

Review

The conservation of Afro-Palaeartic migrants: What we are learning and what we need to know?

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The global long-term decline of migrant birds represents an important and challenging issue for conservation scientists and practitioners. This review draws together recent research directed at the Afro-Palaeartic flyway and considers its implications for conservation. The greatest advances in knowledge have been made in the field of tracking. These studies reveal many species to be highly dispersed in the non-breeding season, suggesting that site-level conservation at a small number of locations will almost certainly be of limited value for most species. Instead, widespread but 'shallow' land-sharing solutions are likely to be more effective but, because any local changes in Africa will affect many European populations, any impact will be extremely difficult to detect through monitoring in the breeding grounds. Targeted action to boost productivity in Europe may help to halt declines of some species but reversing declines for many species is also likely to require these 'shallow' land-sharing approaches in non-breeding areas. The retention or planting of native trees in the humid and arid zones within Africa may be a generic conservation tool, especially if planting is concentrated on favoured tree species. Overall, and despite a growing knowledge, we remain largely unable to progress beyond general flyway-level actions, such as maintaining suitable habitat across an increasingly anthropogenic landscape for generalists, targeted site-based conservation for specialists and at stop-over sites, protection of species from hunting, and individual species-level solutions. We remain unable to assess the cost-effectiveness of more specific conservation

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action, mainly because of uncertainty around how migrant populations are affected by conditions during passage and on the non-breeding grounds, as well as around the efficacy of implementation of actions, particularly in non-breeding areas. For advances in knowledge to develop and implement effective conservation, scientific approaches need to be better integrated with each other and implemented across the full annual cycle. However, we urge the immediate use of available scientific knowledge rather than waiting for a complete understanding, and that any action is combined with species monitoring and adaptive management across the flyway.

Keywords: connectivity, dispersal, East Atlantic flyway, tree establishment, trial solutions.

Migrant birds have been in decline in flyways across the globe for decades (Robbins *et al.* 1989, Berthold *et al.* 1998, Sanderson *et al.* 2006, Studds *et al.* 2017, Rosenberg *et al.* 2019). But their complex annual life cycles, with long migration routes and a dependence on different sites at different times of the year, makes the diagnosis of their declines and subsequent conservation action particularly challenging. Developing and implementing cost-effective solutions to arrest, and ultimately reverse, population declines of any species usually requires knowing whether insufficient breeding success or survival is responsible, and their environmental causes. Intensive studies of single species, or single sites, have produced such information for only a small number of migrant bird species, particularly waders and raptors, but very few of the small migrant passerines (but see, for example, Marra *et al.* 1998, 2015, Kamp *et al.* 2015), particularly within the Afro-Palaeartic flyway (Vickery & Adams 2020).

In an earlier synthesis of factors driving the declines of Afro-Palaeartic migrants, Vickery *et al.* (2014) concluded that, although our knowledge of declining species is generally better in the breeding than the non-breeding season, significant gaps exist throughout the annual cycle for many species. On the breeding grounds, degradation of breeding habitats emerged as a key factor, particularly within agricultural and woodland or forest habitats. In the non-breeding areas, the interacting factors of anthropogenic habitat degradation and changing climatic conditions, particularly drought in the Sahel zone, appeared to be the most important factors. Four priority research areas were identified to address the declines: (1) use of new and emerging tracking technologies; (2) detailed field studies of migrant birds in sub-Saharan Africa; (3) use of

survey and demographic data from the European breeding grounds; and (4) use of remote sensing earth observation data of land cover change in sub-Saharan west Africa in relation to migrant bird populations.

In the 8 years since that review, populations of Afro-Palaeartic migrants have continued to decline. There have been advances in all four areas and yet that knowledge has not contributed to the development of new policies to address declines. In this paper, we assess knowledge acquired since 2014 in the light of the needs of conservation policy and action for the Afro-Palaeartic flyway. First, we provide up-to-date population trend data for Afro-Palaeartic migrant birds derived from Europe-wide survey and census data. Second, we assess progress in each of the four key areas identified by Vickery *et al.* (2014) and how this knowledge informs conservation. Finally, we derive recommendations for future conservation science, policy and practice for migrant birds in the Afro-Palaeartic flyway.

