



The State of Migratory Landbirds in the East Asian Flyway: Distributions, Threats, and Conservation Needs

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With nearly 400 migratory landbird species, the East Asian Flyway is the most diverse of the world's flyways. This diversity is a consequence of the varied ecological niches provided by biomes ranging from broadleaf forests to arctic tundra and accentuated by complex biogeographic processes. The distribution and migration ecology of East Asian landbirds is still inadequately known, but a recent explosion in the number of studies tracking the migration of raptors, cuckoos, kingfishers and passerines has greatly increased our knowledge about the stopover and wintering ecology of many species, and the migratory routes that link northeast Eurasia and the Asian tropics. Yet the East Asian Flyway also supports the highest number of threatened species among flyways. Strong declines have been detected in buntings (Emberizidae) and other long-distance migrants. While the conservation of migratory landbirds in this region has largely focused on unsustainable hunting, there are other threats, such as habitat loss and increased agro-chemical use driven directly by land cover change and climate-related processes. Important knowledge gaps to be addressed include (1) threats affecting species in different parts of their annual cycle, (2) range-wide population trends, (3) ecological requirements and habitat use during the non-breeding season, and (4) the conservation status of critical wintering sites (including understudied farming landscapes, such as rice fields) and migration bottlenecks along the flyway.

Keywords: biome, climate change, ecosystem role, habitat loss, hunting, land use change, migration, tracking

INTRODUCTION

The decline of migratory species is a global conservation concern (Wilcove and Wikelski, 2008) across the world's major flyways (Lloyd-Evans and Atwood, 2004; Galbraith et al., 2014; Beresford et al., 2019). Migratory species declines and the associated drivers are well documented for birds that migrate between North America and the Neotropics (Robinson and Wilcove, 1994; Lloyd-Evans and Atwood, 2004; Bennett et al., 2018) and for species that breed in Europe and winter in Sub-Saharan Africa (Bibby, 1992; Sanderson et al., 2006; Vickery et al., 2014;

Beresford et al., 2019), but less so for other regions. The decline of many species has been linked to anthropogenic changes in habitat conditions, such as habitat loss and fragmentation (Robinson and Wilcove, 1994) intensified by climate change (Lloyd-Evans and Atwood, 2004; Sanderson et al., 2006; Vickery et al., 2014; Gilroy et al., 2016). Over time, climate change is expected to disrupt ecological and environmental processes that may affect migration and reproduction, for instance, by driving spatio-temporal mismatches in food resources (Carey, 2009). Given that migratory species have geographically complex life cycles that connect breeding, stopover and non-breeding sites over large areas, they are especially vulnerable to threats along their migratory routes (Runge et al., 2014, 2015).

The East Asian Flyway (EAF) as defined here overlaps with the eastern hemisphere (east of the 90th meridian), including the western Pacific Ocean (McClure, 1974, 1984; Nisbet, 1976; Yong et al., 2015), and spans arctic, boreal, temperate and tropical biomes (Figure 1). Compared to the African-Eurasian and the American flyways, the EAF is geographically more varied with an uneven distribution of landmass across boreal-temperate and tropical latitudes (Nisbet, 1976). While there are few ecological barriers in the west in the form of mountain ranges, the EAF contains extensive island chains at its eastern fringe and the vast Indo-Australian archipelago spanning the tropical belt. These island chains collectively pose complex barriers in the form of sea-crossings for migrating landbirds (Kuroda, 1961; Ellis et al., 1990; Yamazaki et al., 2012; Nourani et al., 2018) unmatched in other flyways.

With almost 400 species (387 species [63% of all migratory species]; see also Appendix I for full list), the bulk of EAF migratory species are in fact landbirds, with passerines and diurnal raptors among the most species-rich groups (McClure, 1974; Yamazaki et al., 2012; Yong et al., 2015). In this flyway, migratory landbirds fulfill diverse ecological roles in boreal, temperate and tropical biomes in terms of their trophic positions (e.g., herbivory, insectivory and predation) and transport processes (e.g., nutrient and parasite transfer, seed and pollen dispersal; see Şekercioğlu et al., 2004; Bauer and Hoye, 2014; López-Hoffman et al., 2017). Across East Asia, migratory landbirds consume and disperse the fruits and seeds of varied tree species, as evidenced by studies in Japan, China and South Korea (Nakanishi, 1996; Corlett, 1998; Choi and Chae, 2007; Cho et al., 2011; Choi et al., 2011; Jeong et al., 2014). Insectivorous species provide significant pest-control services to agroecosystems (Kim et al., 2012b) and directly reduce disease transmission through predation and scavenging (Kim et al., 2012a). Yet, despite their contribution to ecosystems at a large scale in East and Southeast Asia, landbirds are the least understood among the diverse migratory bird assemblages in Asia (Yong et al., 2015; Heim et al., 2020).

The declines in populations of many migratory waterbirds, and especially shorebirds, across East Asia and Australasia have been well documented (Szabo et al., 2016; Studds et al., 2017) and are far better understood than landbird declines. However, *Emberiza* buntings and many other East Asian landbirds have suffered dramatic population declines in recent years (Kamp et al., 2015; Edenius et al., 2017; Choi et al., 2020a), driven in part by habitat loss (Higuchi and Morishita, 1999)

and unsustainable hunting (Kamp et al., 2015). Meanwhile, the lack of understanding of regional population trends and status of many East and Southeast Asian species continues to hamper conservation actions targeting landbird species. They are similarly affected by inconsistent and incomplete levels of protection offered by national and international legal frameworks for wildlife conservation (Runge et al., 2015; Yong et al., 2015, 2018).

Since 2010, growing interest in the ecology and conservation of migratory landbirds in the EAF has yielded fresh insights on their migration ecology and migratory connectivity (Yamaura et al., 2017; Heim et al., 2018b, 2020; Choi et al., 2020b; Uemura et al., 2020), species-specific population declines (Tamada et al., 2014, 2017; Kamp et al., 2015; Edenius et al., 2017; Choi et al., 2020a), and threats (Amano and Yamaura, 2007; Iqbal et al., 2014; Kamp et al., 2015). While large-bodied hawks and eagles (Accipitriformes) have traditionally been easier to study during migration (Higuchi et al., 2005; Reading et al., 2020) and at key bottleneck sites (Zalles and Bildstein, 2000; Yamazaki et al., 2012; DeCandido et al., 2015; Limparungpatthanakij et al., 2019), studies on migratory passerines and other landbirds are fast catching up thanks to emerging tracking technology and methods.

Against this ‘migratory landbird renaissance,’ we aim to synthesize existing knowledge on the conservation status of migratory landbirds (see Table 1 for definitions) in the EAF. We also identify key knowledge gaps for further work in this traditionally data-poor migratory flyway. We define the taxonomic scope of landbirds in our review based on the widely accepted definitions used in the literature (Kirby et al., 2008; Faaborg et al., 2010), which encompasses passerines, raptors and several near-passerine families (see Supplementary Data for full taxonomic scope). We (1) summarize recent advances in landbird migration ecology research in the EAF, (2) review emerging evidence of declines and associated drivers in key biomes, (3) discuss the ecological implications of these changes on Asian ecosystems in the wider context of land use change and unsustainable hunting, and (4) identify knowledge gaps and describe how addressing them can translate into conservation actions.

ADVANCES IN LANDBIRD MIGRATION ECOLOGY IN THE EAF

Understanding the different migration strategies used by landbirds is crucial to conservation at sites used over the annual cycle of migratory birds. Building on long-term bird ringing work in Japan, the Russian Far East, China and South Korea (reviewed in McClure, 1974; Yong et al., 2015), several new large-scale ringing projects have been established in this region, for instance in India and Mongolia (Buner et al., 2015; Davaasuren, 2018).

Research on Migration Strategies and Stopover Ecology

In general, the migration strategy of a species is fundamentally shaped by its habitat requirements and physiology. Many species that cover long distances need to refuel several times to replenish



TABLE 1 | Definitions of key terms mentioned in the text.

Term	Definition	Example
Altitudinal migrant	Species that breed at higher altitudes and migrate across elevational gradient over seasons. Some species may also cross latitudinal gradients.	scarlet finch <i>Haematospiza sipahi</i> , collared grosbeak <i>Mycerobas affinis</i> , various genera in Leiothrichidae
Biome	Distinct (broad) communities of plants and animals that have formed in response to a shared climate.	
East Asian Flyway	A broad network of migratory routes used by populations of landbird species that connect the northern and eastern Asian breeding areas with non-breeding areas at lower latitudes, especially in tropical Asia and extending to insular Southeast Asia. Also referred to as the East Asian-Australasian Flyway when used in the context of the many shorebirds species that migrate to overwinter in Australasia.	
Intra-tropical migrant	Migratory species that breed, migrate and winter largely within the tropical/subtropical latitudinal belt.	blue-winged pitta <i>Pitta moluccensis</i> , Asian emerald cuckoo <i>Chrysococcyx maculatus</i> , Asian drongo cuckoo <i>Surniculus lugubris</i>
Long-distance migrant	Species that migrate large distances (c. 2,000–10,000 km) at a continental scale annually, typically covering several biomes and a wide range of latitudes. These species usually lack sedentary populations.	common stonechat <i>Saxicola torquatus</i> , Japanese sparrowhawk <i>Accipiter gularis</i> , oriental cuckoo <i>Cuculus optatus</i>
Migratory corridor	A series of migratory routes used by multiple species, defined by particular geography of the region (See Figure 2).	
Migratory connectivity	Linkages between migratory populations of a species at the breeding and non-breeding areas, including stopover sites.	
Short-distance migrants	Species that migrate relatively short distances (<2,000 km) annually within the same biome or across a few latitudinal degrees. Many intra-tropical migrants are short-distance migrants.	gyrfalcon <i>Falco rusticolus</i> , long-tailed rosefinch <i>Uragus sibiricus</i> , blue-winged pitta
Stopover site	Sites that are used by migratory species for resting and refueling for a day to several weeks (but not months) during migration.	
Wintering range	Geographical area consistently used by a migratory species during the non-breeding period after fall migration, within which it does not perform any significant directional movements.	

