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RESEARCH ARTICLE

Telecoupling framework for research on migratory species in the Anthropocene

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Migratory species are an important component of biodiversity and provide essential ecosystem services for humans, but many are threatened and endangered. Numerous studies have been conducted on the biology of migratory species, and there is an increased recognition of the major role of human dimensions in conserving migratory species. However, there is a lack of systematic integration of socioeconomic and environmental factors. Because human activities affect migratory species in multiple places, integrating socioeconomic and environmental factors across space is essential, but challenging. The holistic framework of telecoupling (socioeconomic and environmental interactions over distances) has the potential to help meet this challenge because it enables researchers to integrate human and natural interactions across multiple distant places. The use of the telecoupling framework may also lead to new conservation strategies and actions. To demonstrate its potential, we apply the framework to Kirtland's warblers (*Setophaga kirtlandii*), a conservation-reliant migratory songbird. Results show accomplishments from long-term research and recovery efforts on the warbler in the context of the telecoupling framework. The results also show 24 research gaps even though the species has been relatively well-studied compared to many other species. An important gap is a lack of systematic studies on feedbacks among breeding, wintering, and stopover sites, as well as other "spillover" systems that may affect and be affected by migration (e.g., via tourism, land use, or climate change). The framework integrated scattered information and provided useful insights about new research topics and flow-centered management approaches that encapsulate the full annual cycle of migration. We also illustrate the similarities and differences between Kirtland's warblers and several other migratory species, indicating the applicability of the telecoupling framework to understanding and managing common complexities associated with migratory species in a globalizing world.

Keywords: Conservation; coupled human and natural system; full annual cycle; governance; management; salmon; sea turtle; telecoupling; warbler wildebeest

1. Introduction

Millions of animals undertake long-distance annual migration around the world, some traveling as far as 80,000 km round trip (Egevang et al., 2010). More than 5,000 animal species migrate over 100 km (Global Register of Migratory Species, 2008). Of these, the Convention on the Conservation of Migratory Species of Wild Animals (2015) identified 154 endangered species and many others as threatened or near-threatened. Over 1,850 species of birds are migratory – roughly 19% of all extant bird species (Kirby et al., 2008). Migratory species provide ecosystem services including insect and rodent control as well as seed dispersal (Whelan et al., 2008). However, 49% of neotropical migratory birds have declined in the last 50 years (Sauer et al., 2014). In addition, migration itself is now considered to be an endangered phenomenon, as long distance migration patterns are disappearing around the globe for whales, warblers, large ungulates, and salamanders due to increasing human impacts (Wilcove and Wikelski, 2008).

To reverse this declining trend, many knowledge gaps regarding the interactions of human and natural systems must be addressed. Thus far, there have been numerous studies on the biology of migratory species that explore topics such as physiological and environmental drivers (Gunnarsson et al., 2006; Weber, 2009), evolutionary patterns (Guttal and Couzin, 2010), variations in individual pathways (Lohmann et al., 2007), and effects of resource availability (Olsson et al., 2006). A number of studies have also begun to address the impacts of migratory species

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on human societies via providing pollination and pest management of agricultural crops (Cleveland et al., 2006), food sources (Jacob et al., 2010), tourism (de Vasconcellos Pegas and Stronza, 2010), and as vectors of diseases like Avian influenza and West Nile Virus (Altizer et al., 2011). For instance, pest control provided by migratory Brazilian free-tailed bats is worth up to $1.7 million per year for the cotton industry in south-central Texas, which is merely a fraction of their range (Cleveland et al., 2006). An increasing number of people have recognized the importance of human dimensions in conservation (e.g., Mascia et al., 2003), but previous studies on animal migration mainly focus on either the environmental or socioeconomic dimension alone. Furthermore, they are often isolated to a particular location that makes up just one part of the migratory pathway, although migratory species must be conserved across their entire geographic ranges to be sustainable (Partners in Flight, 2013). Therefore, it is necessary to integrate socioeconomic and environmental dimensions across multiple distant sites (breeding, wintering, and stopover sites) and other areas that affect these sites. To effectively manage the integration of differing fields, a cohesive framework is needed (Liu et al. 2015a). Here we discuss the applicability of the telecoupling framework (Liu et al., 2013), which is an integrative approach that considers socioeconomic and environmental interactions among different sites simultaneously.

Telecouplings are socioeconomic and environmental interactions that occur over distances. The telecoupling framework considers each site as a coupled human and natural system (Liu et al., 2007a; Liu et al., 2007b) to help researchers and managers analyze the interactions between socioeconomic and environmental components across distant sites (Liu et al., 2007b; Liu et al., 2013). The framework consists of five interrelated components: systems, agents, flows, causes, and effects (**Table 1**).

Table 1: Comparisons between conventional and telecoupling frameworks, and examples of new conservation actions from applying the telecoupling framework. DOI: https://doi.org/10.1525/elementa.184.t1

Components	Conventional Framework of Studying Migratory Species	Telecoupling Framework	New conservation actions from applying the telecoupling framework[a]
Systems Features	Natural systems (e.g., migratory species)	Coupled human and natural systems	Systematically incorporate humans into conservation among distant places; minimize human impacts on natural systems, and enhance benefits of natural systems to humans across distant places.
Types	Breeding, wintering, stopover sites	Breeding, wintering, stopover sites, and other places affecting migratory species directly and indirectly	Manage other places that can affect the species; and coordinate the management across all relevant places.
Agents	Focal species, biologists and wildlife managers, landowners, investors, scientific institutions, and governments	Focal species, biologists and wildlife managers, landowners, investors, scientific institutions, and governments; other agents affecting flows of information, material and people (e.g., traders, consumers, industry, business communities)	Engage all agents and facilitate cooperation among all types of agents across distant places.
Flows	Environmental connections through flows of nutrients, energy, and species	Environmental and socioeconomic connections through flows of nutrients, energy, species, information, and materials	Regulate flows of species, information, materials, and people across distant places; control the interactions among flows of focal species and other types of flows across distant places for focal species (e.g., generate funding and reduce predatory mortality).
Causes	Environmental factors	Environmental factors, socioeconomic factors	Create and use socioeconomic incentives and disincentives such as social norms for people to conserve migratory species across distant places.
Effects	Effects on species (population, habitat)	Effects on species (population, habitat) and people	Reduce trade-offs and enhance synergies between environmental and socioeconomic effects across distant places.
	Environmental feedbacks among distant places	Environmental and socioeconomic feedbacks among distant places	Steer socioeconomic feedbacks and the interplays between socioeconomic and environmental feedbacks across all distant places.

[a]For the sake of simplicity, traditional strategies (e.g., management in breeding and wintering sites) are not included in the table, but are still needed in conservation.

Systems refer to coupled human and natural systems in which humans and their environments interact (Liu et al., 2007a). They may be classified as sending (origins or breeding sites), receiving (destinations or wintering sites), or spillover (other systems that affect or are affected by interactions between sending and receiving systems, such as stopover sites during migration). Agents are the decision-making entities involved in the telecoupling, which affect flows of energy, materials, and information within and between the systems. Causes are factors that create the telecoupling and change its dynamics, resulting in socioeconomic and environmental effects (Liu et al., 2013). More details and examples about the telecoupling components and their relationships are available in a number of publications (Liu et al., 2013, 2014, 2015b; Liu and Yang, 2013).

The framework has already been applied to address several important issues, including international trade [e.g., food, forest products, energy (Fang et al., 2016; Liu, 2014; Liu et al., 2014, 2015b)], species invasions (Liu et al., 2013, 2014), global land grabbing and investment (Liu et al., 2014), global land use (Eakin et al., 2014), and distant ecosystem services (Deines et al., 2015; Liu and Yang, 2013; Liu et al., 2016a). These applications have led to the identification of research gaps (e.g., spillover systems) and hidden linkages (e.g., feedbacks) among different geographic regions of the world that have implications for sustainable resource management. However, the framework has not systematically been applied to migratory species research and conservation. The applications of the framework to other issues demonstrate its potential for use in research and conservation of migratory species because their annual cycles involve interactions between distant locations and their status is largely determined by human activities (Czech et al., 2000). Such an approach is needed because human activities such as land use have increased in various places in the Anthropocene, and because the often profound and hard-to-predict unprecedented effects create a new set of governance and management challenges for migratory species.

To illustrate the potential of the framework in research on migratory species, we first use the Kirtland's warbler (*Setophaga kirtlandii*) as a demonstration. The Kirtland's warbler is the rarest songbird in North America (Wilson et al., 2012), but is a relatively well-studied species. The Kirtland's Warbler Recovery Team, an inter-agency advisory group established by the U.S. Fish and Wildlife Service in 1973, has spearheaded research and management efforts for the species with measurable success. As a conservation-reliant species, Kirtland's warblers still face numerous, ever-evolving threats and require active management to maintain populations in human-influenced forest systems (Bocetti et al., 2014). The telecoupling framework can help incorporate various factors including human dimensions for sustaining Kirtland's warblers across their geographic range. We then highlight some novel insights and lessons learned from applying the framework (e.g., research and conservation gaps, and applicability of the framework to other migratory species). Finally, we discuss constraints on and opportunities for framework operationalization.

2. Applying the telecoupling framework to Kirtland's warbler research

This section applies the telecoupling framework to Kirtland's warblers in terms of the five interrelated components: systems, agents, flows, causes, and effects. Besides biological interactions typically considered in a flyway assessment, the telecoupling framework also considers socioeconomic interactions and includes areas beyond the flyway that may influence migration (**Figure 1** and **Table 1**). Systems refer to coupled human and natural systems in the breeding, wintering, and migratory stopover sites as well as any areas that affect or are affected by these sites. Agents, such as Kirtland's warblers, government agencies, non-government organizations (NGOs), and the public, affect flows of not only organisms, but also energy, money, and information within and between the systems. Causes include Kirtland's warblers' search for suitable habitat and other human factors that alter the dynamics of the telecoupling, such as tourism and land conversion. Socioeconomic and environmental effects that result from the telecoupling range from establishment of conservation programs to habitat management.

