of research (Fig 3). It is also a response to the multitude of man-made factors that threaten migratory animals and the increased awareness of the role of migrants for ecosystem functions and for human economy and agriculture.

Our post-hoc analyses of scoring the challenges along a novelty and urgency gradient yielded several important insights (Fig. 2). First, the novelty-urgency scores were surprisingly similar between the US and Europe (not shown) – suggesting that the identified challenges are shared globally. The greatest differences in scores emerged between the three major taxa of aerial migrants – birds, bats and insects (Fig. 2). Most challenges scored less novel or urgent for birds, bats were intermediate, and for insects, the majority of challenges was scored either urgent or novel. This pattern clearly reflects, and is probably a consequence of, the research history in these taxonomic fields: For birds, radar aeroecology has already provided insights into biomasses, abundances, large-scale or long-term patterns (Box 1) – information that cannot be attained from individual tracking devices (Kelly and Horton 2016). For bats, radar is a vastly underused research tool and very little is known about bat migratory behaviour, for example flight altitude or the use of migration corridors. Unlike birds, bats are not thought to migrate in large aggregations that would facilitate detection on weather radar. Thus, the few studies of bat behaviour using weather radar are of high-flying species using large communal roosts (Horn and Kunz 2008, Frick et al. 2012, Stepanian and Wainwright 2018). For insects, the individual tracking perspective has hardly ever been an option and therefore, dedicated insect radars have been used for decades but have mainly been employed for economically important applications of pest insects (Drake and Reynolds 2012).

The high-scoring challenges and their overarching patterns have also identified where future research in radar aeroecology should be targeted, namely at a) challenges that have generally scored high, b) extending the range of spatial and temporal scales, c) fundamental 'catch-up' research in insects and bats and comparative studies between taxa, and d) providing various stakeholders with knowledge for efficiently mitigating human-wildlife conflicts.

High-scoring challenges

Challenges that have generally scored 'urgent' were those that identify human influences on fitness-relevant aspects of migration or attempts to mitigate them – from the degree to which artificial structures such as high buildings, power lines, Box 1. Selected recent key works from within radar aeroecology and their contribution to answering the challenges that were identified in our horizon scan, separately for the three major taxa of aerial migrants.

		Birds	Bats	Insects
Description	Migration routes, sites	Nilsson et al. (2019): European-wide patterns of avian migration along the West European flyway from weather radar data.	Horn and Kunz (2008): estimation of colony size, direction of movement, speed of dispersion, and altitude gradients of bats emerging at night from colonies.	Chapman et al. (2012): numbers of insects immigrating into UK each spring. Chapman et al. (2010): migration route of silver-Y moth in western Europe.
	Biomass, numbers	Dokter et al. (2019): seasonal abundance and survival of North America's migratory avifauna from weather radar.	Stepanian and Wainwright (2018): quantification of bat population fluctuations at a roost.	Hu et al. (2016): quantification of insect bio-flows over southern UK, their seasonal and annual variation over a 10-year period.
Mechanisms	Orientation, navigation	Horton et al. (2016b): migrants in flight often drifted sideways on crosswinds, and compensation for drift varied geographically and over time.		Reynolds et al. (2016): orientation in high-flying migrant insects in relation to flows. Chapman et al. (2015b): comparisons of orientation strategies of songbirds and moths.
	Weather	Many studies, e.g. Kemp et al. (2013): wind conditions influence flight altitude selection during migration.	Frick et al. (2012): migratory bats emerged earlier to forage under drought conditions during maternity season.	Chapman et al. (2015a): strategies in nocturnally migrating insects and songbirds and their responses to wind.
Services and disservices	Transport effects		Horn and Kunz (2011): General over- view of bat services.	
	Warnings, forecasts	Van Belle et al. (2007): operational model for prediction of bird migration intensities three days ahead, used to issue warning to flight safety and in rescheduling of training flights.		Leskinen et al. (2011): warning system for immigration of pest insects (bird-cherry aphid). Westbrook et al. (2014): radar-detection of emigratory flights of noctuids during a major pest outbreak. Boulanger et al. (2017): monitoring of spruce budworm exodus flights.
Human influences	Climate change	Kelly et al. (2012): phenology of purple martins at a summer roost.	Stepanian and Wainwright (2018): quantification of changes in bat migration phenology over 20-year period.	
	Sensory pollution	McLaren et al. (2018): broad-scale attraction of migratory birds to artificial light at regional scales, which decreased within a few kilometers of brightly-lit sources. Van Doren et al. (2017): urban light installation dramatically altered behaviours of nocturnally migrating birds; effects disappeared when lights were extinguished.		
	Man-made structures	Fijn et al. (2015): daily, monthly and seasonal patterns in fluxes at rotor heights and influence of wind direction on flight intensity.		
	Conser-vation	Buler and Dawson (2014): identification of locally important stopover sites and habitat associations of migratory landbirds in the northeastern U.S.		
Technical challenges	Classifi-cation	Dokter et al. (2011): fully automated method for detection and quantification of bird migration from operational C-band weather radar.	Mirkovic et al. (2016): prediction of radio scattering properties from an anatomical model to improve identification of bat targets.	Drake et al. (2017): compilation of all available insect radar cross-section results.
	Data infra-structure	Shamoun-Baranes et al. (2016): visualization of dynamic radar data for an intuitive representation of scale and dynamics. Ansari et al. (2018): big-data partnership and collective effort among federal government, private industry, and academia for applications of NEXRAD data.		
	Integration with other data	Horton et al (2018): combination of radar and citizen science data for avian flight strategies during spring migration over USA. Laughlin et al. (2013): combination of radar, citizen science and individual tracking data to identify flight strategies, habitat use over the year. Dokter et al. (2013), Komenda-Zehnder et al. (2010): Ground-truthing of radar data using field observations and mist-netting.	McCracken et al. (2008): presence of insects confirmed at altitudes where bat echolocation calls were recorded. Cryan et al. (2014): combination of radar with echolocation and thermal imaging at wind energy site. Smith and McWilliams (2016): incorporation of reflectivity data in analysis of bat echolocation data.	