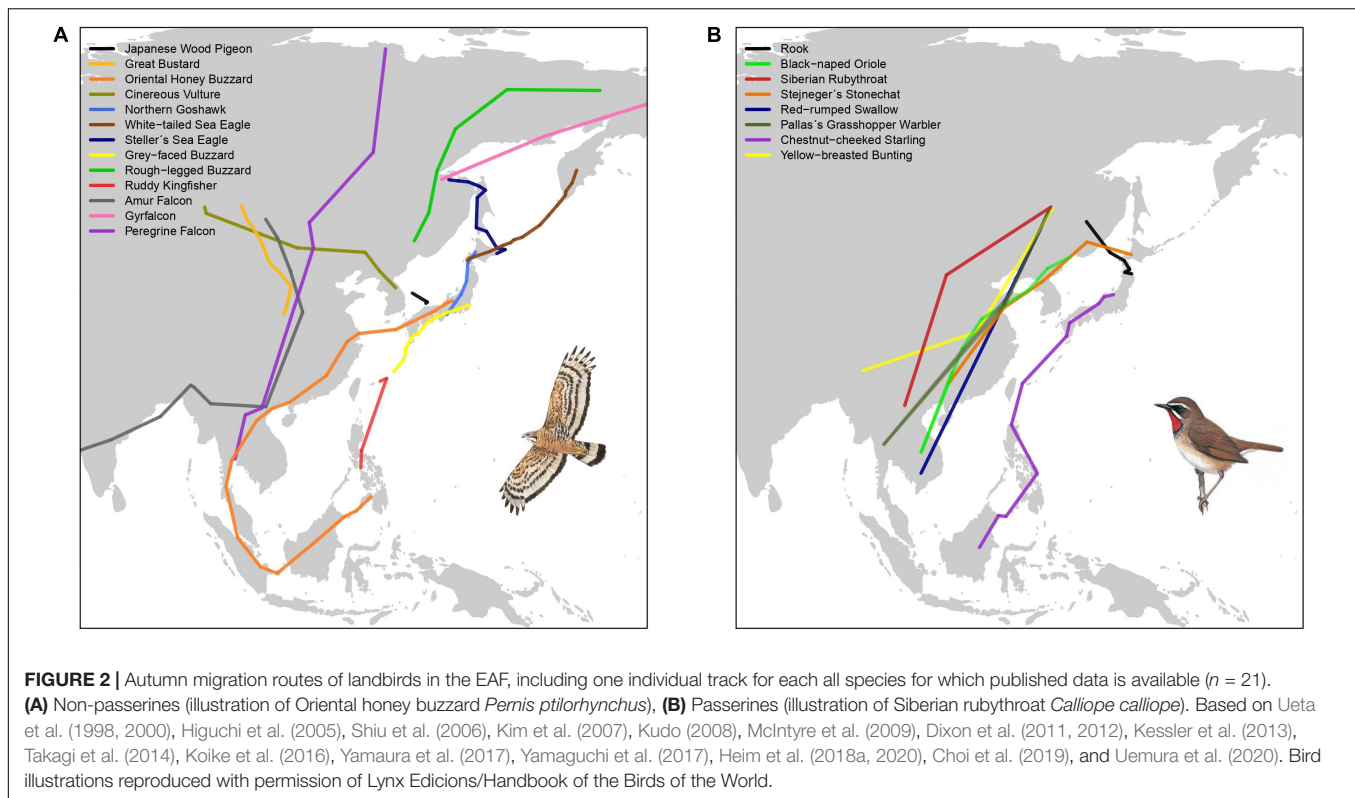
fat reserves before reaching their wintering grounds (Bairlein, 2002), and thus the availability of suitable stopover habitat is critical (Warnock, 2010). Ongoing studies at key stopover sites for landbirds at Muravioka Park in southeast Russia, in China, on various islands off South Korea and elsewhere in the region are beginning to unveil the diverse migration strategies (Nam et al., 2011; Heim et al., 2018b). Sander et al. (2017, 2020) describe the different strategies adopted by warblers to increase their fat stores during autumn migration: Pallas's leaf warbler *Phylloscopus proregulus* carries more fat, fuelling longer flight bouts with fewer stops. Others, such as the thick-billed warbler *Arundinax aedon*, carry less fat, necessitating more frequent stopovers on migration (Bozó et al., 2019; Sander et al., 2020).

Stopover habitats utilized by landbirds range from old-growth, deciduous forests (Tojo, 2015) to a variety of human-modified landscapes and habitats (Kim et al., 2010). While many migratory landbird species may occupy a broader or different niche away from the breeding areas, some rely on similar environmental conditions throughout their annual cycle (Zurell et al., 2018). *Phylloscopus*, *Acrocephalus* and *Locustella* warbler species are among the most abundant landbirds in East Asia, and show species-specific habitat preferences at both breeding and stopover sites (Bozó et al., 2018b). On the other hand, *Emberiza* buntings often show a large overlap in habitat use at stopover sites (Heim et al., 2018a).

While migration strategies undoubtedly vary widely across taxa, temporal differences in migration within a species over

different seasons have also been described. For instance, stopovers for many species (e.g., yellow-browed warbler *Phylloscopus inornatus* and red-flanked bluetail *Tarsiger cyanurus*) have been found to be considerably shorter in the spring than in the autumn, suggesting faster spring migration (Wang et al., 2006; Bozó et al., 2021), a generally well-described pattern for many migratory species (Kokko, 1999; Smith and Moore, 2005; Nilsson et al., 2013). This may be explained by competition to arrive at the breeding grounds before conspecifics (Nilsson et al., 2013). On the other hand, no significant differences between spring and autumn migration speed/duration are evident in non-passerines, e.g., in satellite-tracked Oriental honey buzzard *Pernis ptilorhynchus* (Yamaguchi et al., 2008) and great bustard *Otis tarda* (Kessler et al., 2013). In addition, specific morphological and behavioral adaptations have been found across various model species in the EAF that improve the efficiency of long migratory flights (Bozó et al., 2018a; Wang et al., 2020).

Analyses of the arrival and departure times of landbirds at key stopover sites have shown that migration distance and the relative locations of the breeding and wintering grounds determine the migratory phenology of *Emberiza* and *Phylloscopus* species and Siberian rubythroat *Calliope calliope* in the Russian Far East (Nam et al., 2011; Maslovsky et al., 2014, 2018; Bozó and Heim, 2015, 2016; Bozó et al., 2017, 2019; Heim et al., 2018a; Park et al., 2020; Wobker et al., 2021). Long-distance migrants generally arrive at stopover sites later in spring, while departing earlier in



autumn, and of these, species breeding at higher latitudes tend to pass earlier during spring migration (Wobker et al., 2021). Additionally, biological factors, such as sex, age and the timing of molt are all known to influence migration phenology in many passerines (Maslovsky et al., 2018; Park et al., 2020; Wobker et al., 2021), with protandry being a common pattern (Nam et al., 2011; Bozó and Heim, 2016; Park et al., 2020).

Monitoring migration phenology is important, given that the ability of a species to adjust its migration timing to events along its annual cycle can indicate its vulnerability to climate change (Møller et al., 2008). Valchuk et al. (2017) suggested that links between the West Pacific climate index and the abundance of migrating landbirds at a stopover site in the Russian Far East can indicate the effects of climatic shifts on migration phenology at a broad scale. Indeed, long-term studies have revealed shifts in spring arrival times for several species in Japan, linked to warmer temperatures (Deguchi et al., 2015), consistent with observations in Europe and the Americas (Thorup et al., 2007; Hurlbert and Liang, 2012).

Research on Migratory Routes and Connectivity

Studying the migratory connectivity of a species is necessary to understand its migration ecology (Marra et al., 2011), and holds important implications for its conservation. Data from ringing recoveries, increasingly complemented with data obtained from various tracking technologies (e.g., light-level geolocators and satellite telemetry) have traditionally been used to map migration routes, and infer migratory connectivity for

species and populations (Finch et al., 2015; Heim et al., 2020; **Figure 2A**). As smaller devices become increasingly available, various small-bodied landbirds can now be effectively tracked. Over the past decade, the number of landbird species tracked in the EAF has steadily risen to at least 26 species, with an increasing number of small passerines (**Figures 2A,B** and **Table 2**).