Below we provide a synthesis of what is known about Kirtland's warblers in regards to these components (**Table 2**). While each piece of information is not new, integrating the isolated information under the telecoupling framework is novel and provides a new approach that links various pieces of scattered and fragmentary information. This is in response to international calls for integrated approaches to research and conservation (e.g., Future Earth, 2016).

2.1. Overview of Kirtland's warblers

Kirtland's warblers were chosen as a demonstration species because there is a relatively large amount of information available on their biology, habitat requirements, and human interventions. The species' migratory behavior connects the jack pine (*Pinus banksiana*) forests of Michigan to the Bahamas archipelago over a distance of approximately 2,300 kilometers (Ewert et al., 2012) (**Figure 2**). Kirtland's warblers are insectivorous, ground-nesting songbirds that prefer early successional forests (U.S. Fish and Wildlife Service, 2012). Humans directly contributed to the songbird's initial declines to as few as roughly 430 breeding males in the 1950s (**Figure 3**), through forest fragmentation and fire suppression that reduced habitat suitability and increased Brown-headed cowbird (*Molothrus ater*) nest parasitism (Rapai, 2012). The population continued to decline in the 1960s until the early 1990s. There has since been a remarkable recovery of the species to reach over 2,000 breeding males as of 2015 (**Figure 3**), a goal accomplished by intensive habitat management (Houseman and Anderson, 2002), including rotational jack pine harvests, prescribed burns, and cowbird removal (Bocetti et al., 2012) coordinated by the inter-agency Kirtland's Warbler Recovery Team. There are also increased efforts to collaborate with managers in the Bahamas to initiate more conservation and research on the wintering grounds, particularly in working with local goat farmers.

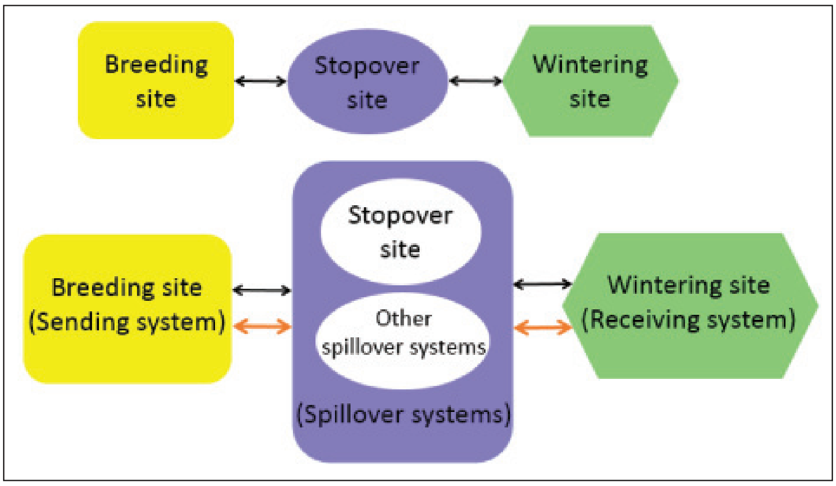

Figure 1: Comparisons between traditional migration research (top) and the telecoupling approach (bottom). Black arrows indicate environmental interactions, while orange arrows refer to socioeconomic interactions. DOI: https://doi.org/10.1525/elementa.184.f1

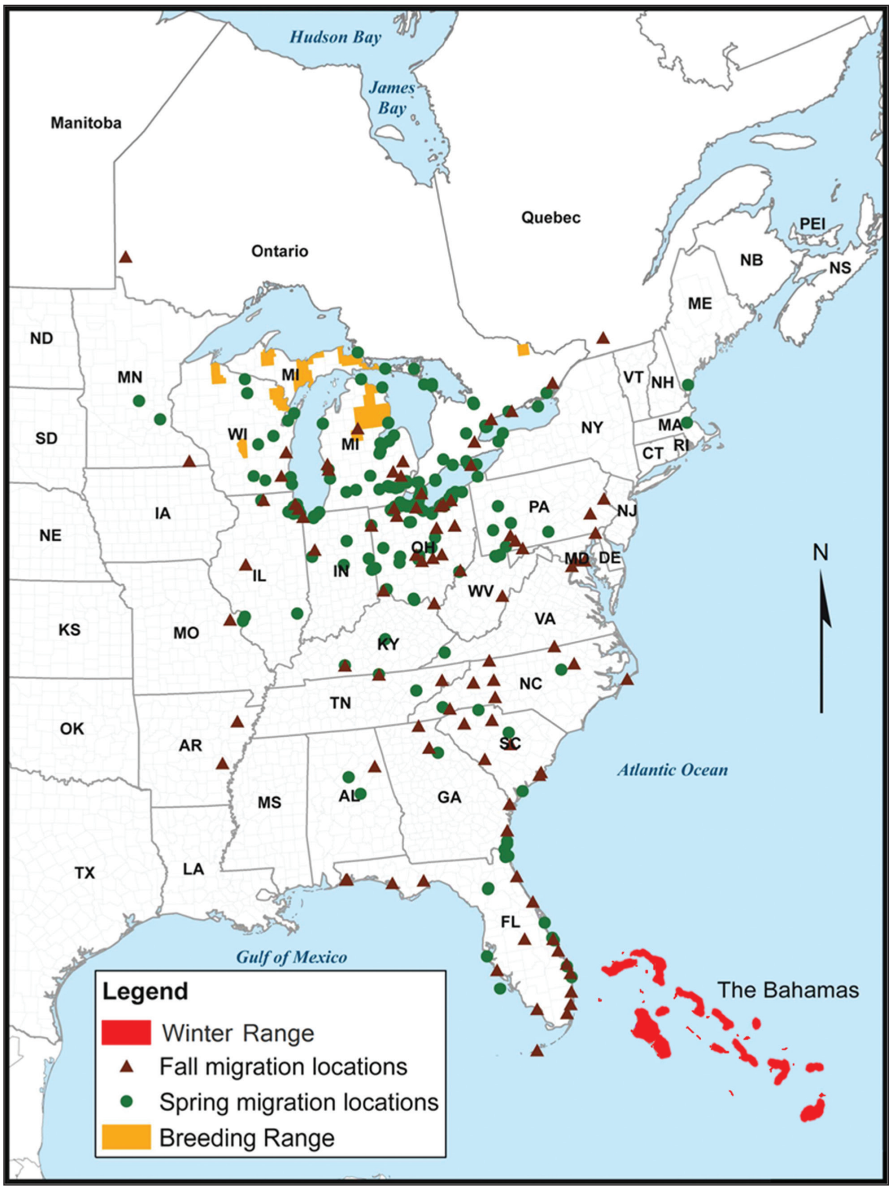

Figure 2: Map of geographic locations of Kirtland's warbler range and migration stopover sites. Map includes migration locations obtained from 1851–2011 (sight, song, and specimen records). Figure adapted from (U.S. Fish and Wildlife Service (2012) using data from Petrucha et al., 2013). DOI: https://doi.org/10.1525/elementa.184.f2

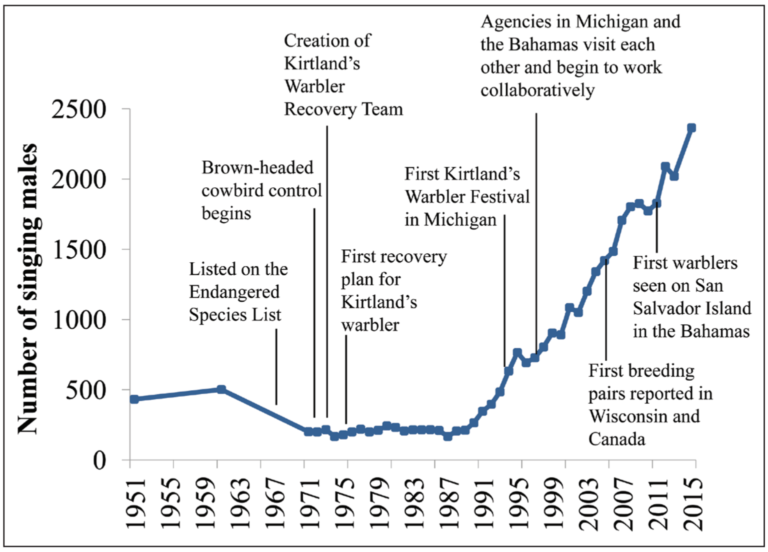

Figure 3: Changes in Kirtland's warbler population size from 1951–2015 (according to number of singing males) and associated timeline of key events in Kirtland's warbler population recovery. Data are recorded in censuses conducted by the U.S. Fish and Wildlife Service during the breeding season and include Michigan, Wisconsin, and Ontario, Canada (U.S. Fish and Wildlife Service, 2016). DOI: https://doi.org/10.1525/elementa.184.f3

Currently, a new Conservation Partnership of government agencies and non-government organizations has been developed to sustain the species if it is removed from the protections of the Endangered Species Act. Despite past successes, the future of the species is uncertain under climate change, continuing human activities such as land use change, and possible reduction of federal funding. These dynamic and unpredictable challenges on the horizon make it all the more important for managers and researchers to adopt a telecoupling approach to understand how to better manage the species across its entire migratory pathways.

2.2. Systems

The two most apparent interacting systems regarding Kirtland's warblers are breeding and wintering sites (**Figure 2**). It is useful to analyze sending and receiving systems from the perspective of fall migration after the breeding season. Breeding sites (mainly in Michigan) are considered the sending system while the Bahamas wintering site is the receiving system. The sending systems in Michigan include Ogemaw, Crawford, Oscoda, Alcona, and Iosco counties (U.S. Fish and Wildlife Service, 2012). The total breeding system in Michigan consists of approximately 89,000 ha of jack pine managed on a 40–80-year rotation length to provide approximately 15,380 ha of 5–23 year-old early successional jack pine forests (Probst and DonnerWright, 2003; U.S. Fish and Wildlife Service, 2012). This requires relevant agents (see Section 2.3 below) to produce 1,550 ha annually in Michigan (Michigan Department of Natural Resources et al., 2014). Recently fewer Kirtland's warblers have also been seen in Wisconsin and Ontario as their range has expanded (BirdLife International, 2014). The receiving system (wintering grounds in the Bahamas) is characterized by 5,535 ha of low, dense shrubs such as *Salvia verbenaca* (Wunderle et al., 2010). The Bahamas consists of a total of 700 islands. The proportion of these occupied by Kirtland's warblers is unknown, but most past sightings have been on Grand Bahama, New Providence, and Abaco islands (Jones et al., 2013). Most of the comprehensive ecological research on Kirtland's warblers and their wintering habitat has been conducted on Eleuthera Island (**Table 2**). The bird was also recently spotted on San Salvador Island in 2012, which is believed to be the first sighting there in 46 years (Jones et al., 2013).

