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Review

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Improving the quantification of waterfowl migration with remote sensing and bird tracking

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Abstract Accurately quantifying waterfowl migration patterns is pertinent to monitor ecosystem health and control bird-borne infectious diseases. In this review, we summarize the current understanding of the environmental mechanisms that drive waterfowl migration and then investigate the effect of intra- and inter-annual change in food supply and temperature (e.g., climate change) on their migration patterns. Recent advances in remote sensing and animal tracking techniques make it possible to monitor these environmental factors over a wide range of scales and record bird movements in detail. The synergy of these techniques will facilitate substantial progress in our understanding of the environmental drivers of bird migration. We identify prospects for future studies to test existing hypotheses and develop models integrating up-to-date knowledge, high-resolution remote sensing data and high-accuracy bird tracking data. This will allow us to predict when waterfowl will be where, in response to short- and long-term global environmental change.

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1 Introduction

Migratory birds are important bioindicators for monitoring the condition of complex ecosystems due to their sensitivity to environmental changes [1–4]. Their migration activities can alter ecological networks and influence ecological community dynamics and ecosystem functioning by transporting nutrients, energy and other organisms worldwide [5]. Migratory birds also harbor zoonotic pathogens and facilitate the long-distance spread of bird-borne infectious diseases [6]. However, our knowledge about the mechanisms underlying the migration patterns and decision rules determining when and where to go, and how long to stay is rather fragmentary, even for the most frequently studied migratory bird species. An improved understanding and accurate quantification of bird migration patterns are needed by conservation organizations, policy makers and other relevant communities to manage bird populations and land, monitor ecosystem health and control bird-borne infectious diseases.

Bird migration is principally driven by internal mechanism (i.e., an internal clock under photoperiodic control) [7] but is fine-tuned by external environmental factors [8]. Although much remains to be understood in terms of the internal cues [9], our understanding of external environmental cues controlling bird migration is particularly limited [10]. The reason is that bird migration activities often stretch over vast distances spanning large, remote and inaccessible areas, and the traditional field measurement method is not feasible. Recent advances in remote sensing and animal tracking techniques enable us to monitor the environment over a wide range of spatiotemporal scales and record detailed spatiotemporal bird migration patterns. These developments will facilitate substantial progress in understanding the environmental mechanisms underlying bird migration patterns.

Among migratory birds, we are particularly interested in waterfowl because: (1) they exhibit stronger phenotypic plasticity than other bird taxa under photoperiod control in response to the constraints of other environmental factors on their aquatic habitats [11–15]; and (2) they are an important spread agent facilitating the global transmission of highly pathogenic avian influenza [16–20]. In this review, we summarize the environmental mechanisms that drive waterfowl migration patterns, with an emphasis on key environmental factors and the role that remote sensing and modern bird tracking techniques could play in improving the prediction of waterfowl movements at a global scale. We conclude our review with prospects for future studies.

2 Understanding the environmental drivers of spatiotemporal waterfowl migration

The annual change in day length is the most reliable indicator of seasonality in governing the annual life cycle of migratory birds [21, 22]. Day length is adopted by many species as the proximal stimulus triggering the onset of the migration cycles [7, 23, 24]. In concurrence with appropriate photostimulation, the photoperiod response might be modified by other environmental factors [24]. However, the photoperiod is consistent year to year, whereas other environmental factors vary. It is advantageous for wild birds to be able to adjust to suit current circumstances. Hence, the effect of day length normally initiates preparatory processes in migration, whereas other environmental factors play a greater role as migration progresses [8].

Migration is most pronounced in environments in which food supplies vary greatly over the seasons and where migration enables birds to exploit a surplus in food resources and avoid seasonal shortages [8, 25, 26]. Migratory waterfowl breed at high-latitude areas with abundant high-quality food during summer and winter toward the equator in areas with mild conditions. Additionally, improved survival of the adults and young at high latitudes due to low predation risks balances the cost of long-distance migration [27, 28]. When migrating to the north, those waterfowl that make best use of resources available along the route are favoured by natural selection. Similarly, waterfowl that efficiently avoid deteriorating conditions at the breeding area (e.g., food shortage, low temperature, frozen water/ground, or snow cover) by migrating to low-latitude areas during autumn migration are at an advantage.