We searched Web of Science and Google Scholar for papers matching key search terms in either 'Topic' (title, abstract, author key words and Keywords Plus) or 'All Fields', with a publication date of 2014 onwards. Different search terms were used for different sections of our review (see Appendix S1 for details), but they generally included 'Afro-Pal(a)earctic' OR individual species names (common name OR scientific name) AND other broad terms, e.g. 'Africa', 'migration', 'land cover', 'tracking', 'demography', OR more specific terms, e.g. individual tracking methods or demographic parameters. Returned papers were assessed for relevance based on their abstracts, and reference lists of included papers were checked to ensure no relevant literature had been missed by the online searches.

POPULATION TRENDS OF AFRO-PALAEARCTIC MIGRANT BIRDS AND POTENTIAL DRIVERS OF THOSE TRENDS

We define Afro-Palaeartic migrants as species in which at least part of the population moves between breeding areas in the Palaeartic region and non-breeding grounds in sub-Saharan Africa each year (as defined in Vickery *et al.* 2014 and following the classification of BirdLife International 2004). Breeding population data are available for a subset of 62 species of long-distance migrants in Europe (Brlík *et al.* 2021: <https://pecbms.info/>). The aggregate population trajectory of this group in Europe, derived from the Pan-European Common Bird Monitoring Scheme (PECBMS: Brlík *et al.* 2021), was significantly negative between 1980 and 2017 (Fig. 1a: long-term change $-26.7 \pm 5.2\%$ standard error (se), $P < 0.01$), whereas the trend for residents and short-distance migrants combined was stable (Fig. 1a: long-term change $-3.0 \pm 1.9\%$ se, not significant). These trends are significantly different from each other (trend difference -0.0071 ± 0.0013 se, $P < 0.05$). Population trends of long-distance migrants that predominantly winter in arid northern Sahelian and Sudan savannah zones (Fig. 2) show a significantly different pattern from those that winter in the humid, more tropical southern areas (Figs 1b and 2: trend difference -0.008 ± 0.004 se, $P < 0.05$). Birds wintering in the arid zone fell in abundance between 1980 and 2017 (long-term change $-39.5 \pm 12.1\%$ se, $P < 0.01$), especially early in the time series, and their populations are now much depleted when compared with the baseline of 1980. Over the same period, birds wintering in the humid tropics of West and Central Africa and wet-season savannahs of southern Africa have also fallen in abundance overall (change $-15.7 \pm 4.1\%$, $P < 0.01$), but the pattern appears different with the declines starting later. Overall, these analyses suggest a continuing long-term downward trend in the abundance of long-distance migrant birds in Europe compared with other bird groups. They also suggest that, although both the arid-zone wintering and humid and southern-zone wintering species have declined, that trend has flattened for arid-zone species.