Spillover systems include migratory stopover sites (or staging sites where migrants can rest and feed). During migration, Kirtland's warblers have been observed in numerous vegetation types from yards to fencerows to dense woodlands with the most preferred vegetation being 1.5m tall (Stevenson and Anderson, 1994). According to the recent synthesis of 425 acceptable sight records during 1851–2011 (Petrucha et al., 2013), migratory routes are widespread in 24 states of the USA and 3 provinces of Canada (**Figure 2**). Besides stopover sites, other potential spillover systems include the hometowns of tourists (**Figure 4**). From 2004 to 2013, over 9,000 tourists attended Kirtland's warbler tours run by the U.S. Fish and Wildlife Service and U.S. Forest Service (U.S. Fish and Wildlife Service and U.S. Forest Service, 2016). Approximately one third of the tourists came from within Michigan, while the rest originated from the other 49 states and 32 other countries (**Figure 4**). The hometowns of tourists may be important because their experiences in sending or receiving systems can result in sharing ideas and wealth that may in turn have positive feedbacks (e.g., inspire other people to come as tourists, contribute to a conservation fund, or influence policy-makers).

2.3. Agents

A number of agents make decisions that influence the flows of information, energy, and materials between systems (**Table 2**, **Figure 5**). For example, Kirtland's war-

Table 2: Research achievements and gaps (At-A-Glance) regarding Kirtland's warblers in the context of the telecoupling framework and example conservation actions based on the information from filling the gaps (see text for details). DOI: https://doi.org/10.1525/elementa.184.t2

Components of telecoupling framework (Liu et al., 2013)	Telecoupling components with regard to Kirtland's warblers	Specific telecoupling components that are already studied	Research gaps (Specific telecoupling components that are not studied yet) (examples of conservation actions based on the information from filling the gaps)
Sending systems	Breeding sites in Michigan	· Environmental characteristics, locations of core breeding habitat, impacts of management on habitat suitability	1. Sustainable habitat management options post-delisting (Include socioeconomics in proactive planning measures for most likely management needs such as funding)
Receiving systems	Wintering sites in the Bahamas	· Environmental characteristics, habitat occupied by Kirtland's warblers on Eleuthera Island · Habitat created by goat farming to manage habitat for Kirtland's warblers on Eleuthera Island	2. Habitat occupied by Kirtland's warblers throughout the Bahamas (Develop measures to conserve the habitat and surrounding areas) 3. Habitat created by goat farming for Kirtland's warblers throughout the Bahamas (Manage goat farming to maximize warbler habitat) 4. Sustainable habitat management options post-delisting (Include socioeconomics in proactive planning measures for most likely management needs)
Spillover systems	Stopover sites and other relevant places (e.g., origins of tourists to see Kirtland's warblers and Brown-headed cowbird wintering and stopover sites)	· General pathway for migration of Kirtland's warblers · Environmental characteristics of Brown-headed cowbird wintering habitats	5. Specific locations and environmental as well as socioeconomic characteristics of migratory stopover sites each year (Conserve these specific stopover sites) 6. Other areas affect or are affected by information on Kirtland's warblers (e.g., tourist hometowns) (Motivate more support from tourists to benefit the warbler) 7. Sustainable habitat management options post-delisting (Take proactive measures to plan for most likely management needs) 8. Environmental characteristics of Brown-headed cowbird migratory stopover sites (Develop most effective measures to control the cowbird) 9. Environmental and socioeconomic impacts of Brown-headed cowbird continental scale control methods (Take measures to prevent or reduce the impacts of control methods)
Agents	Kirtland's warblers, Brown-headed cowbirds, Government agencies, NGOs, and other public/private organizations that affect Kirtland's warblers, farmers, tourists	· Government agencies and NGOs in sending systems such as U.S. Fish and Wildlife Service, U.S. Forest Service, Michigan Department of Natural Resources, Canadian Wildlife Service, Ontario Ministry of Natural Resources, The Nature Conservancy, Audubon Society, Huron Pines, Arbor Day Foundation collaborate with one another to conserve the Kirtland's warbler in the sending system · Government agencies and NGO's in receiving systems such as The Bahamas Ministry of the Environment, Bahamas National Trust, The Bahamas Ministry of Tourism, and The Nature Conservancy work together on conservation issues in the receiving system. · Agents from sending and receiving systems work together on shared warbler conservation issues in both systems. · Tourists view warblers in the sending system in Michigan. · Goat farmers affect warbler habitat in the receiving system in the Bahamas.	10. U.S. Fish and Wildlife Service – Migratory Birds Division, eastern flyway state government agencies are found in spillover systems but aren't engaged in Kirtland's warbler conservation (Engage these agents and promote cooperation between them and other agents) 11. Role of tourists and landowners in spillover systems is unknown (Engage those agents in stopover areas together those in sending and receiving systems) 12. Institutional frameworks and dynamics among multi-agency collaborations have not been analyzed in detail (Promote good collaboration among different agencies within and between systems)

Flows	Movement of Kirtland's warblers, energy, information, materials and money between systems	· Initial qualitative studies of movement of energy via Kirtland's warblers between wintering and breeding sites · Initial studies of movement of money between agents of recovery program and local communities · Initial qualitative studies on movement of money from spillover systems (e.g., Tourists pay for tours and spend money in local economies in sending and receiving systems)	13. Numbers of Kirtland's warblers lost during each season of annual cycle (Develop measures to reduce the loss of warblers) 14. Movement of information/materials between sending (or receiving) system and spillover systems (Develop measures to manage the flows between systems that affect the warbler) 15. Quantitative studies of movement of energy via Kirtland's warblers between wintering and breeding systems (Improve habitat quality to ensure sufficient energy intake by the warbler) 16. Further studies of movement of money between agents of recovery program and local communities (Provide adequate conservation incentives for local communities) 17. Quantitative studies on movement of money from spillover systems (e.g., Tourists pay for tours and spend money in local economies in sending and receiving systems) (Promote financial contribution from spillover systems for conservation) 18. Movement of money from sending and receiving systems to spillover systems (e.g., via government agencies or NGOs) (Take measures to maximize the benefit of the money to the warbler)
Causes	Socioeconomic and environmental factors affecting Kirtland's warblers across Michigan, Bahamas, stopover sites, and other spillover systems	· Kirtland's warbler migration for food/habitat availability · Increased drought intensity reduces Kirtland's warbler breeding success · Impacts of brood parasitism by Brown-headed cowbirds · Impacts of land conversion, tourism, and timber harvesting on warblers in sending systems · Impacts of information spread on tourism · Interagency cooperation within sending and receiving systems	19. Impacts of land conversion, tourism, and timber harvesting on warblers in receiving and spillover systems 20. Magnitudes of interaction (environmental and socioeconomic) of climate change and human disturbances on food and habitat availability for Kirtland's warblers (Take adaptive conservation measures in response to interaction effects between climate change and human disturbances) 21. Magnitudes of interaction (environmental and socioeconomic) between Kirtland's warblers and Brown-headed cowbirds on continental scale (spillover and sending systems) (Control the cowbird in spillover and sending systems) 22. Spread of information on Kirtland's warblers with technological advances in sending, receiving, and spillover systems (Coordinate conservation across sending, receiving, and spillover systems)
Effects	Socioeconomic and environmental effects on Michigan, Bahamas, stop-over sites, and other spillover systems; feedbacks among systems	· Seed dispersal by migrating Kirtland's warblers · Changes in habitat management by private landowners in sending and receiving systems to promote conservation · Creation of tourism and education programs in the sending and receiving systems · Feedbacks between conservation efforts in the sending system and goat management in the receiving system	23. Magnitudes and relative strengths of socioeconomic and environmental effects on spillover systems (Regulate the effects on spillover systems to enhance conservation in sending and receiving systems) 24. Feedbacks between spillover systems and both sending and receiving systems (Develop new policies based on habitat quality in receiving/spillover systems)

blers are decision makers, as they search for habitat and travel long distances. Brown-headed cowbirds are also agents that have profound effects on Kirtland's warblers, as they significantly reduce warbler survivorship by acting as brood parasites. Government agencies, NGOs, academics, the timber industry and the general public facilitate Kirtland's warblers' search for habitat and other behaviors through habitat management for Kirtland's warblers, other wildlife, timber, and recreation, education, and tourism in the breeding system. Other agencies and local landowners influence Kirtland's warbler habitat in the breeding and spillover systems (**Table 2**, **Figure 5**). Kirtland's warblers are unique among migratory species due to the unusually high level of cooperation among different agents spread across sending and receiving systems (**Figure 5**). For example, the Kirtland's Warbler Recovery Team is a multi-agency group that coordinates ongoing conservation efforts for the species. This group has consisted of members from U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Geological Survey, Michigan Department of Natural Resources, academia, Canadian Wildlife Service, the Bahamas Department of Agriculture, the Bahamas National