Two main migratory corridors in the EAF are now well established, (1) the ‘island’ or ‘oceanic’ route linking eastern Russia (Kamchatka and Sakhalin) and Japan to the Philippines and eastern Indonesia, and (2) the ‘mainland’ route, linking eastern Russia, China and continental Southeast Asia (Higuchi, 2005; Yamazaki et al., 2012; Concepcion et al., 2017; Heim et al., 2020). Data from recent tracking studies (**Figure 2**) further illustrate the use of the ‘island route’ by passerines and raptors breeding in Japan (Koike et al., 2016; Nourani et al., 2018; Uemura et al., 2020) and species shared with Kamchatka (e.g., barn swallow *Hirundo rustica* and Siberian rubythroat) (Heim et al., 2020). These results corroborate direct observations in the Philippines and eastern Indonesia (Germi et al., 2009, 2013; Concepcion et al., 2017).

The specific island route(s) used remain poorly studied. Observational data show that two raptors, grey-faced buzzard *Buteo indicus* and Chinese sparrowhawk *Accipiter soloensis*, pass south through the Japanese archipelago, Taiwan and the Philippines (Ellis et al., 1990; Yamazaki et al., 2012; Concepcion et al., 2017). Similarly, some passerines, including wagtails, pipits and yellow bunting *Emberiza sulphurata*, also follow this least energetically costly route (Nourani et al., 2018). Certain species may take a more direct route from south Japan passing east

TABLE 2 | East Asian landbird migrants for which tracking data have been published in the peer-reviewed literature ($n = 23$) with the tracking technique (Tech) used for each species (GLS = light-level geolocation, GPS = Global Positioning System data logging and SAT = satellite tracking), the number of individuals tracked (N, adults/juveniles), the country where the birds were tagged (RUS = Russia, MNG = Mongolia, JPN = Japan, USA = United States of America), and the source(s) where the original data were published.

Species	Tech	N	Country	Source
<i>Cuckoos</i>				
Common cuckoo ¹	SAT	4/0	RUS	Bulyuk et al., 2018; Thorup et al., 2020
<i>Bustards</i>				
Great bustard	SAT	3/0	MNG	Kessler et al., 2013
<i>Raptors</i>				
Oriental honey buzzard	SAT	>33/1	JPN	Higuchi et al., 2005; Shiu et al., 2006; Yamaguchi et al., 2008, Yamaguchi et al., 2012; Sugasawa and Higuchi, 2019
Cinereous vulture	GPS/PTT	10/53	KOR/MNG	Kim et al., 2007; Reading et al., 2020
Northern goshawk	SAT	2/0	JPN	Kudo, 2008
White-tailed sea eagle	SAT	2/0	JPN	Ueta et al., 1998
Steller's sea eagle	SAT	9/25	JPN/RUS	Meyburg and Lobkov, 1994; Ueta et al., 2000; McGrady et al., 2003
Grey-faced buzzard	SAT	9/0	JPN	Shiu et al., 2006; Nourani et al., 2018
Rough-legged buzzard	SAT	4/0	JPN	Yamaguchi et al., 2017
<i>Pigeons</i>				
Japanese wood pigeon	GPS	2 ³	KOR	Choi et al., 2019
<i>Kingfishers</i>				
Ruddy kingfisher	GPS	3/0	JPN	Uemura et al., 2020
<i>Falcons</i>				
Amur falcon ¹	SAT	1/0	MNG	Dixon et al., 2011
Gyrfalcon	SAT	0/15 ⁴	USA	McIntyre et al., 2009
Peregrine falcon	SAT	17/0	RUS	Dixon et al., 2012
<i>Passerines</i>				
Black-naped oriole	GLS	1/0	RUS	Heim et al., 2020
Brown shrike	GLS	3/0	JPN	Aoki et al., 2020
Rook	SAT	20/0	JPN	Takagi et al., 2014
Pallas's grasshopper warbler	GLS	1/0	RUS	Heim et al., 2020
Red-rumped swallow	GLS	1/0	RUS	Heim et al., 2020
Barn swallow	GLS	1/0	RUS	Heim et al., 2020
Willow warbler ²	GLS	3/0	RUS	Sokolovskis et al., 2018
Chestnut-cheeked starling	GLS	16/0	JPN	Koike et al., 2016
Chinese blackbird	SAT	0/1	KOR	Choi et al., 2020c
Siberian rubythroat	GLS	10/0	RUS	Heim et al., 2018b, 2020
Common stonechat	GLS	12/0	JPN	Yamaura et al., 2017
Yellow-breasted bunting	GLS	3/0	RUS	Heim et al., 2020

Note that the migration routes of some species extend beyond the East Asian Flyway^{1,2}. ¹Migrates to Africa via India; ²migrates to Africa via West Asia; ³ages unknown; ⁴only four individuals migrated from Alaska to East Asia.

of Taiwan, most likely aided by seasonal weather conditions, as suggested by tracking data of ruddy kingfisher *Halcyon coromanda*, chestnut-cheeked starlings *Agropsar philippensis* and grey-faced buzzards (Koike et al., 2016; Uemura et al., 2020). The northward migration route(s) in spring is less well known, with some species supposedly leaving the northern Philippines heading for southern China (Welch, 2011). The low number of observations of species such as Gray's grasshopper warbler *Locustella fasciolatus* in Taiwan and the Philippines is unusual (Severinghaus et al., 2017; Allen, 2020) – either they largely overfly or bypass these islands, or are simply overlooked.

Meanwhile, recent tracking data from Russia, Mongolia and northern China are providing insights on precise migration paths along the 'mainland route' for small passerines (e.g., Siberian

rubythroat, Pallas's grasshopper warbler *Locustella certhiola* and yellow-breasted bunting *Emberiza aureola*) (Heim et al., 2018b, 2020), as well as for great bustard (Kessler et al., 2013) and cinereous vulture *Aegypius monachus* (Kim et al., 2007; Reading et al., 2020). Although there are no major geographical barriers, species using the 'mainland route' may cross uplands and mountains in central and southern China, northern Indochina (Wang et al., 2000; Tordoff, 2002; Fei et al., 2015) and the Malay Peninsula (Medway and Wells, 1976).

Based on satellite tracking studies, Oriental honey buzzards breeding in Japan (Higuchi et al., 2005; Yamaguchi et al., 2008, 2012; Sugasawa and Higuchi, 2019) and probably yellow-breasted buntings from Kamchatka (Heim et al., 2020) make major sea crossings to the mainland before migrating to

southern China and Southeast Asia (Yamaura et al., 2017), potentially avoiding longer sea crossings further south. Such migratory patterns may suggest that these species colonized Japan from the mainland relatively recently (Agostini and Mellone, 2007). Satellite telemetry has demonstrated strong migratory linkages for large (soaring) species, particularly rough-legged buzzards *Buteo lagopus* moving between eastern Russia and Japan (Yamaguchi et al., 2017), while highlighting the importance of Japan for wintering Steller's sea eagles *Haliaeetus pelagicus* and white-tailed sea eagles *H. albicilla* breeding in eastern Russia (Ueta et al., 1998; McGrady et al., 2003). Similarly, tracking studies and field observations at key watch sites have demonstrated the role of the Japanese archipelago as a land corridor for bird migration into tropical Asia (Shiu et al., 2006; Yamazaki et al., 2012; Koike et al., 2016; Nourani et al., 2018).

Nevertheless, whilst the majority of EAF landbird species migrate largely along latitudinal gradients into temperate and tropical Asia, a few species deviate from these two major migratory corridors to reach non-breeding grounds in India or Africa. These landbirds have migratory routes that partially overlap with the EAF; they eventually migrate westward toward Africa crossing the large ecological barrier of the Indian Ocean. Two of the best studied examples are Amur falcon *Falco amurensis* and common cuckoo *Cuculus canorus*, both known to cover the longest migratory distances among East Asian landbirds (Dixon et al., 2011; Townshend, 2016a; Bulyuk et al., 2018; **Figure 2A**).

BREEDING DISTRIBUTION OF MIGRATORY LANDBIRDS

The varied ecosystems of northeast Asia form the core breeding grounds of most migratory landbirds in the EAF (McClure, 1974; Nisbet, 1976; Yong et al., 2015). These include temperate broadleaf forests in China, Japan and the Korean Peninsula, which support the highest diversity of (migratory) breeding landbirds, as well as boreal (taiga) forests and Arctic tundra, which support a more depauperate breeding landbird fauna (Ganter and Gaston, 2013; **Figure 3**). There are fewer than 20 landbird species regularly breeding in the Arctic, only five of which are strictly associated with this biome (Vaughan, 2010; Ganter and Gaston, 2013). The migration patterns of Arctic-breeding landbirds are not well known, as the movements of only one species, the snow bunting *Plectrophenax nivalis*, have been tracked and only in an American flyway (McKinnon et al., 2016). The natural history of the landbirds of eastern Russia, which forms the largest part of the EAF, has, however, been relatively well studied for over a century (Dementiev and Gladkov, 1951–1954). Extensive regional reviews are also available for northeast Russia (Kistchinski, 1968, 1988; Krechmar et al., 1991), Sakhalin Island (Nechaev, 1991) and the diverse broadleaf temperate forest of Primorsky Krai (Gluschenko et al., 2016). Similarly, reviews have been published on the Chinese, Korean and Japanese breeding bird fauna since the 1960s (Cheng and Li, 1955; Yamashina, 1961; Won et al.,