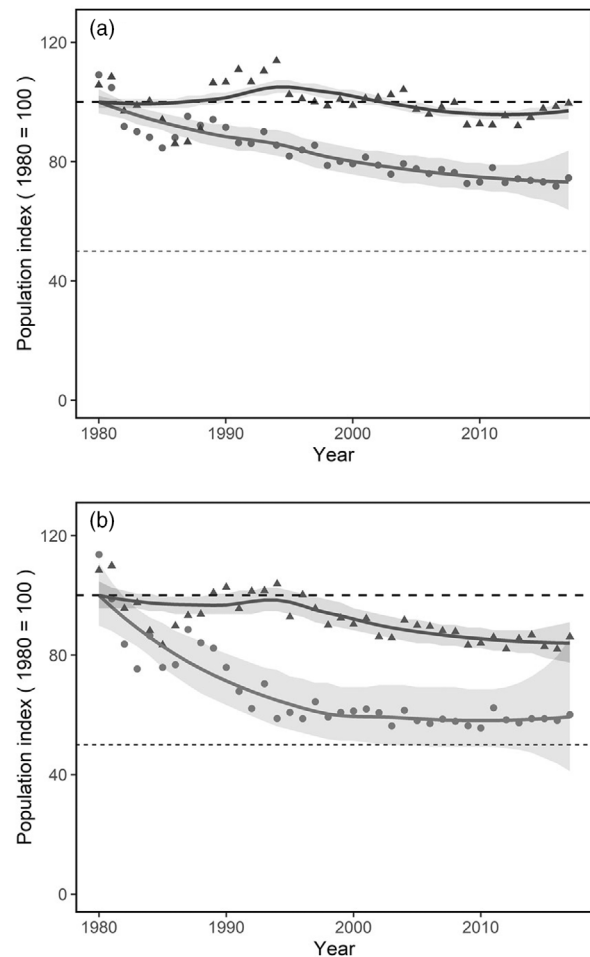


Figure 1. Aggregate multi-species indices for widespread and common European (a) long-distance migrants (62 species: circles) and short-distance migrants and resident breeding birds (108 species: triangles), and (b) long-distance migrants spending the non-breeding season predominantly in the arid zone (22 species: circles) and humid and southern zones (29 species: triangles) of Africa. Horizontal dashed lines mark index values of 100 and 50. Trend data from 1980 to 2017 come from 28 countries covered by the Pan-European Common Bird Monitoring Scheme (Brlík *et al.* 2021: <https://pecbms.info/>). Statistically smoothed indices are derived using the Multi-Species Indices Tool (MSI-tool: Soldaat *et al.* 2017) and fixed to a value of 100 in 1980 with grey-shaded 95% confidence limits. We also used the MSI-tool to test for significant differences in trend slopes and statistical change points in the slopes based on Monte Carlo procedures (Soldaat *et al.* 2017). The predominant non-breeding zone of long-distance migrants in Africa is classified broadly as either 'arid' or 'humid & southern' following the studies of Hewson and Noble (2009), Thaxter *et al.* (2010) and Ockendon *et al.* (2012). For full details see Table S2.

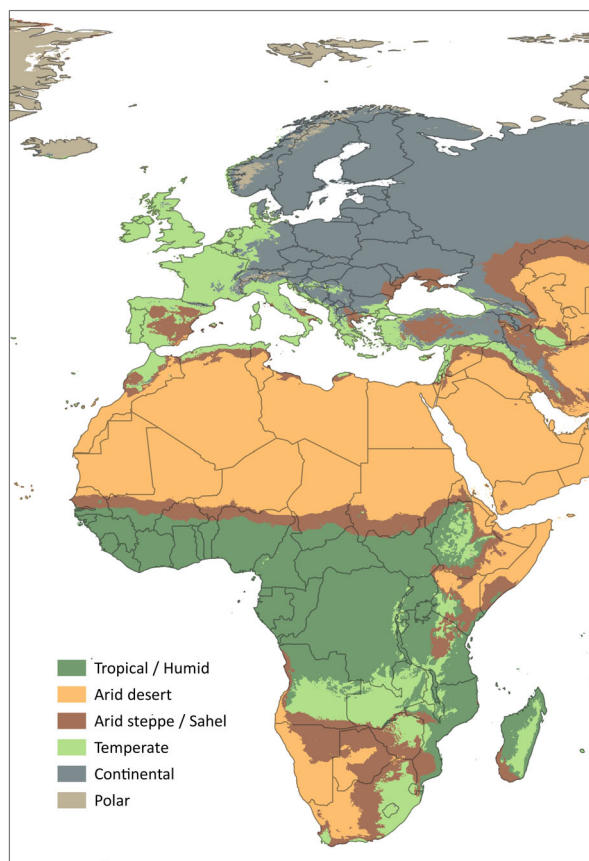


Figure 2. Climate zones of Africa and the western Palearctic: Köppen–Geiger climate classifications for the present day (1980–2016) are from Beck *et al.* (2018). First-level classifications are shown except for the ‘arid’ category, which has been subdivided using level 2 categories to make the distinction between desert climate and the Sahel, which has a steppe climate.