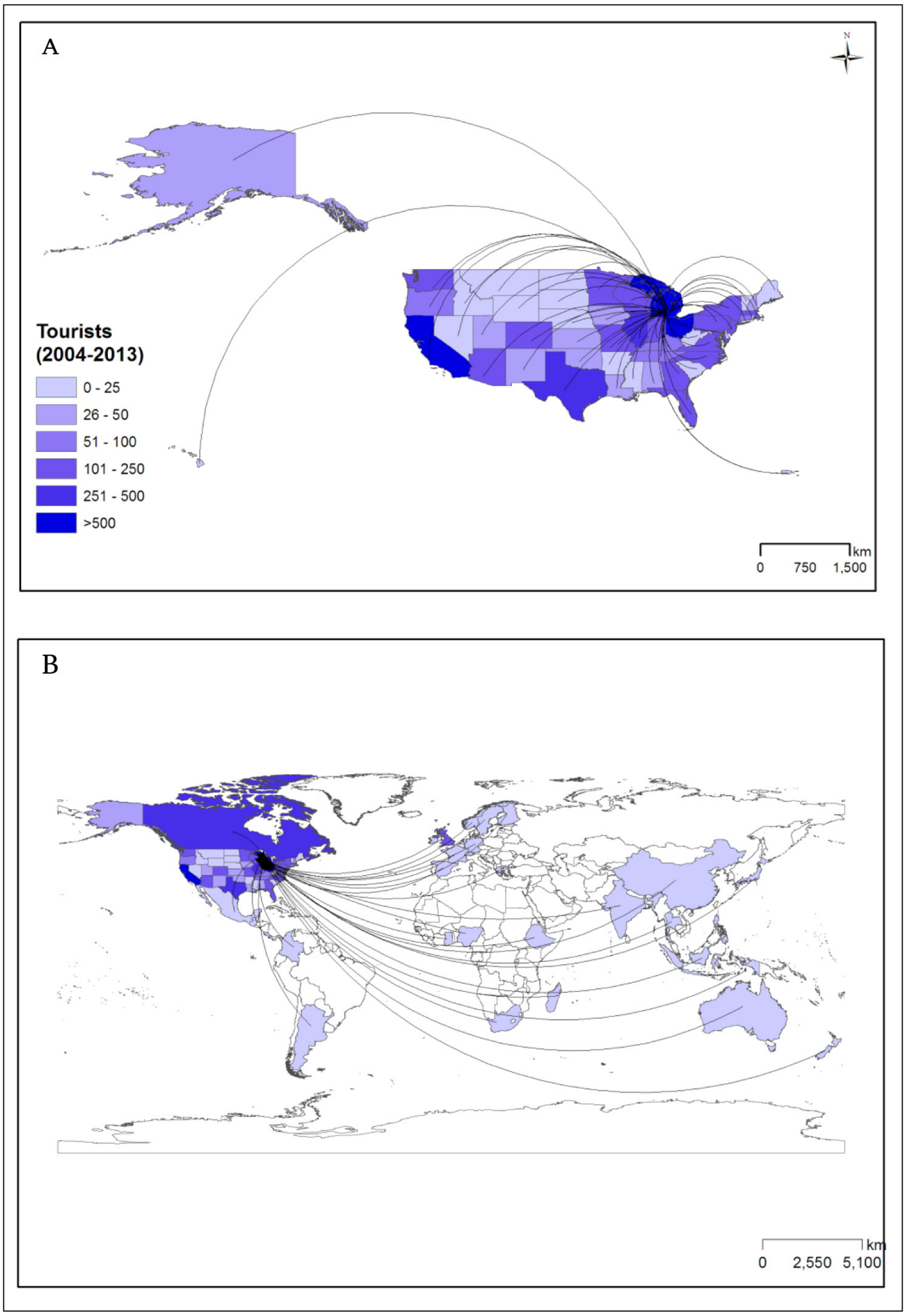

Figure 4: U.S. state origins (a) and country origins (b) of tourists attending Kirtland's warbler tours administered by the U.S. Fish and Wildlife Service and the U.S. Forest Service in Michigan from 2004–2013 (U.S. Fish and Wildlife Service and U.S. Forest Service, 2016). Note that these numbers only include people who attended the formal tours arranged by USFWS/USFS and people who were willing to participate in a survey. DOI: https://doi.org/10.1525/elementa.184.f4

Trust, Audubon Society, and Huron Pines. In the wintering system, agents often facilitate land use decisions, such as harvesting timber, planting crops, raising livestock, and abandoning agricultural sites, which inadvertently creates ideal warbler habitat (Wunderle et al., 2010). New agents are also becoming a part of the telecoupling as the range of the Kirtland's warbler expands into new agency jurisdictions in Wisconsin and Canada, bringing additional state and national level governments to the table.

Other key agents include the agricultural industry, tourism industry, and tourists (**Table 2**). Landowners involved in the agricultural industry make land use decisions that affect the survivorship of cowbirds in the southern states, and open landscapes that provide access for cowbirds to breeding systems in the Great Lakes region (Brittingham and Temple, 1983). Tourists (e.g., wildlife tourists) make decisions to experience wildlife, including travel and donations for conservation (Perkins and Brown, 2012). The tourism industry promotes activities for tourists. For example, the Ramada Inn in the city of Grayling in Michigan offers a meeting place for tours of the warbler's habitat (Grayling Visitor's Bureau, 2013). In the Bahamas, a resort owner allows use of his land for research in exchange for researchers providing ecotourism opportunities for resort guests (Rapai, 2012).

2.4. Flows

The major flows are exchanges of energy, species, information, and money among systems (**Table 2**). Energy flows occur when Kirtland's warblers consume insects and berries in the Bahamas, converting them to fat stored for migration (Rockwell et al., 2012). Some agents can also be part of the flows as they move from one system to another (e.g., Kirtland's warblers, Brown-headed cowbirds, tourists). Information about Kirtland's warblers may be shared in different locations through research, education, tourism, and the media. Agencies and the tourism industry facilitate flows of information to consumers, for example, by offering presentations or tours to tourists at the Kirtland's Warbler Wildlife Festival (Grayling Visitor's Bureau, 2011) and through government-sponsored tours that are offered daily from mid-May through mid-July. From 1981 to 2013, U.S. Forest Service provided guided tours to an average of 437 (range: 270–1001) tourists annually (U.S. Forest Service, unpublished data) and U.S. Fish and Wildlife Service did the same for 683 (range: 436–917) tourists (U.S. Fish and Wildlife Service, unpublished data). Tourists may then cause a flow of information by communicating their experiences to friends and relatives who may then visit warbler sites. Researchers provide a flow of information that affects habitat management through publications, and the media can help disseminate research findings to the general public. Researchers may also provide a flow of information through training students, particularly in the Bahamas, where students return to build conservation capacity (J. Wunderle and D. Ewert, personal communication).

Monetary flows also occur, bringing money from other areas of the world (spillover systems) into the Bahamas and Michigan. The timber industry results in major monetary flows into Michigan, contributing approximately $14.6 billion to the state's economy annually (Leefers, 2013). The Kirtland's warbler management program in Michigan

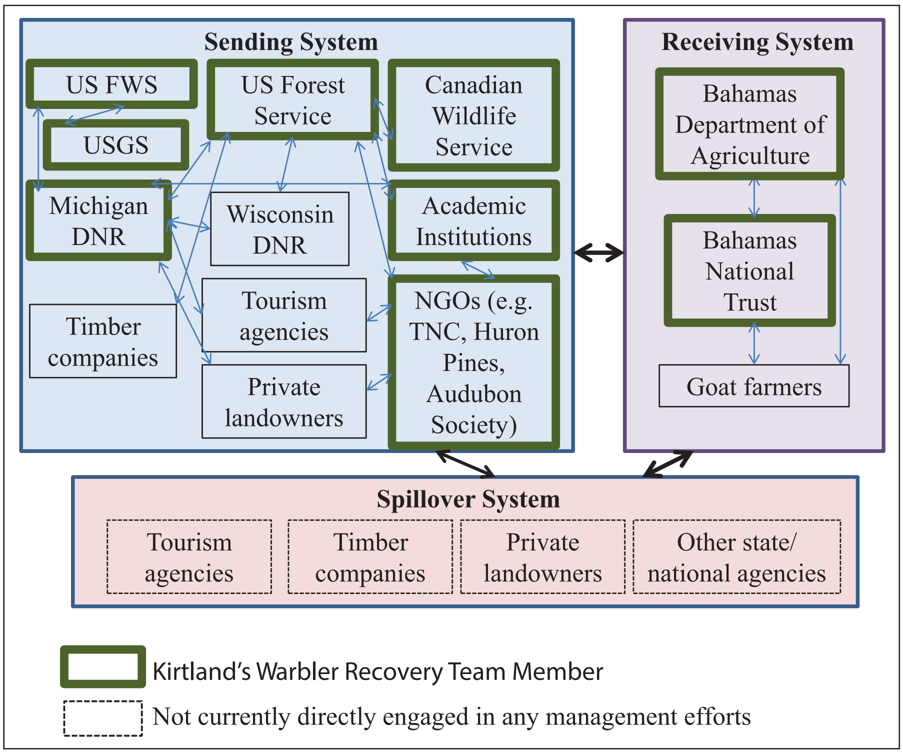

Figure 5: Key agents involved in the Kirtland's warbler migration telecoupling and their interactions with one another. Thick green boxes represent agencies that have served as core members of the Kirtland's Warbler Recovery Team, solid boxes represent agents that are associated with current recovery efforts, and dotted boxes indicate agents not currently engaged in Kirtland's warbler management efforts (but perhaps should be included in the future). DOI: https://doi.org/10.1525/elementa.184.f5

specifically provides average annual timber sale revenue of $239 (range: $121–$499) per ha (Michigan Department of Natural Resources et al., 2014). However, it annually costs on average of $81–$155 per ha to regenerate habitat in Michigan (Kirtland's Warbler Recovery Team, 2008, unpublished data). Work related to managing breeding and wintering sites may cost about $1.7 million and $1.0 million a year, respectively (BirdLife International, 2014; Meyerson, 2013), but there are caveats in these rough estimates (e.g., not all the money is spent on habitat management and they may also include expenses for training). On a smaller scale, tours of the breeding system in the cities of Grayling and Mio can generate monetary flows from tourists to local businesses via the purchase of products, lodging, and food or through donations by tourists to support habitat management. Similarly, tourism programs in the wintering system have successfully produced a monetary flow into the Bahamas (Bahamas National Trust, 2011).

2.5. Causes
Migration is one of the least understood biological components across the animal kingdom (Faaborg et al., 2010) and for the Kirtland's warblers specifically (Byelich et al., 1985; Petrucha et al., 2013). The research done on this topic thus far suggests that a number of environmental factors influence the Kirtland's warbler migration patterns. The birds migrate for breeding and to find suitable habitat and food (Mayfield, 1988). Increases in droughts (Rockwell et al., 2012) and presence of Brown-headed cowbirds (Dinets et al., 2015) also affect breeding success and subsequent migration.