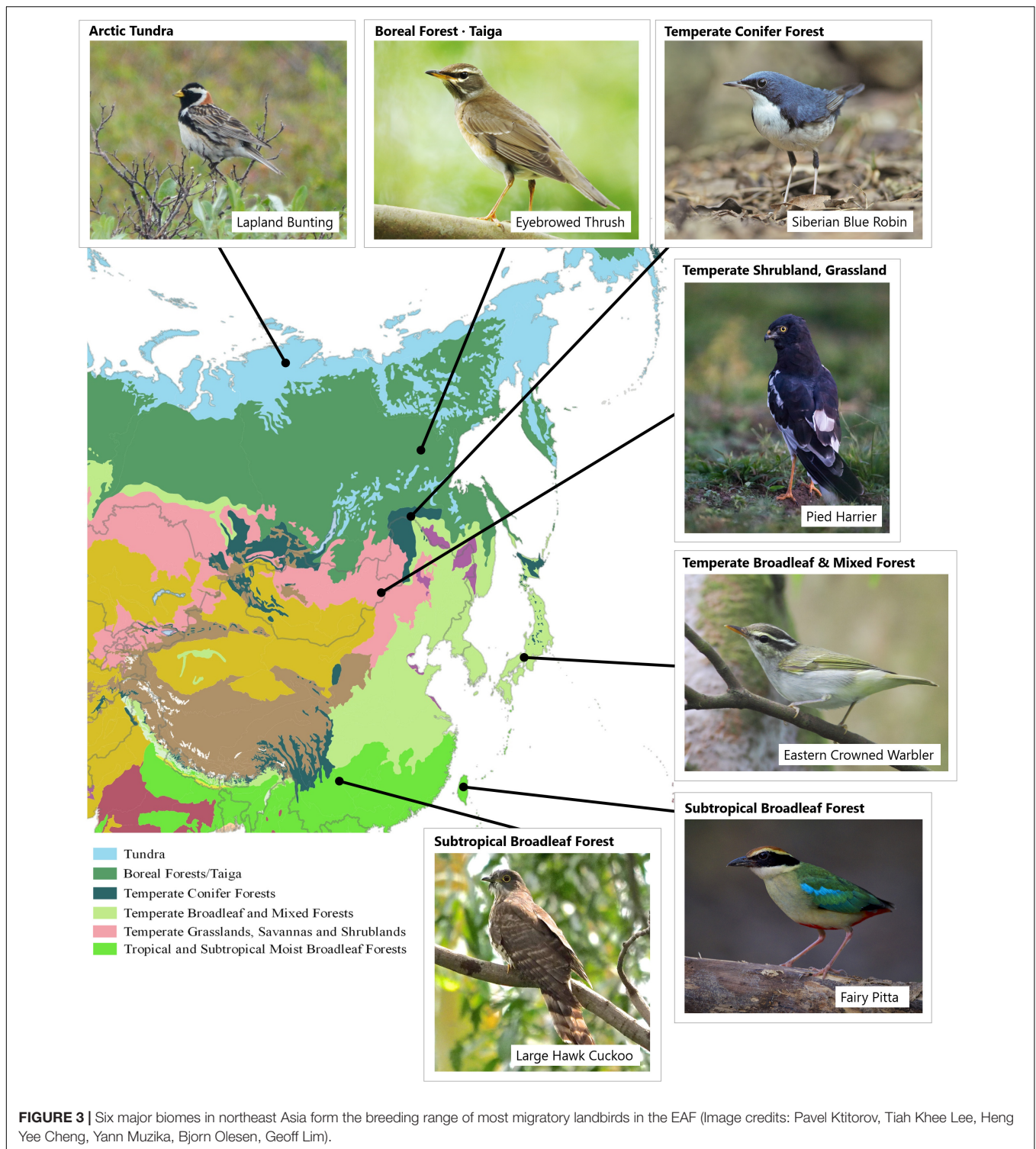
1966; Won and Gore, 1971), whilst natural history studies of many species exist.

The broad distribution of birds in the eastern Palearctic (which overlaps in its entirety with the northern EAF) was first described by Shtegman (1938), who defined seven major habitat-associated groups across the wider Palearctic region. Based on this classification, most migratory landbird species in the EAF (finches, chats, thrushes, buntings and *Phylloscopus* warblers) belong to the Siberian (usually boreal forest or taiga species) or the Chinese faunal group (usually species of mixed broadleaf forests; see Shtegman, 1938). The ratio of migratory species progressively increases with latitude: the handful of Arctic-breeding species are almost all migratory, while the proportion of migratory species drops to 60–80% in the boreal and temperate biomes (Ganter and Gaston, 2013; Somveille et al., 2013), and even lower in the subtropics (Yong et al., 2015).

DISTRIBUTION AND ECOLOGY OF MIGRATORY LANDBIRDS IN THE TROPICS

The broad patterns associated with wintering landbird diversity and distributions across tropical Asia are relatively well described (Nisbet, 1976; White and Bruce, 1986). The diversity of wintering landbirds is highest in mainland Southeast Asia, followed by southern China and the Greater Sundas (McClure, 1974; Nisbet, 1976; Yong et al., 2015; **Table 3**), declining progressively through the Philippines and Wallacea toward Australia (White and Bruce, 1986). Unlike other Eurasian migratory systems, the EAF hosts a large number of insectivorous species that overwinter in forests, many with putative and/or narrow distributions (e.g., rufous-headed robin, blackthroat *Calliope obscura*, Gansu leaf-warbler *Phylloscopus kansuensis* and Ijima's leaf-warbler *Phylloscopus ijimae*; see Yong et al., 2015). A few species, such as Gray's grasshopper warbler *Locustella fasciolata* may be considered 'extreme eastern' landbird migrants that largely overwinter in eastern Indonesia (White and Bruce, 1986; Coates and Bishop, 1997; Allen, 2020). A handful of taxa have their core wintering ranges in New Guinea or continental Australia (e.g., white-throated needletail *Hirundapus caudacutus*) (White and Bruce, 1986; Tarburton, 2014; Menkhorst et al., 2017).

Tropical broadleaf forests form the dominant wintering habitat for at least 90 migratory landbirds in the Southeast Asian tropics (Medway and Wells, 1976; Wells, 2007; Yong et al., 2015; **Figure 4**). An additional 60 species that rely on this habitat are Sino-Himalayan and/or short-distance migrants that breed at higher (subtropical and tropical) latitudes. The ecological niches occupied by these forest-dependent species vary considerably. Many occupy seasonal deciduous and evergreen forest mosaics, species wintering in the Greater Sundas mostly use evergreen (lowland) rainforests, while the few species reaching southern Wallacea are largely eurytopic (Schellekens et al., 2011). The elevational distribution of most forest-wintering taxa has been poorly defined, although some seem to be confined to lowlands or mountains (15 and 23 species, respectively). At least 36 species use inland freshwater wetlands, opportunistically



exploiting wetland-like rice paddies (Figure 4) that represent the dominant anthropogenic land cover in many parts of tropical Asia (Round, 2008). As the region was formerly dominated by forests, the historical distribution of species assemblages currently associated with open anthropogenic landscapes is unclear. Nevertheless, some almost certainly have expanded

their distribution to colonize new habitats created by the clearance of the climax vegetation (Yamaura et al., 2017). In Indonesia, starlings and other wintering species are now reported from urban areas and heavily modified mosaics of coastal vegetation (Diniarsih et al., 2016), suggesting some level of adaptability.

TABLE 3 | Non-breeding distribution of migratory landbirds in different Southeast Asian regions and Australia.

Region	Number of species (exclusive)	Shared with	Number of species
Australia	1	Philippines	1
Philippines	13	Greater Sundas and Thai-Malay Peninsula	16
Greater Sundas and Thai-Malay Peninsula	14	Philippines, Indochinese Peninsula*	9
Indochinese Peninsula*	124	Greater Sundas and Thai-Malay Peninsula	23
Wide-ranging species	29		

*Includes species in adjacent southern China (e.g., Yunnan and Hainan).

POPULATION TRENDS OF LANDBIRDS IN EAST ASIA – THE CURRENT EVIDENCE

Ever since *Silent Spring* (Carlson, 1962) raised the alarm on bird declines globally, landbird population declines have been widely reported in Europe and North America (Terborgh, 1992; Vickery et al., 2014; Rosenberg et al., 2019). Long-term population trends for European species became available based on the large datasets collected by various large-scale bird monitoring and ringing schemes (Vorisek et al., 2008). In East Asia, the first worrying trends were detected in Japan, with declines found to be associated with forest-dependent and long-distance migrant species (Higuchi and Morishita, 1999; Amano and Yamaura, 2007), and further evidenced in Japan's national-level bird atlas (Japan Bird Research Association, 2021). Wells (2007) reported larger declines for landbirds that rely on tropical forests as wintering habitat in the Thai-Malay Peninsula and data from Thailand also suggest a decline of at least some species (e.g., tiger shrike *Lanius tigrinus*; Round, 2010).

In the past decade, drastic declines in the yellow-breasted bunting (**Figure 5**) have raised major conservation concerns (Kamp et al., 2015). This species used to be one of the most abundant Palearctic birds with a vast breeding distribution from Fennoscandia to eastern Russia and Japan (Dementiev and Gladkov, 1951–1954; McClure, 1974). However, since the 1990s, its global population has declined by almost 90% (Kamp et al., 2015), with national-level declines reported from Russia, Japan and Korea (Tamada et al., 2014, 2017; Choi et al., 2020a; Park et al., 2020; Heim et al., in press) and the species was uplisted to Critically Endangered in 2017 (BirdLife International, 2020).