and wind energy installations pose substantial mortality risks, the role of artificial light and noise in distorting migration routes and survival, or the role of climatic changes in altering migration phenology. Also the technical and methodological challenges of classifying radar targets, data infrastructure and integration with other data scored high. This shows that researchers recognize the big-data nature inherent to continental-scale radar data, the specific approaches required, and the greatest limitations of radar data namely its limited taxonomic resolution.

The effects of migrants scored somewhat intermediate, indicating that understanding the effects of migrants on ecological communities and their services and disservices are deemed important. However, in many cases it is not clear yet how specific applications should be designed (with the exception of insect warnings) and which auxiliary studies are needed at which spatial and temporal scales. For instance, if a future warning system would be desired for the dispersal of zoonotic parasites by migrants, where and when would an epidemiological screening be needed?

Although not scoring as highly novel or urgent in itself, research on basic migration knowledge such as routes, timing, numbers and biomasses is recognized as fundamental to many of the more applied challenges and should therefore be continued.

Range of spatial and temporal scales

The scales in the majority of radar aeroecological studies to date do not cover the full spectrum of spatial and temporal scales possible but are biased towards studies at local to regional spatial scales or short time-scales (Supplementary material Appendix 1 Table A1). Research that focuses on large-scale AND long-term scales is still largely missing, yet, urgently required for factors that act mainly over larger spatial or long time-scales, e.g. land-use change and climate change. The NEXRAD archive is probably unique in that it already provides the opportunity to attain this whereas for other continental radar networks national differences in radar systems need to be harmonized and legal agreements produced for the access and use of radar data across nations.

'Catch-up' research in bats and insects and cross-taxon studies

Although it will be unrealistic to expect that the level of knowledge on insect and bat migration will soon catch up with the level of knowledge of bird migration, studies on fundamental migration characteristics in insects and bats are urgently required. While it is inherently difficult to identify bats in radar signals, it is possible that bats using corridors may be detected using weather radar networks, for example movements of *Leptonycteris* long-nosed nectar bats from Mexico into the southwestern U.S. Perhaps a better application of radar in studying bat migration might be deployment of specialized fixed-beam radar (Schmidt et al. 2017) near suspected migratory stopovers such as Long Point (McGuire et al. 2012) or corridors such as the Baltic coastline (Ijäs et al. 2017). Such radar systems could also be an important monitoring tool in cases where bats do not always use echolocation during migration (Gorresen et al. 2017).

In parallel to taxon-specific advances, we need comparative studies across taxa that identify common patterns and mechanisms in, e.g., the movement strategies of flying animals and their responses to environmental factors and human-induced changes.

Stakeholders and target audiences

A variety of stakeholders can benefit from better knowledge, real-time information or forecasts of timing, extent and intensity of aerial migrations (Fig. 3, Bauer et al. 2017). Obviously, the specific information that can support the work and products of stakeholders also varies: Habitat associations of migrants, demographic trends and the influence of weather on migrations are crucial information for conservationists developing efficient management and protection measures or for national and international legislation and policy makers passing bills.

The general public is probably the most numerous stakeholder that we hope to reach – not only to spark the interest in migration as an iconic natural phenomenon but also to raise the awareness of the threats that migrants are facing. Making real-time information about aerial migrations publicly accessible (e.g. <http://birdcast.info/live-migration-maps/>) can enthral a broad audience from laymen to professionals but also making use of observational data can engage citizen scientists and provide positive feedback to their contributions.

Our analysis has shown that radar methods have significantly contributed to advance our knowledge of aerial migrations in the past and can do so even more in a variety of present and future, fundamental and applied challenges. Particularly, the large spatial and long temporal scales that radar monitoring can cover are a unique feature that cannot be attained by any other technology.

We are also aware of the strong geographical bias in using radar data with the US and Europe being highly studied regions whereas the situation is different in many other areas of the world. Although there are large numbers of migrants in these regions as well, very little is known about their movements and fates. Thus, our call for using existing radar data for monitoring aerial migrants applies even more to regions where very basic knowledge about migratory systems is lacking. For these areas, issues no longer considered novel in the US and Europe may be both novel and urgent, and this particularly applies to regions undergoing rapid environmental change.

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Supplementary material (Appendix ECOG-04083 at <www.ecography.org/appendix/ecog-04083>). Appendix 1.