Other factors influencing the dynamics of the telecoupling are human-related, involving economic, political, cultural, and technological factors that affect populations and habitats of Kirtland's warblers (**Table 2**). For example, the timber industry, which accounts for an important portion (3.6% of GDP as of 2013) of Michigan's economy (Leefers, 2013), affects breeding habitat. Tourism, which generates more than half of the GDP in the Bahamas (A.M. Best Company, 2012), influences wintering areas. It is important to minimize the negative impacts of human population growth and economic development, which have been long identified as the primary drivers of ecosystem degradation and habitat loss through overexploitation of natural capital and land conversion (Kahuthu, 2006; Millennium Ecosystem Assessment, 2005; Resendiz, 2012). Land conversion also has environmental impacts by changing the types of species that use the region, including regionally non-native species. In spillover systems, economic factors determine the amount of rice waste that is left in agricultural fields, which provides ideal food for cowbirds (Brittingham and Temple, 1983). Politically, sustainable habitat management in the wintering system is difficult due to complex Bahamian land ownership laws (Rapai, 2012). Local residents cannot own land, even if they have occupied it for several hundred years. Residents may thus be inclined to raze forests on the land they inhabit to demonstrate their occupancy and deter government takeover. Residents may also be distrustful of researchers who express interest in working on the land. Despite these challenges, active management in the form of livestock rearing by locals may help Kirtland's warblers. Goats reared for local livestock industries have been found to improve Kirtland's warbler habitat suitability by generating adequate foliage of fruit-bearing plants (e.g., snowberry) (Wunderle et al., 2010). Public perceptions of land use in the breeding system heavily impact the politics that define how habitat should be managed for Kirtland's warblers, timber harvest, and recreational uses (DJ Case and Associates, 1998). Culturally, people around the world are accepting the responsibility of trying to save declining species (Hvenegaard, 1994). As such, activities such as donating for conservation and tourism have increased. Technological advances have increased the speed of sharing information and the distances to which tourists can travel, allowing for more frequent national and international interactions. For instance, visitors representing all 50 states of the U.S. and 32 countries traveled to Michigan between 2004 and 2013 to see Kirtland's warblers ((U.S. Fish and Wildlife Service and U.S. Forest Service, 2016), **Figure 4**). Furthermore, the telecoupling dynamics have been heavily influenced politically by the high level of cooperation among government agencies (U.S. Fish and Wildlife Service, 2009), which have contributed to the increased Kirtland's warbler population numbers.

2.6. Effects
The effects of Kirtland's warbler migration can be environmental and socioeconomic (**Table 2**). Environmental effects of Kirtland's warbler migration are centered on the bird's role in ecosystem services such as seed dispersal across its range (Rapai, 2012). Economically, there is an inflow of money into breeding systems via funds allocated for Kirtland's warbler conservation by state agencies, federal agencies, and the timber industry. Government agencies allocate funds for cowbird and habitat management in jack pine stands in the sending system, which must be maintained to have marketable products for timber harvest and provide suitable warbler habitat. Money earned from timber harvesting feeds back into the state to fund future conservation efforts. Tourism results in monetary flow to the sending system benefiting local communities and generating political support for land management for Kirtland's warblers. In Michigan, tourism activities include guided tours. For many years the Kirtland's Warbler Wildlife Festival held at Kirtland Community College provided a strong link to other tourism opportunities like the guided tours or canoeing/kayaking on local rivers. Tourists may also participate in the Jack Pine Viewing Tour to learn about the warbler, jack pine management and other wildlife species occurring throughout the glacial outwash plains. Tourism also results in monetary flow to the wintering system, where Bahamians additionally gain an education and a sense of pride about local species. The Bahamas Ministry of Tourism advertises birding tours as tourism options, several of which mention Kirtland's warblers (Bahamas Ministry of Tourism, 2013; Field Guides, 2016). Increases in opportunities to view the Kirtland's warbler may also play a role in improving spiritual and psychological well-being of tourists (cultural ecosystem

services), given the importance of experiences in nature for human health and well-being (Maller et al., 2006).

Feedbacks between sending, receiving, and spillover systems also occur. Threats to the Kirtland's warbler that are observed in the receiving system in the Bahamas have been a concern for agents in the sending system in Michigan. Therefore, multiple agencies have come together to send teams over to the receiving system to conduct conservation efforts, with the goal that these efforts will later improve migration back into the sending system. For example, the multi-agency organization of the Kirtland's Warbler Recovery Team has teamed up with The Nature Conservancy to work with Bahamian goat farmers to promote further habitat improvement for Kirtland's warblers (D. Ewert, 2013, personal communication), inspired by recent increases in Kirtland's warbler wintering in goat-managed regions. The interactions between breeding and wintering systems have also inspired education programs in the Bahamas run by organizations from Michigan, bringing together agents from different parts of the Kirtland's warbler migration pathway. Members of The Nature Conservancy in Michigan and U.S. Forest Service in Michigan and Puerto Rico travel to the Bahamas to train local residents to conserve Kirtland's warblers, other species, and their habitat.

3. Novel insights and lessons learned from applying the telecoupling framework

There are many new lessons and insights learned from applying the framework to Kirtland's warblers. Below, we discuss one set of research-oriented insights (the identification of research gaps for Kirtland's warblers), one set of management-oriented insights (flow-centered management of Kirtland's warbles), and the application of the framework to other migratory species.

3.1. Identification of research gaps

3.1.1. Gaps related to each component of the telecoupling framework

In the previous section, we outlined what is known about Kirtland's warblers using the telecoupling framework. The telecoupling framework also indicates that many knowledge gaps still exist (24 gaps, **Table 2**). While some of the gaps were also identified by the Kirtland's Warbler Recovery Team (Michigan Department of Natural Resources et al., 2014), the telecoupling framework offers a comprehensive tool that can help systematically identify more gaps as well as interrelationships among the gaps and existing knowledge. We hope this systematic effort under the telecoupling framework that built on the success of the Kirtland's Warbler Recovery Team can help direct future research efforts and inform future conservation by addressing potential limiting factors such as impacts of climate change across all systems (see the underlined examples of potential future conservation actions in **Table 2**). We provide further details on some of the key gaps and associated conservation actions below.

Spillover systems hold the most opportunities for future research because they have been rarely studied (Gaps 5–11, 14, 17–19, 21–24, **Table 2**). Because the warbler migration period lasts nearly five months (approximately 86 days in fall and 59 days in spring) (Petrucha et al., 2013), as climate change continues, it is imperative to learn how changes in spillover systems can impact warblers, even if sending and receiving systems are ideal. For example, little is known about specific locations as well as environmental and socioeconomic characteristics of Kirtland's warbler migratory stopover sites and other areas affecting the warblers (such as tourist hometowns) (Gaps 5, 6). Habitat quality likely affects individual warbler migration performance (Ewert et al., 2012), but has not been studied at stopover sites. Environmental characteristics of stopover sites of the Brown-headed cowbird and the environmental and socioeconomic effects of various cowbird control methods have also not been adequately studied (Gaps 8, 9). Agricultural activities in the areas with Brown-headed cowbird wintering habitats and migratory stopover sites may affect cowbird population size (Brittingham and Temple, 1983), and landscape manipulations that provide open or closed corridors from other parts of the Midwest to Michigan may also affect ecological encounters between cowbirds and warblers, perhaps even more so than cowbird management in the sending system alone. Kirtland's Warbler Recovery Team is evaluating the current scope of the cowbird control program to assess cost-effectiveness and efficacy within the breeding range of the species, but not on the continental scale that includes the interaction effects of cowbird ecology and human disturbances in spillover systems. Further research in each of these areas would allow for conservation efforts to be initiated in key stopover sites for the first time in addition to more effective measures for cowbird control to be implemented. The role of spillover systems may be even more important in the future if recent proposals to delist the Kirtland's warbler from the Endangered Species List are implemented, which would require revisions to management and conservation funding structures, with potential increases in funding required from sources outside the sending and receiving systems (Gap 7).

The biggest research gap for agents is in understanding agents that may be affecting Kirtland's migration in these spillover systems, such as farmers or developers that may affect habitat along migratory stopovers through changing required vegetation types to agricultural and/or development lands (Gaps 10, 11, **Table 2**). Filling this gap would help to bring new stakeholders to the table to weigh in on how to design future management plans for the species.

Agents in spillover systems are currently not engaged in collaborative management efforts undertaken by agents in sending and receiving systems (**Figure 5**). For example, the U.S. Fish and Wildlife Service's Migratory Birds Division works with U.S. state agencies. These agencies have to date not been active participants in Kirtland's warbler conservation in spillover systems, but could conceivably initiate conservation efforts in the warbler stopover sites and integrate them with other programs targeting other species underway in the region in the future.

Little is also known about many flows among receiving, spillover, and sending systems (Gaps 13–18, **Table 2**). For instance, there is no reliable estimate available regarding how energy is transferred throughout the migration process. Estimates for Kirtland's warbler population numbers are well understood annually in the sending system (**Figure 3**), but numbers in the receiving and spillover systems each year are poorly understood, which makes pinpointing potential areas of concern along with the migrant pathways difficult (Gaps 14, 15). In addition, little is known about how money moves through the migratory pathways (Gaps 16–18). How much money do tourists from spillover systems spend in the sending system when they visit? Is money spent in sending systems for Kirtland warbler viewing by tourists ever applied back to conservation in receiving systems? Could governments find ways of allocating funding for Kirtland's warbler conservation in the spillover systems (i.e., to protect stopover sites)? Answering questions like these could help eliminate financial leakage and reveal ways that money might be better distributed to meet conservation needs.

With respect to causes of the Kirtland's migration telecoupling, the greatest knowledge gaps exist in the lack of understanding how diverse environmental and socioeconomic factors interact with one another to impact the migratory population and pathways (Gaps 20, 21, **Table 2**). For instance, climate change and land use likely affect one another, such as if drought further promotes agricultural range expansion (see also discussion on cross-cutting research gaps below). These interactions are further complicated when considering the Brown-headed cowbird, which has its own complex environmental and socioeconomic influencing factors (e.g., host species richness (Cummings and Veech, 2014), forest cover and fragmentation (Hovick and Miller, 2013), and livestock grazing (Goguen and Mathews, 2001)). But there are no data on how these cross-sector interactions in turn impact the Kirtland's warbler across different parts of the migratory pathways. Such data would help tease apart and quantify the relative contributions of different sources of threats to the Kirtland's warbler and identify new management measures to account for evolving threats. In addition, little is known about information spread about Kirtland's warblers throughout the migratory pathway and beyond (Gap 22). How is information about conservation shared across systems? How do tourists receive information about warbler viewing opportunities and how can these information outlets be augmented?