On top of this, hypotheses have been formulated to address how the seasonal environment affects the migration patterns of waterfowl. In regard to spring migration, the “green wave hypothesis” predicts that herbivorous birds track a succeeding spring flush of plants on their way from the temperate wintering grounds to the Arctic breeding sites [29, 30]. For example, water birds that migrate along the western Palearctic continental flyway in spring often stopover at sites where fresh spring grasses are available [31]. This food-based prediction has been extended to also explain other bird species: Insectivorous species track the emergence of insects that coincides with the vegetation green-up [32] and fish-eating species track a “silver wave” of fish spawn during spring migration [33].

In contrast to a successively northern food flourishing in spring, autumn migration could be explained by the “food shortage hypothesis”. Migratory birds have to leave the high latitudes before their food supplies collapse and continued survival becomes precarious [8]. The harsh winter at high latitudes causes food to become completely unavailable for waterfowl due to plant senescence and/or food being locked by frozen soils or waterbodies [34]. Therefore, when food conditions at their present staging area deteriorate, waterfowl tend to progressively move to more southern sites until they reach a site where food is available throughout the winter. Birds might leave some perfectly available food behind if using these stocks would not be energetically profitable enough in the long run. Recent work has also demonstrated continuous movement and rapid turnover among duck populations wintering at the southern or southwestern edge of their range, likely because these birds constantly track subtle changes in the availability of their food [35–37]. Waterfowl tend not to migrate further south than necessary in order to save energy and avoid the dangers of traveling, as well as to be able to return to their breeding ground as soon as conditions allow [8, 26]. European waterfowl are often observed wintering along the southern part of the winter 0 °C isotherm [38], just beyond the snow line where grass growth has stopped.

Climatic factors are often used as surrogates for seasonal ecological conditions in the study of waterfowl migration patterns. Temperature is frequently used because of its effects on energy needs, food supply (vegetation growth and insect activity), water availability, wind condition and other relevant climatic events [8, 14, 39–42]. In general, warm temperatures in spring (both globally and locally) trigger northward waterfowl migration toward high altitudes, and cold temperatures in autumn (e.g., freeze-up) lead to southward departure from high-altitude sites. Wind condition can also influence migration timing and stopover patterns due to its effects on travel speed, flight times and energy expenditure [8, 43, 44]. Tailwinds facilitate a direct migration strategy, allowing the bypassing of potential stopover sites, whereas headwinds can prevent a nonstop migration due to the need for refueling [45, 46]. Snow cover can affect the timing of spring arrival at the breeding grounds and also the breeding success of many Arctic-breeding species [39], and frost is assumed to trigger waterfowl autumn migration [47]. Furthermore, precipitation shows a pronounced effect on changes in waterfowl migration timing in southwestern Australia, where vegetation growth is largely limited by soil water availability [48, 49].

Other factors such as human disturbance (e.g., land use and hunting/poaching), predation and competition for food may overrule the above effects locally and result in changes in migration patterns. For example, geese are found to stay a much shorter time at sites with a high disturbance level by local farmers and hence are forced to stay longer at non-disturbed sites with deteriorating foraging conditions during spring migration [50]. The opening of the hunting season triggers the autumn departure of ducks from Finland [51]. Geese also tend to depart earlier, stay shorter or bypass area with increased predation risks or increased food competition that might cause a low-energy deposition rate [52–54]. The hypothesized external environmental effects influencing waterfowl migration are summarized in Fig. 1.