A similar trend has been documented for the closely related rustic bunting *Emberiza rustica*, based on data from the breeding grounds in Russia (Yakovleva and Sukhov, 2017; Gerasimov and Lobkov, 2019), Fennoscandia and from stopover sites in China and Japan (Edenius et al., 2017). Buntings are typically widely distributed and thus data on their status and trends are available from multiple sites across their breeding range. Yet, for the majority of East Asian species with narrower distributions, little or no long-term monitoring data are available and it is nearly impossible to confidently elucidate population trends or conservation status (Yong et al., 2015).

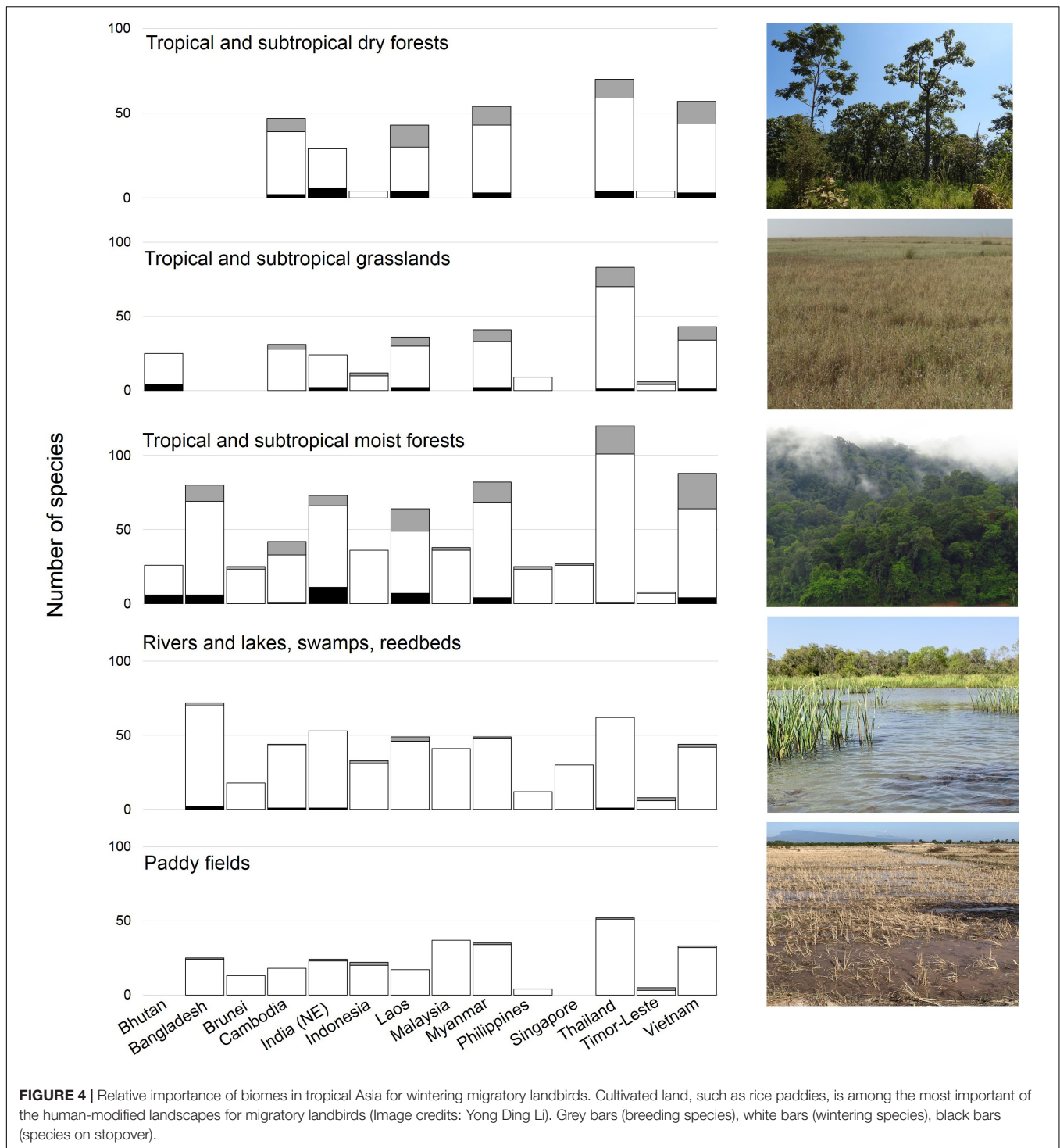
Across the region, evidence for the decline of migratory landbirds has been growing steadily based on studies at stopover sites and the breeding grounds (see **Supplementary Table 1**). Based on diverse data sources, six breeding and migrating bunting species, including the once abundant rustic and chestnut

buntings *Emberiza rutila*, were found to have declined in South Korea (Choi et al., 2020a). In Russia, significant declines have been detected for Pallas's *E. pallasi* (Heim, 2017) and chestnut bunting (Valchuk et al., 2017) on migration and at breeding sites (Ananin, 2011). These patterns are consistent with the declining trends of passerine landbirds reported at ringing stations in mainland China (Jiao et al., 2016; Xu et al., 2017) and at breeding sites surveyed in Japan and Taiwan (Tamada et al., 2014, 2017; Kitazawa et al., 2020; Japan Bird Research Association, 2021), including the threatened fairy pitta *Pitta nympha* (Lin and Pursner, 2020). Meanwhile, population trends of landbirds on their wintering grounds remain largely unknown, even though the available evidence suggests declines for species that winter in India (SoIB, 2020) and Australia (Tarburton, 2014; see also **Supplementary Table 1**).

While many long-distance Asian migrants including those wintering in the tropics have suffered larger declines (Amano and Yamaura, 2007; Bourski, 2009; Ananin, 2011), consistent with patterns observed in the Western Palearctic (Vickery et al., 2014), the trends are inconsistent, even among species that share apparently similar migration strategies. The yellow-browed warbler has declined at both its breeding and wintering grounds (Ananin, 2010, 2011; Xu et al., 2017; SoIB, 2020), while increases have been documented for the closely related dusky warbler *Phylloscopus fuscatu*s (Ananin, 2011; Gerasimov and Lobkov, 2019). There is an urgent need to understand overall population trends for migratory landbird species, drawing from monitoring work across the region. This will also help elucidate the specific threats and drivers of decline.

RANGE SHIFTS OF LANDBIRDS

Some observed changes in species population trends and densities of landbirds can be explained by shifts in breeding distributions and range limits. Many European and North American species show recent range shifts likely driven by changes in habitat availability accelerated by climate change (Virkkala and Lehikoinen, 2014; Whitaker, 2017). Similarly, in the EAF, northward and eastward shifts have been detected in the breeding distribution and range limits of several species across eastern Asia. Some Chinese breeding species (e.g., red-billed starling *Sturnus sericeus*, light-vented bulbul *Pycnonotus sinensis* and yellow-bellied tit *Parus venustulus*) were not recorded in the Korean Peninsula until 2000. All three have since expanded their distribution ranges northeast across the Yellow Sea and became



locally common breeding species in South Korea (Choi et al., 2011). The range of the yellow-bellied tit has expanded even further north and it has colonized the Russian Far East (Fetting et al., 2016; Redkin et al., 2020). The widespread Palearctic-breeding fieldfare *Turdus pilaris* has shown a recent eastward expansion across Siberia. At the end of the 20th century, fieldfares bred as far east as Yakutia, west of the Aldan River, with no

records east of the Verkhoyansky Mountains. Since 2009, the species has rapidly spread eastward, reaching Magadan in 2014 (Kondratyev, 2014), Kamchatka (Lobkov, 2015) and the Anadyr River by 2020, a range extension of more than 1,000 km.

There are other examples of range shifts at smaller spatial scales, as well as longitudinal shifts along the tundra-forest-tundra gradient, and in the northern taiga transition zones. Little



FIGURE 5 | Yellow-breasted bunting *Emberiza aureola* is the best example of an Asian landbird that has suffered steep declines in the recent decade (Kamp et al., 2015; Image credits: Michelle and Peter Wong).

bunting *Emberiza pusilla*, Arctic warbler *Phylloscopus borealis* and Common stonechat *Saxicola torquatus*, all characteristic boreal species, have shifted northwards and breed more regularly in the tundra and at more diverse locations than previously known (Andreev et al., 2015; Syroechkovskiy et al., 2019). On Sakhalin Island, black-browed reed warbler *Acrocephalus bistrigiceps* (Ktitorov and Zdorikov, unpublished data), and White's thrush *Zoothera aurea* (Ktitorov et al., 2019) have recently

colonized the northern parts of the island. In temperate and subtropical areas of China, several migratory cuckoo species have exhibited northward and eastward shifts (Sun et al., 2018).

Shifts in distributions and range limits of many species may be explained by changes in vegetation cover and associated habitat dynamics, often anthropogenically caused, or may arise due to the broader effects of warming driven by climate change (Virkkala and Lehikoinen, 2014; **Box 1**). According to modeled climate change scenarios, the distributions of most East Asian species are expected to be affected, including many that are already threatened (Hu et al., 2020). These distribution shifts need to be considered when planning conservation actions for migratory species. While there is a risk that observed distribution shifts may arise from geographical biases in sampling, they need to be monitored and carefully documented, as they may manifest in precipitous local declines, as seen in the near-endemic Japanese breeding subspecies of brown shrike (Kitazawa et al., 2020).