Effects of the telecoupling are also understudied (Gaps 23, 24, **Table 2**). Assessments of the efficacy of management measures being implemented in the Bahamas (receiving system) for Kirtland's warbler are in progress, but are not yet as well-developed as those for the sending system (**Figure 6**). For instance, the potential efficacy of tourism programs for raising awareness and improving conservation in the receiving system is not well documented. New efforts to promote goat farming to improve habitat suitability for Kirtland's warblers in the receiving system are currently being examined and should be further developed in the future. There is also little data to document the impact of Kirtland's warbler migration on spillover systems, since they are normally not studied. Further, environmental and socioeconomic effects of potential landscape-scale cowbird control measures across spillover systems are also understudied, despite the documented evidence of the measurable impacts of cowbird control on warbler survival in sending systems. Data that fill these research gaps would help tease out the relative magnitudes of the interactions and diverse effects and in turn help promote effective policies and discourage ineffective ones.

One of the biggest research gaps pertains to feedbacks occurring among receiving, sending, and spillover systems (Gap 24, **Table 2**). For instance, how have the recent intensive measures to manage the Kirtland's warbler in Michigan (e.g., Brown-headed cowbird control and jack pine harvest control) had an impact on the number and distribution of warblers in the Bahamas? And how have these changes in turn impacted local human activities and economies in the Bahamas? Recent surveys suggested that the Kirtland's warbler may have expanded its range to areas such as San Salvador Island, Bahamas (Jones et al., 2013). These results imply that the measures in Michigan may have had profound impacts in the Bahamas, which may have then promoted expansion in the sending system to Wisconsin and Ontario. But the nature of the changes remains understudied. On the other hand, how will persistent threats in the Bahamas dampen the success of efforts being made in Michigan? Filling the gaps would help better conserve the species across the telecoupled systems.

3.1.2. Cross-cutting research gaps

The telecoupling framework can also shape the direction of new research priorities that cross-cut all of the components in the telecoupling framework, such as the timely and pressing example of the interaction effects of climate change and other human disturbances. Climate change may result in the extinction of many species (Hannah, 2012; Sekercioglu et al., 2008) or reduce or shift species' ranges, which can make species more vulnerable to threats by human activities (Schneider et al., 2007; Summers et al., 2012). Climate change may also impact plant germination and growth, thereby altering wildlife habitat quality (Walck et al., 2011).

Climate impacts are even more complex for warblers and other migratory species, which are affected by human activities [e.g., habitat fragmentation, (Herkert et al., 1996)] at varying places that may offset conservation efforts being conducted in other parts of the migratory pathways. For example, droughts in the Bahamas may reduce habitat quantity and quality, delaying warbler departure for migration, and reducing breeding success via delayed nest initiation in Michigan (Rockwell et al., 2012), resulting in fewer warblers returning to the Bahamas (**Figure 7**). Climate change may also reduce or fragment breeding areas because changes in temperature and precipitation can alter fire regimes (Cleland et al., 2004), prescribed burning management practices, and population dynamics of insect prey and pest species (Stange and Ayres, 2010) in warbler habitats in Michigan. Consequently, warblers may face challenges if management plans do not consider how they may adapt to climate change in multiple systems

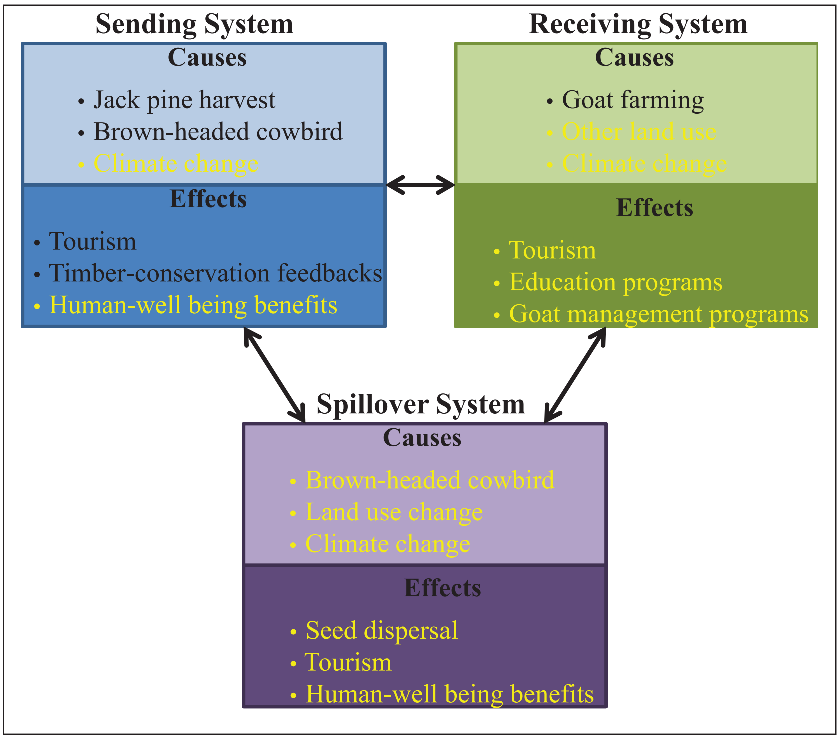

Figure 6: Key causes and effects of the Kirtland's warbler migration telecoupling. Yellow font indicates causes and effects that are understudied and should be targeted for future research. Also understudied are the interactions among the different causes and effects shown. DOI: https://doi.org/10.1525/elementa.184.f6

simultaneously. For example, sea-level rise would make habitats in coastal areas and many islands in the Bahamas disappear (**Figure 7**). Even if these sites still exist, temperature rise and changes in precipitation patterns would affect plant growth, which in turn harm warblers because those plants are essential components of warbler habitat.

The Kirtland's Warbler Recovery Team is currently working with an interagency research group to model the effects of climate change on the ecology of the warbler in wintering and breeding systems. However, the project does not include socioeconomic effects in those systems nor does it include any effects in spillover systems although there may be substantial potential impacts of climate change on spillover systems such as stopover sites. The lack of this information could lead to biased conclusions since factors (e.g., food, socioeconomic conditions) in spillover systems might play a critical role in the biological conditions (e.g., body size, body weight) and behaviors (e.g., duration of stopover) of migrant birds. Climate change might also affect the number of tourists visiting breeding and wintering sites (e.g., climate change impact may cause economic damage to the origin areas of tourists and thus affect the affordability of tourism for people who may be interested in seeing warblers).

As climate change intensifies, interactions between climate change and other human disturbances may have increasing impacts on the persistence of warblers across the telecoupled system. The telecoupling framework can help improve full annual cycle models by identifying interactions between climate change and human activities across telecoupled systems. The interaction effects can be detected by comparing results from separate and simultaneous evaluation of climate change and human disturbances on the components of the telecoupling framework via simulation modeling. Human disturbances may include the selection of timber species like red pine versus jack pine, selection of stocking density and rotation length on various timber products like pole, pulp, chip, or biofuel products in Michigan, and development and agricultural practices in the Bahamas and at stopover sites which affect warbler and cowbird movements.

3.2. Flow-centered management

In addition to identifying research gaps, adopting the telecoupling framework can also help with on-the-ground management. The framework can expand existing practices from site-centered management (focusing on management of individual sites) to flow-centered management (management of flows such as organisms, money for research and conservation, and tourists across sites). Such an expansion would help link various organizations in breeding, wintering and spillover systems and manage them as an interrelated whole (e.g., integration of agents, flows, causes, and effects across all systems). The flow-centered governance emphasizes that governance of land in one area should consider its relationships (e.g., flows of agricultural products through trade) with land elsewhere (Sikor et al., 2013). Similarly, for warblers, we propose to expand the management paradigm from site-centered to flow-centered across sites. Some studies have accounted for biological dependence (through flows of migratory species) among sites (Runge et al., 2014), indicating that the population size in wintering sites may depend on population size in breeding sites, and vice versa. Flows of