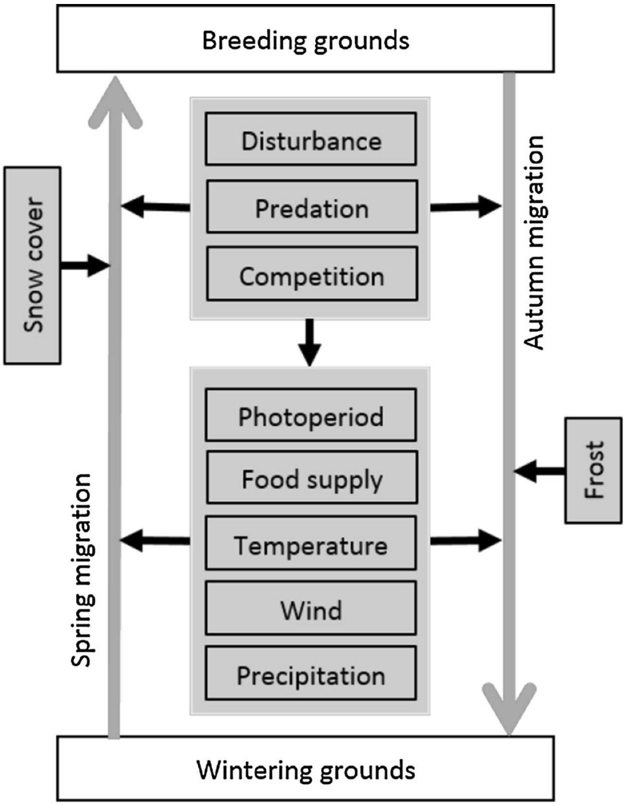

Fig. 1 Hypothesized environmental factors underlying waterfowl migration patterns

3 Testing environmental effects on waterfowl migration patterns

Two types of effects have been explored regarding the environmental mechanisms of waterfowl migration patterns: the intra-annual environmental change effect on seasonal bird migration patterns and the inter-annual environmental change effect (e.g., climate change) on migration phenology. We mainly focus on two key environmental factors, namely food and temperature.

3.1 The effect of intra-annual variation in food supply on waterfowl migration

Many studies suggest that herbivorous waterfowl consistently follow the onset of spring along their migration routes. The onset of spring, quantified by growing degree days (GDD), or the peak of temperature increase (GDD jerk), has a stronger correlation with the departure, arrival and staging decisions of geese migrating from West Europe to Arctic, than other energetic cues (e.g., intake rate) or environmental cues (e.g., latitude and snow cover) [55–57]. The onset of spring in general indicates the start of the growing season. However, as total plant biomass increases after the onset of spring, digestibility decreases. Therefore, immature plants at an intermediate development stage offer the optimal intake rate of digestible nutrients as predicted by the "forage maturation hypothesis" [58–60].

Considering the food maturation effect, it has been demonstrated that waterfowl track different levels of plant developments at different stages of their migration. A field experiment study found that barnacle geese *Branta leucopsis* in Europe follow the peak in nutrient biomass (plants with the highest amount of nitrogen per unit area) during spring migration, but arrive at their Russian breeding site early so the subsequent food peak coincides with the time of gosling rearing [61]. This overtaking of green wave has been recently demonstrated by two studies. Kolzsch et al. [62] found that barnacle geese arrive at the southern stopover sites after the onset of spring (calculated based on the peak of temperature acceleration) and at the breeding ground before it. Facilitated by detailed satellite-derived plant development stages, Si et al. [63] demonstrated that barnacle geese arrive at the southern stopover site at the peak in nutrient biomass and gradually overtake the green wave, arriving at their breeding sites at the onset of spring. When simulating the spring migration timing of European geese using an individual-based model and the onset of spring as a rule (without considering the overtaking process) [56], the match between the observed and simulated timing shows a poorer fit at the southern stopover site than the northern ones. However, this overtaking of the green wave needs to be further validated using other bird species migrating along different flyways over extended period of time.

Piscivorous waterfowl time their spring migration schedule based on the availability of food, and some omnivorous waterfowl overtake the peak of food supply. The northward migration of surf scoters *Melanitta perspicillata* along the Pacific coast from Baja California to Alaska shows a close association with herring spawning events [33]. Based on field measurement of food abundance, Eurasian teal *Anas crecca* leave their wintering and spring staging site before a sharp increase in invertebrates and seeds, and time duckling hatching at their breeding grounds in Sweden to coincide with the local peak in food abundance [64]. However, whether birds adopt this overtaking strategy to optimize food conditions for offspring and/or because of a lower predation risk and longer feeding time (due to longer day length) at the breeding site [27, 64] needs further investigation.

The effect of intra-annual variation in food supply on waterfowl autumn migration patterns has hardly been investigated. Geese are observed to use a more direct and shorter migration route than they use in northward spring migration, especially when wind conditions are favorable [45, 46]. A possible reason could be that during spring migration, birds need to accumulate body store via detour route for a successful breeding, whereas in autumn migration, minimizing travel distance might overrule maximizing body store. On the other hand, ducks ringed in southern France seem to migrate faster in spring than in autumn [65]. Further investigation on the effect of food conditions could shed more light on the different strategies employed during spring and autumn migration.