THREATS TO MIGRATORY LANDBIRDS

The threats faced by migratory landbirds in the EAF are poorly understood compared with those faced by waterbirds, which have been extensively studied in the past decade (Studds et al., 2017; Gallo-Cajiao et al., 2020). Given that most landbirds in the region (**Figure 4**) are somewhat dependent on forests as stopover and non-breeding habitat, forest loss and degradation are predicted to be major threats. Intensive land management, especially intensive agriculture, often with heavy pesticide use, presumably also affects species stopping over or wintering in rice paddies or other cultivated land. It remains unclear how complex

BOX 1 | Land cover change in eastern Siberia and the Russian Far East: impacts on breeding birds.

The varied and complex ecosystems of eastern Siberia and the Russian Far East provide breeding grounds for most long-distance migratory landbirds in the EAF (**Figure 3**). Much of eastern Russia has a sparse human population and thus appears little disturbed, based on the limited extent of built environments, population density and infrastructure (Venter et al., 2016). Not surprisingly, this understudied, but ecologically complex region is frequently perceived as being covered by vast tracts of boreal forests. However, recent global assessments of intact forested landscapes reveal that the extent of old-growth forest cover is less than expected and is declining even in the most remote areas of eastern Russia (Potapov et al., 2008, Potapov et al., 2017; Global Forest Watch, 2014).

The main drivers of deforestation and land use change in eastern Russia include legal and illegal logging, both which are unsustainable (Vandergert and Newell, 2003), and fire. While most forest fires (65%) are anthropogenic, their prevalence has increased as a result of the earlier spring and summer thaw, presumably exacerbated by climate change (Achard et al., 2008). Logging and forest fires mostly affect the more developed, southern regions of the Russian Far East (Kurdykov and Volkovskaya-Kurdyukova, 2016; Heim et al., 2019), but forest fire hotspots are becoming increasingly prevalent further north, particularly in central Yakutia and have even penetrated the forest-tundra zone of southern Chukotka (Achard et al., 2006).

Land cover changes associated with shifting agricultural policies have attracted less attention, but have a discernible effect in shaping Siberian ecosystems. The collapse of the Soviet Union in 1991 triggered the abandonment of vast areas of cropland and pasture, especially in southern Siberia and in the Far East. Since 2016, some areas have reverted to agriculture (Prishchepov et al., 2020), but these remain negligible in eastern Russia, mostly concentrated along the Chinese border (Teluguntla et al., 2015; Global Cropland Database). This synergy of anthropogenic drivers and natural ecological processes is re-shaping landscapes in eastern Russia and has resulted in the replacement of the mosaic of old-growth forests and cultivated land by more uniform early- and mid-successional shrub or forest habitat (Heim et al., 2019), although some areas of old-growth forest show signs of recovery (Potapov et al., 2008, Potapov et al., 2017).

In the Arctic and sub-Arctic regions of eastern Russia, changes in the vegetation cover, particularly in the tundra and taiga-tundra ecotone have received little attention from ecologists. One of the most visible features of the Arctic landscape associated with climate change is 'shrubification,' characterized by an increase in cover, height and thickness of shrub vegetation (Tape et al., 2006; Forbes et al., 2010). In the eastern Russian tundra, larch *Larix* spp. and willow *Salix* spp. are growing taller, leading to gradual transformation of the taiga-tundra transition zone into true taiga and the encroachment of shrubland into tundra (Forbes et al., 2010; Frost and Epstein, 2014; Heim et al., 2021). Remote sensing analyses show hotspots of tundra greening in many areas of the Russian Arctic (Frost and Epstein, 2014).

The large-scale consequences of land cover change for migratory landbirds have not been studied, partly due to the lack of a nation-wide bird monitoring scheme in Russia. However, these changes are presumably complex and multi-directional, affecting species dependent on old-growth forests negatively, but favoring species that exploit post-fire successional vegetation and forest edges (Osipov and Biserov, 2017). Based on the observed directionality of vegetation change, it is possible to make some broad predictions: (1) forest edge and shrub-dwelling species (i.e., most boreal-breeding migratory passerines) should benefit from increased habitat availability, while (2) old-growth forest species (e.g., large diurnal and nocturnal raptors) and (3) open habitat species (e.g., various bunting species) may suffer from a reduction of habitat.

land use changes and land management regimes will impact bird populations across Asia under different climate change scenarios. Meanwhile, the intense harvesting of wildlife for use as food or pets has been directly implicated in the decline of several migratory landbirds in the EAF, the best known being the yellow-breasted bunting *Emberiza aureola* (Chan, 2004).

Habitat Loss and Degradation

Forest loss and degradation affect many migratory landbirds throughout their distributions in the EAF, particularly at the tropical wintering grounds (Amano and Yamaura, 2007; Yong et al., 2015). Asian tropical lowlands have suffered the highest rates of forest loss globally (Corlett, 2014; Stibig et al., 2014; Namkhan et al., 2021). Extensive deforestation throughout the lowlands of the Greater Sundas is predicted to affect both globally threatened and more common species that winter predominantly in lowland forest (Wells, 2007; Yong and Liu, 2015). In one of few assessments of wintering forest landbird assemblages, Wells (2007) observed that the densities of Siberian blue robin *Larvivora cyane* were substantially lower in Malaysian hill-slope forests and in disturbed or agricultural habitats compared to old-growth lowland rainforests, suggesting that this common wintering species is sensitive to lowland deforestation.

Montane forest cover in Southeast Asia has been relatively less affected compared to the lowlands (Soh et al., 2019), and therefore species wintering in montane forests have been presumed to face lower risk. Yet, montane forests are also under increasing pressure (Peh et al., 2011; Zeng et al., 2018). In northeast India and Bangladesh, deforestation on mountains is driven by illegal logging and clearing for tea plantations and other fast-growing plantation species, exacerbated by ongoing shifting cultivation (Rasul, 2007; Lele and Joshi, 2009); in upland parts of Southeast Asia, expansion of vegetable farms is known to drive deforestation (Poudel et al., 1998). In mainland Southeast Asia and southern China, shifting cultivation has affected large tracts of montane forest landscapes (Fox et al., 2014). It remains unclear how such extensive land use change (perhaps in synergy with climate-change shifts) may impact species using tropical montane habitats. Anecdotal evidence suggests that montane species, including wintering landbirds, may be better adapted to exploit habitat mosaics and successional growth (e.g., Diamond and Lovejoy, 1985) and are therefore less sensitive to habitat degradation compared to lowland-dependent species.

The impact of wetland conversion on migratory landbird communities is another major knowledge gap. Until recently, only anecdotal observations were available, along with a few studies from coastal marshes in China and Japan (Ma et al., 2007). Across the floodplains of the major rivers in southern China, Southeast Asia, Bangladesh and northeast India, most climax wetland vegetation (e.g., seasonally inundated grasslands and marshland on floodplains) has been heavily modified and largely replaced by extensive areas of rice paddies, tea gardens and other agriculture (Round, 2008; Prokop, 2018). Rice paddies can support a subset of the migratory bird assemblages associated with freshwater wetlands (Round, 2008; Wong et al., 2009; Fujioka et al., 2010; Wood et al., 2010). For instance, on the Chao Phraya floodplains in central Thailand, the rice

harvest period coincides with the arrival of migratory species. The leftover stubble is used by raptors, insectivores, such as bluethroat *Luscinia svecica* and eastern yellow wagtail *Motacilla tschutschensis*, and granivores, such as yellow-breasted bunting (McClure, 1974; Round, 2008). Similar examples have been documented in Indochina, Malaysia and southern China (Wong et al., 2009; Azman et al., 2019). In Timor in Wallacea, heavily grazed and modified floodplains support a few migratory species, such as eastern yellow wagtail (Trainor et al., 2007).

Widespread land-use change, in particular agricultural intensification with the associated loss of fallow and increased pesticide use, may have contributed to the declines of wintering buntings in Southeast Asia, and species that feed on large insects, such as shrikes and drongos (Round, 2008; Kitazawa et al., 2019). Meanwhile, changing water management and cropping regimes in rice paddies may affect wintering landbird assemblages to the detriment of species with specialised ecological needs. Across Southeast Asia, formerly rain-fed, single-crop rice (including floating rice) has now been extensively replaced by multi-cropped rice that demands intensive irrigation (Round, 2008). An associated reduction in fallow duration and the extent of fallow fields and paddy stubble may reduce food resources and habitat available to wintering birds. In the floodplain wetlands of Candaba in Luzon (the Philippines), which was the only known regular wintering site for the Endangered streaked reed-warbler *Acrocephalus sorghophilus*, the original natural wetlands have been converted to rice paddies, while intensive land management practices limit natural succession, reducing possibly essential habitat diversity (Round and Allen, 2010).