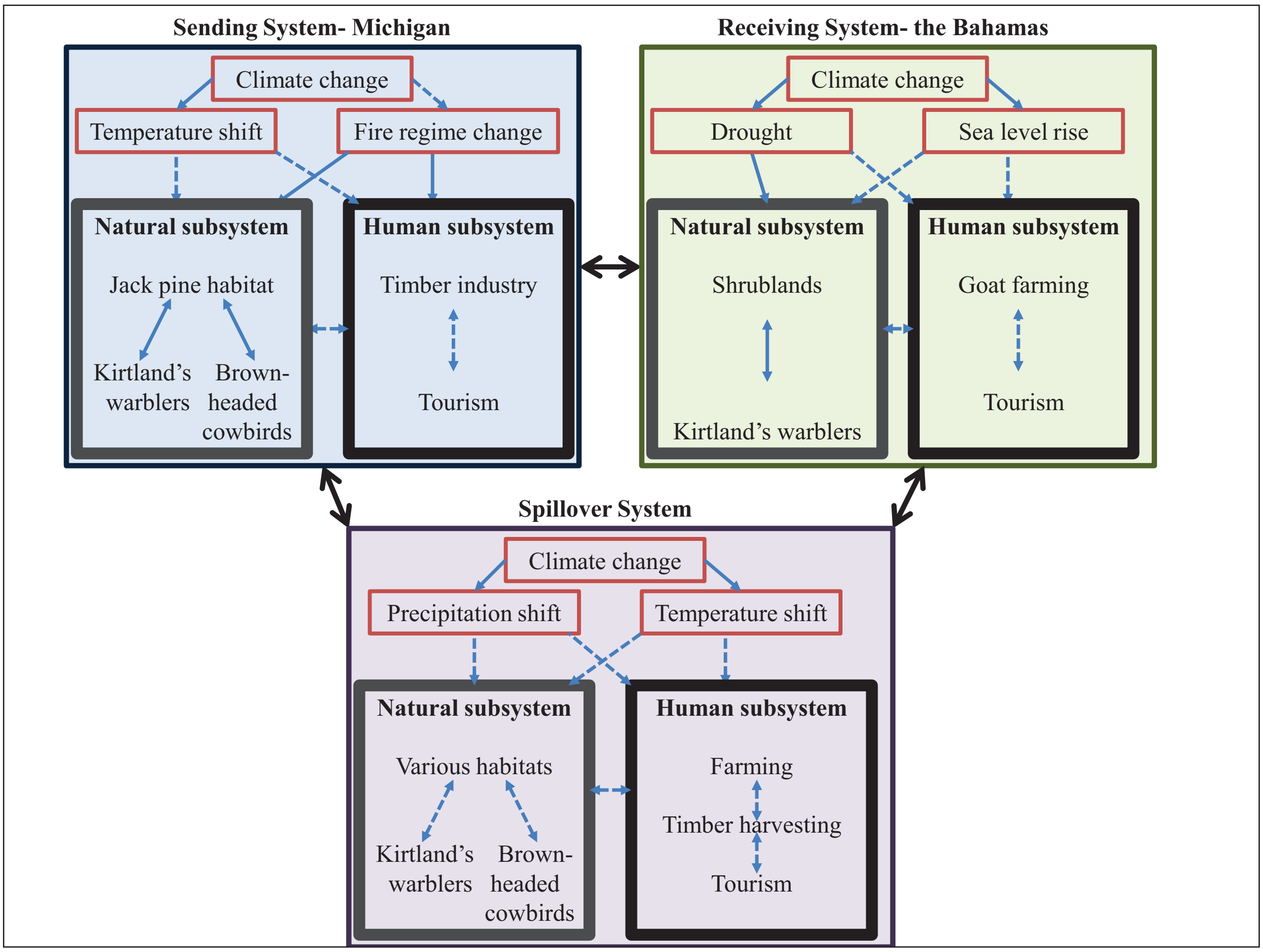

Figure 7: Schematic illustrating select hypothesized effects of climate change on Kirtland's warbler migration in sending, receiving, and spillover systems. Dashed arrows represent understudied interactions. DOI: https://doi.org/10.1525/elementa.184.f7

money and tourists from other places (spillover systems) to wintering and breeding sites may be crucial for generating funds to sustainable conservation. On the other hand, cowbirds from other places to breeding sites may reduce the warbler population. Thus, eliminating or minimizing the flows of cowbirds to breeding sites of the warbler is needed.

Achieving such flow-centered management requires cooperation among agents in sending, receiving, and spillover systems. Flow-centered management goes beyond the conservation social network approach suggested for large-scale conservation efforts such as the Yellowstone to Yukon in North America and The Greater Easter Ranges in Australia that focus on large continuous regions (Guerrero et al., 2015). The social network approach uses social network theory to understand collaboration and formal (e.g., Sandström and Carlsson, 2008) or informal modes of conservation governance (e.g., Vance-Borland and Holley, 2011). It employs network metrics to quantify network characteristics (e.g., Cohen et al., 2012) and evaluate how specific stakeholder interactions are represented. Such analysis of the relationships between stakeholders could help identify options to improve collaboration planning and management. For example, if a particular type of stakeholder interaction is underrepresented in the stakeholder network, efforts should be made to enhance the interaction. Network theory has recently been applied to develop the concept of "network governance", which describes how complex networks of multiple institutions across space can develop relationships that allow them to collectively manage natural resources at larger scales than one institution alone could handle (Scarlett and McKinney, 2016). A key flow that maintains network governance is the flow of information, which maintains communication across the different institutions and helps them to work toward common goals as situations change over time (Bixler et al., 2016). The flow-centered management approach could be an effective tool for understanding such flows as it lends itself to addressing challenges in not only continuous systems but also discontinuous telecoupled systems that may be far apart from each other. Besides the within-scale and cross-scale interactions among stakeholders in large-scale conservation within a particular system (Guerrero et al., 2015), flow-centered management also considers cross-system interactions and coordination (i.e., among sending, receiving, and spillover systems) and reveals key agents and their connections within and across systems that would be most important.

So far, cooperation among different agents for conserving the warbler has largely been within the sending or receiving systems, or across the two, but does not include spillover systems. For example, for managing warblers in Michigan, there are collaborative efforts in planning and implementation by U.S. Forest Service and Michigan Department of Natural Resources to provide essential habitat for warblers with additional lands provided by the U.S. Fish and Wildlife Service and Michigan National Guard (Ryel, 1980). These agencies have also partnered with several NGOs (e.g., Trout Unlimited, Hoot Owl Gun Club, and Huron Pines) and private companies (e.g., Plum Creek) for habitat management. In the Bahamas wintering area, The Nature Conservancy collaborated with private landowners (D. Ewert, 2013, personal communication). Inter-agency collaboration across the sending and receiving systems has been achieved via the sustained efforts of the Kirtland's Warbler Recovery Team and its associates, which includes the above organizations in Michigan and the Bahamas plus Kirtland Community College and College of the Bahamas, The Nature Conservancy and The Bahamas National Trust (**Figure 5**). Members of organizations in both systems travel to the other system to hold workshops and exchange ideas about Kirtland's warbler management. The Nature Conservancy also funds a project (in collaboration with universities and agencies in Michigan) that brings students from the College of the Bahamas to train in Michigan to learn about Kirtland's warbler management efforts that they could then apply in the Bahamas system. These efforts are commendable and should continue and expand. All stakeholders that affect breeding, wintering, stopover sites, and other relevant systems should collaborate to sustain the migratory species.

The flow of money may also be important for the future of Kirtland's warbler management. With the current proposal to delist the Kirtland's warbler from the Endangered Species List, private contributions (Bocetti et al., 2012) and revenues through businesses such as tourism (e.g., from spillover systems) will be essential. Tourism has become a popular way to support conservation goals because of its potential to generate funds specifically for sustaining ecological health (He et al., 2008; Krüger, 2005; Liu et al., 2012). It is important to expand upon current forms of tourism in breeding and wintering systems, and perhaps stopover systems. Few tourism activities in the Bahamas mention warblers (Bahamas National Trust, 2011), but the Kirtland's Warbler Recovery Team is interested in creating more eco-friendly tourism opportunities because regulated tourism has worked well in the sending system. Funds obtained from various sources should be allocated to address important knowledge gaps such as those discussed in the previous section and **Table 2**. Filling these gaps may also lead to more opportunities for generating funding.

3.3. Applicability of the framework to other migratory species

The application of the telecoupling framework to Kirtland's warblers also provides good lessons for applying the framework to other species. Kirtland's warblers share essential attributes with many other migratory species (e.g., with annual cycles across breeding, wintering, and stopover sites that are affected by human activities) although there are some species-specific differences. While the Kirtland's warbler has specific habitat requirements in relatively narrow breeding and wintering ranges, the telecoupling framework is also applicable to other migratory species such as habitat generalists with broad breeding and wintering ranges. This is because the telecoupling framework is flexible to accommodate differences in characteristics of migratory species such as habitat requirements and distribution ranges. This flexibility was similarly demonstrated with the recent applications of the telecoupling framework to flows of different types of ecosystem services (e.g., water – (Deines et al., 2015; Liu and Yang, 2013; Liu et al., 2016a); food – (Liu, 2014; Liu et al., 2015b); forest products – (Liu, 2014)). In **Table 3**, we use the telecoupling framework to highlight three example migratory species to illustrate the similarities and differences with the Kirtland's warbler example. Of the three examples, one is currently experiencing global population declines (leatherback sea turtle, *Dermochelys coriacea*), one species has stable population numbers (blue wildebeest, *Connochaetes taurinus*), and one species has variable population trends depending on the location (Chinook salmon, *Oncorhynchus tshawytscha*).

With regard to systems, all migratory species have breeding, wintering, and stopover sites (**Table 3**). Some species such as the blue wildebeest are similar to Kirtland's warbler in that they have very specific and narrow destinations for breeding and wintering grounds (Hopcraft et al., 2014), but others such as leatherback turtles have broader ranges and are found on many continents (Fossette et al., 2014). The Chinook salmon and leatherback turtle also follow a river or coastline to ocean pathway that differs from terrestrial system (Fossette et al., 2014; Mantua et al., 2015). The blue wildebeest is also an example of a species for which some individuals migrate and others do not if there are enough resources available to them in a particular site to sustain them year-round.

The general types of agents related to other migratory species tend to be largely similar to those for the Kirtland's warbler, as all involved governments from different countries that have a vested interest in conservation or management of the species (**Table 3**). For instance, Chinook salmon management brings together governments and associated agencies in relevant countries (the U.S., Canada, Russia, and Japan), and the leatherback turtle management involves institutions from 10 or more countries. Many of the telecouplings also relate to land owners whose land use decisions affect the migration pathway. For instance, tourist agencies that develop coastlines alter leatherback sea turtle nesting habitat (Roe et al., 2013). Some agents may even harvest migratory species for consumption (e.g., anglers of Chinook salmon or hunters of wildebeest) (Fenichel et al., 2010; Rentsch and Packer, 2015).

Flows are also similar across the telecouplings (**Table 3**). Some species share the same flows as we found in the Kirtland's warbler such as money that flows across systems (e.g., for the fishing industry in Chinook salmon (Welch et al., 2014), for hunting and conservation of wildebeest (Mfunda and Røskaft, 2010). Nutrient or seed flow is also seen in many species like we saw with the warbler, as was information about how to manage or conserve the species. New flows also included disease spread (e.g., for wildebeest (Wambua et al., 2016)) or parasite spread (e.g., for Chinook salmon (Claxton et al., 2013)). Both of these flows could also be playing a role in the Kirtland's warbler example, although to our knowledge no research has been done on them yet.