3.2 The effect of inter-annual variation in food supply on waterfowl migration

Only a few studies have explored the effects of the inter-annual variation in food supply (and/or quality) on bird migration, and they suggest that waterfowl adjust their migration according to this inter-annual variation. Tombre et al. [66] found the Svalbard-breeding populations of geese migrate earlier in years with an earlier onset of spring (quantified by a satellite-derived vegetation index). Straub et al. [67] measured plant and invertebrate food for spring-migrating ducks in the Upper Mississippi River and Great Lake Region and found the food biomass varied widely between years and among habitats. They suggest future studies should investigate how duck migration patterns are influenced by the spatiotemporal variation of food supply, but no further attempt has been carried out. Based on a long-term field observation of foraging habitat quality of dabbling ducks *A. platyrhynchos* in the Illinois River valley, O'Neal et al. [68] found a considerable variation of inter-annual stopover duration during autumn migration, positively related to the foraging quality of stopover sites. Using long-term ringing datasets for common teal *A. crecca* from southern France, Guillemain et al. [69] found that teal arrive much earlier at their winter quarters in autumn migration due to the increased food availability in these areas. So far knowledge about the effects of the inter-annual variation in food supply on waterfowl migration is relatively limited, probably due to the difficulty of measuring the long-term food variation over large geographical scales in the field.

3.3 The effect of intra-annual variation in temperature on waterfowl migration

Temperature is often used as a surrogate of food conditions due to the difficulty of measuring food supply in the field along the migration route. Local accumulated temperature (degree days) is found to be a more accurate predictor for the spring migration schedule of European waterfowl than the actual temperature at departure or arrival dates [56, 70]. Local accumulated temperature can be used to infer the advance of spring and help birds to adjust the progress of their northward migration, for example by accelerating their migration when it is warmer [70].

Frost pattern derived from temperature (the first time the night land surface temperature drops to below zero) has been used to explain the waterfowl autumn migration pattern [47], but this relationship has not yet been validated using empirical bird migration data. Waterfowl wintering phenology has seldom been investigated. Waterfowl wintering in three tropical Indian wetlands is found to arrive earlier in autumn and depart earlier next spring in sites/years with higher overwinter temperatures [71].

3.4 The effect of climate change and inter-annual variation in temperature on waterfowl migration

Many studies focus on the impact of climate change on spring migration phenology and breeding success of migratory waterfowl [1]. For example, some waterfowl have altered their arrival and departure dates in accordance with the recent decades of climate warming [11–13, 52, 72–74], whereas for other bird species that maintained their migration schedule or advanced little relative to spring phenology, mismatches between arrival time and breeding season were found [75–77]. In areas where a long-term temperature increase was not reported, waterfowl are able to adjust their spring migration timing with the inter-annual variation in temperature [78]. In general, short- or medium-distance migrants can cope better with climate change than long-distance migrants [11, 13–15, 74].

A pronounced negative effect has been reported for European and American waterfowl between the timing of spring migration and the temperature (spring temperature and/or winter temperature) at the breeding grounds [11, 14, 73, 74], stopover sites [41, 78] and passage sites [13, 15]. Some large-scale temperature events, such as a higher winter North Atlantic Oscillation (NAO), also promote an earlier waterfowl passage over Europe [15] and an earlier arrival at European breeding grounds [14, 74]. In regard to the departure time from wintering grounds, next to a warmer temperature, other factors such as increased competition and a high level of accumulated fat store also trigger an earlier departure of waterfowl from their wintering sites in Europe [52, 79].

However, different responses of early and late migrants to temperature conditions at different migration stages have been reported. At the breeding grounds, peak arrival time of American duck species is strongly correlated with local spring temperature [73]. On the other hand, bird species that arrive early, as well as the earlier cohorts within species, show a stronger response (i.e., a stronger correlation) to temperature change at the wintering grounds and along the migration route in Europe and North America [13, 15]. Similarly, the earlier departure of waterfowl from the wintering site in Ireland due to an increased February temperature is more pronounced for early departing individuals (the first 50 % of population) than for late ones [52]. Further investigation is needed to explain these different responses at different migration stages.