Hunting as a Threat to Migratory Landbirds

The hunting or trapping of wild birds in East and Southeast Asia is driven by diverse socioeconomic forces, with considerable variation across the region. Bird trapping to supply the pet trade is undoubtedly the leading driver of take in Southeast Asia and parts of China (Dai and Hu, 2017; Harris et al., 2017). It has been implicated in the fast deteriorating status of robins, thrushes, white-eyes, bulbuls, starlings and many other species (Eaton et al., 2015). Bird trapping has been most severe in Indonesia, where the practice of keeping pet birds is a well-established local tradition (Jepson and Ladle, 2005; Nijman, 2010) and it is estimated that 66–84 million individuals of songbirds are kept in Java alone (Marshall et al., 2020). Although surveys have revealed migratory songbirds, such as Siberian thrush *Geokichla sibirica* and Siberian rubythroat, in the Southeast Asian pet trade (Yong et al., 2015; Chng and Eaton, 2016; Chng et al., 2018), the degree to which trapping pressures have impacted their populations remains unclear.

Even less is known about the extent to which migratory raptor populations have been impacted by trapping in northern Asia. There is robust evidence that illegal capture in Mongolia, China and Russia to supply falconry and taxidermy markets outside the region has decimated saker *Falco cherrug* and other migratory falcon populations (Gombobaatar et al., 2004; Lobkov et al., 2011; Stretesky et al., 2018). In Russia, several thousand falcons were illegally caught for export in 2012–2016 and trade in falcons increased between 2006 and 2017 (Lobkov et al., 2011; Wyatt,

2011; Krever and Ivannikova, 2020), despite law enforcement efforts. In Southeast Asia, raptors including various migratory species are commonly traded in pet shops or on social media platforms (Iqbal, 2016; Paridi and Noske, 2017).

Hunting of wildlife for subsistence and the trade in wild meat and traditional medicines directly threaten a wide range of vertebrate species in much of Southeast Asia, the Philippines and parts of southern China (Nijman, 2010; Lee et al., 2014; Harrison et al., 2016). Unsustainably high levels of exploitation to supply local, domestic and international demand for wild meat have decimated vertebrate fauna and hunting is now recognized to be a more immediate threat to Southeast Asian vertebrate fauna than deforestation and logging (Tilker et al., 2019). Recent work is beginning to unravel the scale and impact of hunting on wild bird populations in Asia (Kamp et al., 2015; Gallo-Cajiao et al., 2020), particularly for small migratory songbirds (Box 2).

In some parts of Southeast Asia, the number of passerines taken to supply domestic demand for wild meat is potentially unsustainably high (Evans et al., 2000; Davenport and Heatwole, 2013), but surprisingly little monitoring exists. Wild meat

markets selling high volumes of birds have been documented in Myanmar, Laos, Indonesia and northeast India (Brickle et al., 2008; Bhupathy et al., 2013). Studies of traditional hunting activities by local people at migration hotspots in China and the Philippines have also warned of the high number and diversity of species taken (McClure, 1974; Alonzo-Pasicolan, 1992; Aquino, 1997; Wang et al., 2000). Commercially produced mistnets, which are now widely available, and improvised fishing nets are extensively used in paddy fields and aquaculture areas for both bird hunting and crop protection (Evans et al., 2000; Gallo-Cajiao et al., 2020). Nets have also been used to reduce bird-strike at airfields (Townshend, 2016b).

In many parts of Southeast and East Asia, the deliberate release of captive wild animals for religious purposes or 'merit release' is well established in Buddhist tradition (McClure, 1974; Severinghaus and Chi, 1999; Chan, 2004). Gilbert et al. (2012) reported 57 species from bird sellers from Phnom Penh, Cambodia alone, with an annual turnover reaching 700,000 individuals, including large numbers of migratory passerines, such as swallows. In Thailand, Cambodia, and Myanmar, countries where religious releases are ubiquitous, the cumulative

BOX 2 | The role of trade in the decline of migratory passerines.

The global demand for wildlife for human consumption and the pet trade affects much of the world's vertebrate biodiversity (Scheffers et al., 2019) and has driven the unsustainable take of many birds, bringing several species in Asia close to extinction (Sodhi et al., 2004; Eaton et al., 2015; McEvoy et al., 2019). Given that long-distance migratory passerines tend to build up significant fat stores in preparation for migration (Bairlein, 2002), it is not surprising that such species are targeted as food by humans. In parts of China and in certain Southeast Asian countries, the illegal capture and trade of small passerines for food occurs at a very large scale (Kamp et al., 2015). For instance, an estimated 120,000 songbirds were confiscated in Dongli, Tianjin in September 2018 alone (Anon, 2018). In another incident, poachers made a profit of over 140,000 USD from 510,000 songbirds trapped illegally within 40 days (Wen, 2018). In many instances, birds are kept in flat cages and are fed chemical agents to be fattened (Li, 2016). Barn swallows are trapped on an industrial scale in northern Laos, exceeding an estimated 100,000 individuals per year (Evans et al., 2000; Figure 6A). Similarly, thousands of eyebrowed thrushes *Turdus obscurus* are harvested in parts of Sumatra, Indonesia (Iqbal et al., 2014).

Until the 2000s, the species most traded for food in China was believed to be the yellow-breasted bunting. Since this species has declined catastrophically (Kamp et al., 2015), poachers appear to have shifted their attention to other species (Heim et al., in press). For example, 33,000 chestnut buntings and 2,000 chestnut-eared buntings *Emberiza fucata* were confiscated in a single raid in November 2019 in Pingle, Guangxi. Other species often found in 'fattening centers' include yellow-browed *E. chrysophrys* and black-faced bunting *E. spodocephala* and common rosefinch *Carpodacus erythrinus* (Let Wild Birds Fly, 2016).

Meanwhile, the pet trade also drives the harvest of large numbers of migratory passerines and raptors. Siberian rubythroats, long-tailed shrikes *Lanius schach*, and black-naped orioles *Oriolus chinensis* are among the more commonly traded species. Surveillance work has revealed a diversity of passerines, including thrushes, starlings, flycatchers and raptors being trapped in the wild and sold in pet bird shops from Vietnam to Indonesia (Iqbal, 2016; Chng et al., 2018; Figure 6B).

Amidst increasing efforts to tackle bird hunting, better monitoring of the vast trade in migratory birds across Asian countries is urgently required. There is a need, (1) to analyze whether the levels of illegal (and legal) hunting are sustainable and, (2) to assess if ongoing hunting could lead to further population declines, as already shown for some migratory taxa, such as waders (Gallo-Cajiao et al., 2020).



FIGURE 6 | Migratory landbirds are heavily hunted in Southeast Asia and parts of China for the pet trade, and for food. **(A)** Grey-faced buzzard *Butastur indicus* for sale at a pet shop, **(B)** various swallow species are caught in large numbers for human consumption in northern Laos (Image credits: Yong Ding Li).

impact of merit release on migratory landbird populations is likely to exceed many millions of swallows, wagtails, reed warblers and other small passerines. While most individuals will be released back to the wild, release often occurs in unsuitable habitat and high mortalities during transport and capture can be expected (Clewley et al., 2018).

Drawing from diverse sources, we found evidence of trapping or trade for at least 180 of the over 380 migratory landbird species, representing nearly half (47%) of all species in the EAF (see **Supplementary Table 2**). The actual number of species involved is likely to be much higher, given that market and community surveys typically fail to identify many individuals to species, especially leaf-warblers, white-eyes and other difficult groups (Rentschlar et al., 2018). In several families (cuckoo-shrikes, pigeons and doves, drongos, starlings and buntings) almost all migratory species are affected by some level of trapping or trade in the region, whereas other families (swifts and accentors) seem to be unaffected.

KNOWLEDGE GAPS

Various knowledge gaps hinder our present understanding of many aspects of landbird migration in the EAF. The basic ecology of many landbirds, their migratory routes and conservation status, as well as the key threats and causes of decline still require study (re-worded due to poor structure). The increasing availability of novel tools to track migration is rapidly improving the situation. Unlike in Europe and North America, the lack of systematic, large-scale monitoring schemes with coordinated data collection across most parts of Asia means that it is difficult to determine broad population trends for migratory species. There is, however, a potential for citizen science to fill such gaps in the coming decades (Tulloch et al., 2013a,b), and there are already good precedents from the region, especially in Japan and Taiwan (Lin and Pursner, 2020; Japan Bird Research Association, 2021).

Gaps in Knowledge of Migratory Routes and Connectivity

Data on migratory routes are now available for some raptors and larger songbirds (**Figure 2** and **Table 2**). Apart from the studies of the eastern populations of some wide-ranging species, conducted by Japanese and Korean researchers, surprisingly few small Siberian passerines have been tracked (Heim et al., 2020). Large knowledge gaps remain for owls, nightjars, rollers, doves, and many passerines, including most thrushes, flycatchers and leaf-warblers. Tracking the migratory routes of particular species and populations has been instrumental in improving our understanding the migration ecology and survival of landbirds. There are ample opportunities for continued work to identify routes under threat, geographical connectivity, habitat use and key stopover areas, all of which have direct implications for conservation (Runge et al., 2014; McKinnon and Love, 2018). Indeed, several projects have been established to track the migration of some species (Townshend, 2019) aided by novel field techniques, such as the use of sound (Senda et al., 2018) and blue

light (Zhao et al., 2020) to attract birds, which have increased the number of birds ringed during migration.