Causes of the telecoupling are similar across species and usually involve climate and need for different resources in different seasons (e.g., food, nesting conditions) (**Table 3**). For instance, leatherback sea turtles require beaches to lay eggs but their main food sources (e.g., jellyfish) are found in open water (Heaslip et al., 2012). Some (but not all) blue wildebeest migrate each year following patterns of rainfall (and resulting vegetation growth) in a dry savanna ecosystem where food is seasonally limited (Hopcraft et al., 2015). Human factors influencing the telecoupling are also similar to the Kirtland's warbler and include land use changes such as farming, logging, and climate change. For example, farms, in addition to roads and other human settlements, have also fragmented wildebeest habitat along the migration pathway, creating bottlenecks that may threaten wildebeest migration (Morrison and Bolger, 2014) in a similar way that dams impede migration patterns of Chinook salmon (Kareiva et al., 2000).

Effects were diverse across migratory species, but many species share similar effects as the Kirtland's warbler (**Table 3**). Tourism is a common theme across migratory species research and is one of the main ways in which humans interact directly with migratory species. For example, tourism is common in leatherback sea turtle conservation, mainly at the sending systems (breeding sites). Tourists actually directly help with conservation for this species, as over 1,000 volunteers participated in nest protection efforts on one beach in the Virgin Islands over a 10-year period, contributing to a 13% increase in the local population size (Dutton et al., 2005).

Many migratory species are less studied than the Kirtland's warblers, and thus more research gaps exist for them. The identification of research gaps for Kirtland's warblers provides a good approach to identify research gaps for other less studied species. The lack of understanding of interactions across sending, receiving, and spillover systems is a common one across other species as well. For example, conservation efforts for the leatherback sea turtle have been focused mainly on the beaches where they nest (sending systems), with comparably less research and management efforts spent on understanding socioeconomic and environmental factors influencing their survival in the deep sea (receiving and spillover systems) (Dutton and Squires, 2011). In addition, stronger multilateral management efforts are needed in the future to better protect this species from fishing pressure coming from multiple countries, such as by reinforcing existing multilateral agreements that regulate fisheries and creating new ones, in addition to sharing technologies to reduce sea turtle bycatch at the global scale (Dutton and Squires, 2011). This species and many others are not as far along in the quest for "full annual cycle" conservation as the warbler and could benefit from understanding the Kirtland's warbler telecoupling example, particularly with respect to the success with inter-agency cooperation and exchange across sending and receiving systems (e.g., via the Kirtland's Warbler Recovery Team).

Applying the telecoupling framework across multiple migratory species also reveals that migration interacts with other types of telecouplings. One that we have already mentioned is disease spread (a process which affects distant coupled human and natural systems in multiple ways in and of itself). Another example is invasive species, which affect distant coupled systems in complex ways including the transformation of food webs and shifting of local economies in invaded systems (Liu et al., 2013). For example, the Chinook salmon was introduced in the Great Lakes for the first time in the 1960s to control invasive alewives, and subsequently had profound impacts on the local ecosystem and economy as it became successfully established in a new system (Fenichel et al., 2010). Transnational land deals are another telecoupling that also affect distant coupled systems through negotiation of land grabbing by multiple companies or governments that are located far away from the parcels of interest (Liu et al., 2014). Transnational conservation agencies and tourism agencies have been buying land and changing the way it is used in Tanzania (Benjaminsen and Bryceson, 2012), processes which may impact wildebeest migration patterns. Trade is another type of telecoupling which may interact with animal migrations, such as the trade of wildebeest as bushmeat (Mfunda and Røskaft, 2010) or incidental mortality of leatherback sea turtles caught in nets used for the fishing industry and fish trade (Kotas et al., 2004). More research is needed to understand the complex relationships among different telecouplings.

4. Constraints on and opportunities for framework operationalization

Like all integrated frameworks, resources (e.g., time, funding, human power) are big constraints to implement the telecoupling framework. Given their broader scope, operationalizing integrated frameworks such as the sustainability framework proposed by the Nobel Laureate Elinor Ostrom in 2007 requires more time and resources than a narrow disciplinary project (Leslie et al., 2015). The telecoupling framework is even broader than existing frameworks that focus on a coupled human and natural system in a single place because it involves multiple coupled human and natural systems across distant places. Thus, there are more challenges to operationalize the telecoupling framework than many other frameworks. Key challenges include lack of data availability and compatibility across different disciplines and distant locations, as well as lack of computational platforms to integrate diverse datasets. Other challenges include lack of funding support for long-term interdisciplinary research and institutional resistance to support cross-departmental and cross-disciplinary research teams (Liu et al., 2016b).

However, opportunities are emerging to implement the telecoupling framework. More researchers and stakeholders have begun to realize the importance of integrated research

Table 3: Application of the telecoupling framework to example migratory species[a]. DOI: https://doi.org/10.1525/elementa.184.t3

Species	Systems			Agents	Flows	Causes	Effects
	Sending (breeding)	**Receiving (wintering)**	**Spillover (stopover, other)**				
Chinook salmon (*Oncorhynchus tshawytscha*)	Rivers along the coast of British Columbia, Washington, and Oregon; rivers along Japan and Siberia, rivers in systems where the salmon was introduced (the Great Lakes, Patagonia, New Zealand)	Pacific ocean, lakes in systems where the salmon was introduced	Other systems that are affected by salmon trade	Fishermen, governments, consumers, predators, fish	Money, management measures, parasites, nutrients	Climate, water temperature, hydropower, irrigation	Disease spread, nutrient deposition, enhance commercial and indigenous fish industries
Leatherback sea turtle (*Dermochelys coriacea*)	Coastlines of all continents- major ones are Carribbean, Mexico, China, Indonesia, and Africa	Atlantic, Pacific, and Indian Oceans	Tourism networks that extend outside of coastlines, ocean areas along migration routes	Fishermen, conservation organizations, governments, fish, turtles	Nutrients, management measures	Need for coastal nesting conditions, beach development	Promote conservation education and eco-tourism, provide food for locals, control of jellyfish populations
Blue wildebeest (*Connochaetes taurinus*)	Ngorongora National Park and Tarangire National Park in Tanzania	Maasai-Mara ecosystem and Gelai Plains in Kenya and Lake Natron in Tanzania	Maswa Game Reserve and Loliondo, Lake Manyara National Park, and Manyara Ranch in Tanzania	Tanzanian government, Kenyan farmers and pastoralists, poachers and hunters, and lawyers; wildebeest	Diseases, seeds, money for conservation, information on management	Rainfall and vegetation growth, increases in roads and farms that created bottlenecks	Enhance tourism, poaching, crop raiding, control of wildfires, disease spread

[a]Relevant citations can be found in the text.

and conservation. Funding agencies such as the National Science Foundation and Belmont Forum (an international consortium of funding agencies) have begun to fund projects that operationalize the telecoupling framework (e.g., Liu et al., 2015a). The existing applications and new opportunities provide a foundation and lessons to operationalize the framework for migratory species research and conservation. These advances in telecoupling can be combined with other recent advances in the migratory species research realm itself, such as use of geolocators and high-resolution global positioning system (GPS) tracking devices to quantify movements of migratory species with greater precision (Hoenner et al., 2012) and stable isotope analysis for identifying locations of stopover and wintering locations from isotope ratios along dynamic "isoscapes" (Hobson et al., 2010; Hobson and Wassenaar, 2008). These approaches and the telecoupling framework can facilitate and guide the collection of relevant quantitative data so that the relative strengths and importance of different interactions can be evaluated in a robust and integrative manner (e.g., via integrative modeling approaches such as systems models, scenario analyses, or agent-based modeling).

The large number of research gaps on this topic may seem overwhelming (**Table 2**). Like research gaps on other topics, they may not be filled overnight simultaneously given limited funding and human capital. Thus, it is important to set priorities. Priority criteria may include availability of resources as well as the importance and urgency of filling specific gaps for best conservation outcomes. Priority setting would require input from relevant researchers, managers, and other stakeholders. Once priorities are set, it is feasible to divide the entire work under the telecoupling framework into multiple smaller yet interconnected projects and integrate results from those projects when they are available. Each smaller project is doable by an individual researcher or a group of researchers. The entire process would consist of several steps. The beginning step would be to determine all components and relationships under the framework. The middle steps would quantify different components and integrate those quantified. The number of middle steps would be determined by the number of components and resources to quantify these components at each step. After two or more projects are completed, they can be integrated and their relationships can be understood. In other words, more integration is increasingly achieved over time. The last step would be to integrate all components, marking the complete operationalization of the framework. Of course, as systems change, it is necessary to repeat some or all steps described above to measure temporal dynamics. The big advantage of this new approach over the traditional approach is that multiple projects can be integrated under the same framework over time.

5. Conclusions

As the world becomes increasingly connected and humans are having greater impacts on migratory species across political and administrative boundaries, it is imperative to take holistic approaches such as the telecoupling framework in research and management of migratory species. Using the Kirtland's warbler as a demonstration species provided a window into understanding the potential for the telecoupling framework to shape new directions in research on migratory species that embrace human-nature interactions occurring across the entire annual migration pathway and beyond. The novel insights include research and conservation gaps identified through applying the telecoupling framework. Furthermore, in contrast to previous studies that often focused on specific components separately, our paper integrated all major components related to Kirtland's warbler research and conservation. The telecoupling framework adds to migratory species research and conservation by allowing us to link various components and understand their interrelationships. Operationalizing the framework is flexible as it allows researchers to divide a large project into smaller ones yet ensures that smaller projects are integrated. Such a new approach avoids the problem in previous smaller projects that produced fragmentary information. The telecoupling framework also bridges interdisciplinary studies, interagency cooperation, and public engagement, all of which are successful tools for on-the-ground conservation efforts (Bocetti et al., 2012; Ewel, 2001; Reed, 2008; White and Ward, 2011). With cooperation among individuals and agencies with relevant expertise and responsibilities, operationalizing the framework has the potential to help discover hidden environmental and socioeconomic patterns and processes, thus transforming research and sustainable management for the Kirtland's warblers and other migratory species around the world.

Data accessibility statement

No new data were created during this study, except those reported in the figures and tables.

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Competing interests

The authors have no competing interests to declare.

Author contributions

- Contributed to conception and design: JH, CB, HC, VH, WY, JL
- Contributed to acquisition of data: JH
- Contributed to analysis and interpretation of data: JH, CB, HC, VH, WY, JL
- Drafted and/or revised the article: JH, CB, HC, VH, WY, JL
- Approved the submitted version for publication: JH, CB, HC, VH, WY, JL

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