4 Remote sensing and bird tracking help the understanding of waterfowl migration

Remote sensing is an efficient tool to monitor environmental conditions over time across large geographical scales [80–82]. Bird tracking data, obtained by satellite telemetry and other tracking techniques, enable us to determine a detailed spatial and temporal resolution of avian distribution patterns [83–85]. The synergy of remote sensing and modern tracking techniques offers a promising way to test the mechanism that shapes waterfowl migration patterns. Bird tracking data could be synchronized with remote sensing data with varying spatial and temporal resolutions to analyze bird migration patterns. Satellite data from a single sensor are often limited by the trade-off between the spatial, temporal and spectral resolutions. Together with detailed bird tracking data, remote sensing data with a high spatial resolution could be used to investigate local environmental conditions and effects, whereas data with a high revisit rate could be used to analyze the effects of environmental changes on bird migration. Additionally, it is possible to derive environmental conditions from imagery with a high spatiotemporal resolution by fusion of data from different satellite sensors. However, such applications integrating bird tracking data and remote sensing data analyzing bird migration patterns have so far been rather limited.

GDD have been frequently used in previous studies to identify the onset of spring, whereas vegetation phenology derived from earth observing satellite data is superior to those derived based on modeling approaches. The onset of spring derived from GDD mainly considers the temperature influences on vegetation growth [86], but both water availability and photoperiod could limit vegetation photosynthetic activities and phenology [87–89]. Satellite-derived vegetation indices offer a more direct and detailed measurement of plant development and provide a unique way to investigate the effect of intra- and inter-annual variation in food supply on bird migration patterns.

The application of satellite-derived vegetation indices in analyzing bird migration patterns is still limited, and phenological events are often identified using relatively coarse-resolution vegetation indices of, e.g., 15-d 8 km [66, 90] or monthly 28 km [91], as well as combined with arbitrary thresholds or relatively broad ranges. Low spatial and temporal resolutions tend to miss necessary details for identifying specific phenological events. Using one predefined threshold of vegetation indices to identify the onset of spring overlooks the differences between plant species and communities. Migration strategies such as the overtaking of the green wave [63] could be overlooked if the plant development stage that is supposed to be chased by waterfowl is defined too broadly, simply because spring migration coincides with the spring growing season. High-resolution imagery such as the moderate-resolution imaging spectroradiometer (MODIS) daily 250 m vegetation indices could be used in future studies, in combination with more sophisticated phenology extracting methods such as the piecewise logistic models [92]. Moreover, a satellite-derived net photosynthesis index could be used to describe plant productivity [32] and study waterfowl migration patterns.

Remote sensing also offers a reliable way to estimate land surface temperature over extended periods of time and across large geographical scales [81], with a relatively high spatial resolution and temporal frequency, e.g., MODIS 1 km daily day and night land surface temperature products. Local accumulated temperature derived from these products could be used to test the change in temperature on waterfowl migration patterns. Frost patterns derived from these land surface temperature products could be used to test how autumn migration schedule of waterfowl is influenced by the timing of frosts [93]. The MODIS snow products (with an overall absolute accuracy of 93 % of the 500 m resolution products) provide fractional snow cover covering a range of spatial and temporal resolutions, from 500 m to 0.25°, and from daily, 8 d to monthly. However, no attempt has been made to utilize satellite-derived land surface temperate in bird migration studies, and satellite-derived snow cover has only been used by Madsen et al. [39] as a surrogate of the availability of the waterfowl breeding sites to investigate the breeding timing of geese.

Although ringing and field counting data are still commonly used in bird migration studies, these data cannot provide a true tracking of the migration routes due to unequal geographical distribution of potential human hunters/observers. The development of bird tracking techniques, from short-distance, short-life radio telemetry, low-positioning accuracy geolocators [94], to long-life, high-accuracy satellite transmitters, enables us to track both local and long-distance migration of birds over multiple years [84, 85, 95]. Tracking devices are becoming lighter, so that ever smaller species can be tracked. Battery life and energy use are improved, and temporal and spatial resolution is increasing, so that more detailed information is collected. Also, the collected bird tracking details can help an efficient future deploy of transmitters (e.g., by discovering molting area where bird capture is more efficient). Moreover, the massive reduction in the cost of these tracking devices now allows switching from the descriptive study of a handful of individuals to proper analyses of numerous birds, relevant to the population level. This enables a more rigid study design: tracking at least 20 birds to make reliable inference about questions with two possible outcomes and at least 75 individuals for a problem with three outcomes [96]. Modern transmitter types used in tracking migratory waterfowl are summarized in Table 1.