Vickery *et al.* (2014) reported that information on potential factors impacting migrants was available for 48% of species in the breeding season and 27% during the non-breeding season ($n = 126$ species). To assess whether this has changed, we reviewed literature published between 2014 and 2021, and we assessed the extent to which they provided evidence for factors operating during the breeding and non-breeding seasons (see Table S1). The evidence was categorized following Vickery *et al.* (2014) as strong (population-level effect), moderate (affecting survival or breeding success) or weak (influenced habitat selection only) and the strongest level identified for each species in each season was assigned to that species. Several studies suggest that population-level effects in the

non-breeding season are based on correlations between population change and broad measures of environmental conditions in Africa. The term ‘strong evidence’ in relation to these studies may be misleading given the spatial variation in environmental parameters across Africa and the lack of data on non-breeding distributions (Beresford *et al.* 2019) but we continue to use this term for consistency.

Knowledge about factors that may affect migrant birds has increased in both seasons (Fig. 3), across a broad range of habitats and particularly in the non-breeding season; information now exists for 51% of species versus 29% previously (Table S1). However, it is important to note that, as previously, very few of these studies have generated new empirical data from the non-breeding grounds. The majority are large-scale correlations of breeding population data with environmental variables derived from non-breeding grounds.

In their review, Vickery *et al.* (2014) concluded that the most important factors driving declines on the breeding grounds were linked to anthropogenic habitat change, particularly within farmland. There was relatively little evidence for other factors, such as climate change and hunting. This overall assessment remains unchanged; of 103 breeding season studies published since 2014, 61% ($n = 63$) have considered habitat preferences and/or land-use change, and only 15% ($n = 15$) of studies have linked climatic variables to demographic parameters, even though widespread population responses to climate change are reported (e.g. Pearce-Higgins & Crick 2019). Two important areas, however, have advanced: first increasing evidence of widespread insect declines in Europe, a key food resource for many Afro-Palaearctic migrants, and second the large scale and impact of legal and illegal hunting.

Insect populations are declining globally, with a number of large-scale studies suggesting dramatic declines in the total biomass and abundance of entire insect assemblages (e.g. Dirzo *et al.* 2014, van Klink *et al.* 2020). For example, it has been estimated that 67% of monitored invertebrate populations globally show mean abundance declines of 45% (Dirzo *et al.* 2014). In Europe, declines of terrestrial insect abundance have averaged c.9% per decade since the 1960s, and have accelerated since 2005 (van Klink *et al.* 2020). National and regional studies have reported similar results for