Light-level geolocators (Aoki et al., 2020; Heim et al., 2020), collaborative tracking network systems, such as the Motus automated radio telemetry arrays (Taylor et al., 2017) and GPS-based tracking systems may all offer cost-effective means to fill knowledge gaps on the migration and distributions of landbird migrants in the EAF. These methods may be complemented by molecular approaches (Seki and Ogura, 2007; Aoki et al., 2020) and intrinsic markers, such as stable isotope signatures in tissues (Choi and Nam, 2011; Choi et al., 2020b). For instance, genetic markers have been used to infer the breeding areas of migrating Ryukyu robins *Larvivora komadori* (Seki and Ogura, 2007). Stable isotopes from feathers have been used to link breeding and non-breeding areas (Choi and Nam, 2011; De Jong et al., 2019) and to determine migration patterns (e.g., leap-frog versus chain migration; Weng et al., 2014; Choi et al., 2020b). Stable isotope analysis can also provide missing data on the diets and molting patterns of migratory birds during stopover. Despite this, some challenges remain. For instance, no calibration algorithm between precipitation and feather isotope values is available for Asian landbirds (Choi et al., 2020b). Broad longitudinal similarities of hydrogen isotope ratios across Siberia make it difficult to pinpoint precise breeding areas for some species (Choi and Nam, 2011; De Jong et al., 2019) and stable isotope ratios may also be influenced by feeding habitats and environmental pollutants (Sun et al., 2012).

Gaps in Knowledge of Species Ecology and Natural History

Compared to other flyways, the ecology of migratory landbirds in non-breeding areas in the Asian tropics remains poorly understood (Newton, 2010; McKinnon and Love, 2018). For instance, the rufous-headed robin *Larvivora ruficeps* is relatively well-documented at its breeding ground in central China (Zhao et al., 2017), but its wintering distribution in the tropics was entirely putative (Medway and Wells, 1976; Nisbet, 1976) until recent observations (Lim et al., 2020). In another example, the streaked reed warbler is on the verge of extinction, yet its breeding distribution remains largely undetermined (Round and Allen, 2010; Allen, 2020). Similarly, until recently, movements of most migratory raptors in Southeast Asia were known only through direct observations at bottleneck sites in northern Vietnam, the Thai-Malay Peninsula, the Greater Sundas and the Philippines (Tordoff, 2002; Nijman et al., 2006; Germi et al., 2009). Tracking studies (Higuchi et al., 2005; Shiu et al., 2006) have substantially improved understanding of the movements and ecology of some species, such as the Oriental honey buzzard. The wintering ecology of most raptors, however, remains scarcely studied (but see Syartinilia et al., 2015).

Furthermore, there are significant gaps in knowledge on how habitat conversion, loss and degradation impact assemblages of migratory landbirds in forests, cultivated areas and freshwater wetlands, especially at their wintering grounds. A better understanding of the ecological traits of a species, such as age at first breeding, clutch size, survival and life history, migration

patterns, population size and trends, and the threats it is facing can all inform conservation actions that may reduce the risk of extinction (Soulé and Orians, 2001). Generation length, migratory habits, habitat preference and diet have all been shown to influence the sensitivity of bird species to habitat loss (Newbold et al., 2013). Studying spatial and temporal changes in life history can help to identify specific threats (Bibby, 1992). Stage-based life histories could provide insight into the likelihood of decline toward extinction for species facing anthropogenic threats (Van Allen et al., 2012).

Obtaining such information is not only costly and labour intensive, but also presents major challenges, particularly for rare and cryptic species (Soulé and Orians, 2001). Citizen science data now occupies a more prominent place in modern ornithology and can help fill many knowledge gaps (Tulloch et al., 2013b; Hu et al., 2020). Besides popular platforms such as ebird.org (1.1 million bird checklists for India, 84,000 for Thailand, 62,000 for China and 23,000 for Russia by December 2020) and iNaturalist.org (81,000 observations for India, 14,000 for Thailand, 18,000 for China and 230,000 for Russia by December 2020), species-specific or threat-based citizen science projects are also becoming more ubiquitous. A bird-window collision study in South Korea received over 16,000 case records in two years, as of December 2020; see Kim, 2018) and citizen science datasets are increasingly informing studies in East Asia (Heim et al., 2020; Tsai et al., 2021). Over time, more structured and focused citizen science effort can complement and enhance studies by professional researchers (Tulloch et al., 2013a).

Gaps in Understanding the Ecosystem Roles of Migratory Landbirds

Birds are among the most abundant and widely distributed group of terrestrial vertebrates in Asian ecosystems. Birds provide key ecosystem services, including the maintenance of food webs, and ecosystems functioning as foragers, predators, prey, seed dispersers, and pollinators (Şekercioğlu et al., 2004; Whelan et al., 2008). Specifically, migratory bird species play important roles in linking ecosystem processes and fluxes over great distances and times (Whelan et al., 2008) by supporting, regulating, and transferring ecosystem processes and the associated benefits along their migratory routes (Bauer and Hoye, 2014; López-Hoffman et al., 2017). Nutrient cycling and flow, and energy transfer across ecosystems and biomes at large spatial scales are key ecological contributions of migratory species (López-Hoffman et al., 2017), yet the specific roles played by migratory landbirds are largely unstudied. Meanwhile, common species play prominent roles in natural and anthropogenic ecosystems by contributing provisioning, regulating, supporting and cultural ecosystem services (Whelan et al., 2008) and by driving biotic interactions (Gaston, 2010). Inevitably, the decline of common migratory landbirds can thus be expected to drive a disproportionate loss in ecological services, with consequences on ecosystem functioning and processes, but the mechanisms of how these services may be impacted remain unstudied.

While there is limited evidence of disease transmission by migratory birds (McClure, 1974; Kim et al., 2012a; Moriguchi

et al., 2016), their role as vectors and transporters of recently identified pathogens is largely unclear (Choi et al., 2015). More research on invasive species, known pathogens and other microorganisms carried by migratory landbirds will increase our knowledge of emerging diseases and protect animal and human health (World Health Organisation, 2017).

The EAF connects at least 20 countries, each with its unique culture and traditions. Migratory birds link these countries by providing cultural services, as they inspire art, local customs and recreation (Higuchi, 2005; Whelan et al., 2008; López-Hoffman et al., 2017). Aggregations of migratory birds often generate direct economic opportunities through ecotourism activities, such as birdwatching, which is rapidly growing in mainland China (Ma et al., 2013) and parts of Southeast Asia and Russia. Clearly, improved knowledge of the ecosystem roles and services provided by migratory landbirds has the potential to increase public awareness, and thus provide a stronger rationale to support conservation efforts targeted at migratory species.

CONCLUSION

The study of migratory landbirds in the EAF has advanced greatly since the 1950–1960s (Dementiev and Gladkov, 1951–1954; McClure, 1974). Novel methods and tools in tracking technology (Higuchi, 2005; Yamaura et al., 2017; McKinnon and Love, 2018; Heim et al., 2020), molecular/stable isotope analyses, (Choi et al., 2020b), and the advent of citizen science platforms offer exciting new sources of data to better infer the migration patterns and ecology of East Asian landbirds (Supp et al., 2015; Heim et al., 2020). Together, these complement other, more traditional approaches in the bird migration ‘toolbox’, such as ringing (Fiedler, 2009). These novel approaches have accelerated efforts to study landbird movements at the EAF continental scale and yielded new insights on the ecology of migrants. The newest tracking technologies, such as geolocators and ICARUS (Curry, 2018) enable the tracking of ever smaller animals to elucidate previously unknown migratory routes and patterns, further demonstrating the connectivity of bird populations, especially for widely distributed species and those with disjunct subpopulations. When contextualized against environmental datasets and ecological theory, the tracking of migratory species can play a major role in informing conservation strategies.

Despite recent advances, large knowledge gaps remain with regard to the migration ecology of EAF landbirds. We still lack an adequate understanding of the life histories and distribution of many landbird species, and their population trends in much of the region. There is an urgency to better understand the ecology of migratory species in tropical Asia, where species are most impacted by hunting and other forms of exploitation, and by habitat loss and land use conversion arising from human population pressure. This is particularly so as these drivers of decline are likely to be exacerbated by climate change, as observed in other migratory flyways (Sanderson et al., 2006; Vickery et al., 2014).

Specifically, there is a need to better understand, (1) the life histories and community ecology of migratory landbirds

across different landscapes at non-breeding grounds, especially in tropical forests and cultivated landscapes, (2) the migration routes and connectivity of different populations, (3) the threats affecting species during their annual cycle, (4) the ecological roles played by migratory landbirds, such as the long-distance dispersal of plants and microorganisms, and (5) the conservation importance of sites used during the non-breeding period and migration bottlenecks.

Last, there is a need to improve monitoring frameworks to assess the population trends of migratory landbirds at broad spatial scales. Monitoring programs are crucial for identifying declines, population shifts and specific threats that underpin conservation actions. Currently, robust country-wide monitoring frameworks are established in South Korea and Japan (e.g., Choi et al., 2020a; Japan Bird Research Association, 2021), but are lacking elsewhere in the countries of the EAF. Going forward, there is much potential for strengthened regional collaboration between countries in the EAF to establish standardized monitoring programs for migratory landbirds.

AUTHOR CONTRIBUTIONS

DY, JS, SC, and WH conceptualized the manuscript. DY, PR, DA, SC, CT, and WH collected and analyzed the data. All authors participated in the writing and editing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.613172/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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