Bird tracking data have been extensively used to describe waterfowl migration routes, stopover patterns and staging periods at the individual level [85]. However, most previous studies are descriptive; studies linking detailed spatiotemporal movements of birds derived from tracking data with environmental conditions are limited. Only recently has the overtaking of the food wave strategy during waterfowl spring migration been tested using tracking data of individual birds [63]. Furthermore, previous studies analyzing the environmental drivers of waterfowl migration patterns mainly used a few traditionally known stopover sites, although the importance of analyzing the whole migration course and multiple stopover sites has been emphasized [15, 55].

When birds are captured for tracking, detailed information about their age, weight and morphology can also be recorded and integrated in the modeling of migration patterns [70]. Other data such as altitude, temperature, light (day/night), speed and acceleration (from which bird behavior can be derived) recorded by tracking loggers can be used as ancillary information to help understand migration patterns. Figure 2 summarizes the methodology used in analyzing the environmental mechanisms in waterfowl migration patterns with remote sensing and bird tracking techniques.

5 Prospects for future studies

We summarized the up-to-date understanding of the environmental mechanisms underlying waterfowl migration patterns, with an emphasis on two key factors, namely food and temperature. We urge that these findings be verified using empirical waterfowl migration and satellite-derived environmental data and be integrated in the modeling process to further improve the prediction of waterfowl migration patterns. Specifically, we identify the following prospects for future studies:

Table 1 Modern bird tracking techniques used in waterfowl migration studies

Transmitter	Position accuracy	Tracking type	Characters
GPS/GSM[a]	±18 m	Satellite	Continuous tracking, rechargeable battery
PTT	3: <150 2: 150–350 m 1: 350–1,000 m 0: >1,000 m	Satellite	Interval tracking, rechargeable battery
Geolocator	186 ± 114 km	Logging	Continuous tracking, power source, recapture to retrieve data

GPS global positioning system, GSM global system for mobile communications, PTT platform transmitter terminals, PPT position accuracy 3, 2, 1 and 0 indicate different accuracy classes

[a] Two types of GPS transmitters with different data retrieval systems: satellite relay or GSM systems

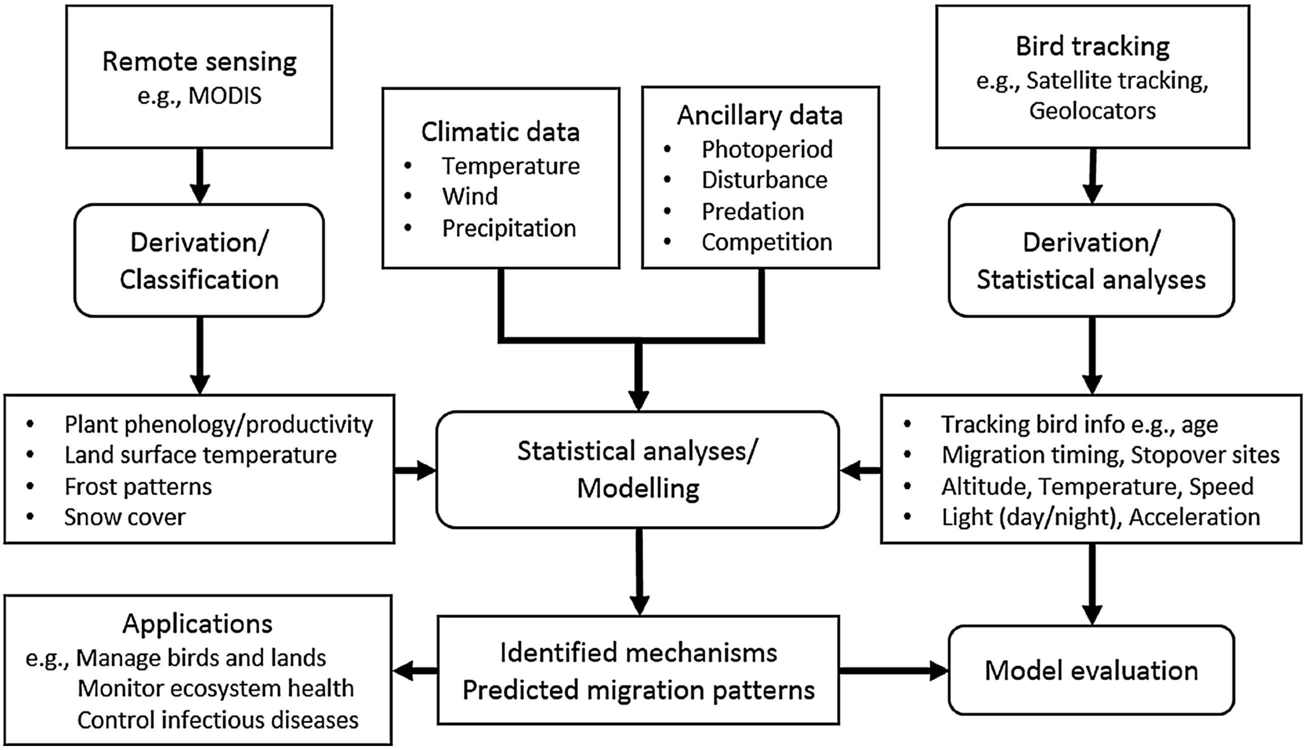

Fig. 2 Methodology for using remote sensing and bird tracking techniques to analyze the environmental mechanisms and predict waterfowl migration patterns

(1) The strategy of overtaking the wave of food availability during waterfowl spring migration needs to be further validated and integrated as one of the decision rules in the modeling of migration patterns. Relying on the onset of spring as a rule over the whole course of spring migration lowers the predictive power of models. The satellite-derived peak in nutrient biomass and onset of spring can be combined to quantify the strategy of the overtaking of the green wave and incorporated in bird migration models (e.g., individual-based model).

(2) The effects of inter-annual variation in food supply on waterfowl migration need further investigation. Future studies can benefit from up-to-date remote sensing techniques and environmental datasets that quantify the long-term food variation at the continental scale. Specifically, food conditions along the migration routes described by, e.g., plant phenology and productivity derived from time-series satellite imagery can be used to investigate how waterfowl react to the change in food conditions across different years.

(3) The environmental mechanisms underlying waterfowl autumn migration patterns need further exploration, given that previous studies mainly focused on spring migration. The effect of plant senescence and lowering temperature on waterfowl autumn migration phenology has not yet been thoroughly investigated, though temperature effects have been taken as a given and commonly used in avian influenza studies. Plant development stages derived from remotely sensed vegetation indices and land surface temperature products retrieved from satellite imagery should be used to further study autumn migration patterns.

(4) More studies are needed to better understand waterfowl migration patterns and environmental conditions along the Asian flyways. The European and American flyways have been most frequently studied, but human–bird conflicts including natural resource utilization conflicts (e.g., habitat deterioration due to land use change), economic risks (e.g., agricultural losses), and human health and safety risks (e.g., diseases transmission) are more pronounced in Asia. Comparative studies should test for similarities and potential differences in underlying environmental mechanisms among the different flyways.

(5) Modern tracking techniques allow spatiotemporal tracking of birds at an accuracy previously unattainable. Satellite-derived environmental data (e.g., plant phenology and temperature) are available in ever-increasing spatiotemporal resolution. Data mining of these datasets is crucial for validating and improving

our understanding of the environmental cues that waterfowl use during migration. For example, a complete stopover network could be derived from bird tracking data; together with the corresponding environmental conditions derived from satellite data, previous findings can be validated and new hypothesis could be generated. Furthermore, these data layers, covering large geographical areas and extended period of time, can be incorporated in models to predict future bird migration patterns.

To further understand the environmental mechanisms underlying waterfowl migration and develop models which integrate high-resolution remote sensing-based environmental datasets and detailed spatiotemporal bird tracking data will allow us to predict when waterfowl will be where, in response to short- and long-term global environmental change, and will facilitate the monitoring of ecosystem health and a better management of waterfowl and land, and minimize the potential economic, health and safety risks birds pose to humans.

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Conflict of interest The authors declare that they have no conflict of interest.

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