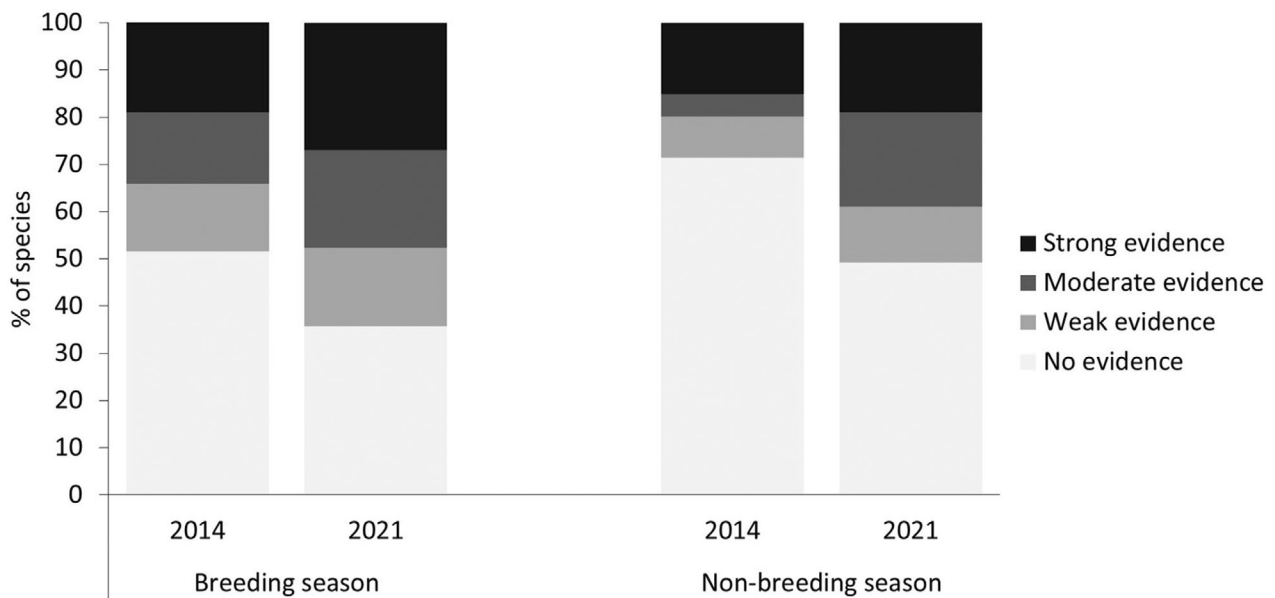


Figure 3. Summary of the extent of evidence available in 2014 and 2021 in relation to environmental factors likely to influence population trends of 126 Afro-Palaeartic migrant species during the breeding and non-breeding seasons. For each species, evidence from published studies catalogued in Table S1 was categorized as either 'strong' (a population-level effect), 'moderate' (effects on survival or breeding success) or 'weak' (an effect on habitat selection). The strongest level identified for each species in each season was assigned and the total number of species in each level was counted.

the insect communities as a whole (e.g. Germany (Hallmann *et al.* 2017a, Seibold *et al.* 2019, or key taxonomic groups (e.g. micro moths (Valtonen *et al.* 2017) and butterflies Thomas *et al.* 2004). It should be noted, however, that other long-term studies, both in Europe (Macgregor *et al.* 2019), and North America (Crossley *et al.* 2020), have found no consistent trends across invertebrate taxonomic groups. Although no studies actually show a direct effect on birds, a number have suggested that declines in insect populations may have contributed to parallel declines in insectivorous birds, including migrants, (e.g. Bowler *et al.* 2019; Hallmann *et al.* 2017b). Insect declines have been reported globally including in tropical regions (Outhwaite *et al.* 2022 although, little data exists for trends of invertebrates in most of Africa (Sánchez-Bayo & Wyckhuys 2021). Though these studies show no direct effect on birds, a number have suggested that declines in insect populations may have contributed to parallel declines in insectivorous birds, including migrants.

Hunting has been identified as an important driver of declines in some species of Afro-Palaeartic migrants, although the demographic impact of

legal and illegal killing on bird population size is difficult to determine because of uncertainty over the estimates of the numbers killed and the flyway population size. However, hunting of European Turtle Dove *Streptopelia turtur* has been shown to be unsustainable under all realistic estimates of bag size and demographic parameters (Lormee *et al.* 2020) and measures to regulate bag size have proved to be ineffective (Moreno-Zarate *et al.* 2021). Similarly, by identifying the origin of breeding populations, Jiguet *et al.* (2019) were able to show that legal hunting of Ortolan Buntings *Emberiza hortulana* in France was unsustainable. Furthermore, although there are several legal quarry species, there is also widespread illegal killing of many Afro-Palaeartic migrants. Reviews of illegal hunting in the Mediterranean and Middle East (Brochet *et al.* 2016, 2019) estimate that tens of millions of birds of hundreds of species may be killed or taken illegally every year (11–36 million in the Mediterranean alone). The potential impact of such illegal killing has been illustrated in the East Asian–Australasian flyway, where the recent widespread decline of the once-abundant Yellow-breasted Bunting *Emberiza aureola* has been

associated with increased trapping of songbirds across Asia (Kamp *et al.* 2015).

RECENT ADVANCES IN KNOWLEDGE AND UNDERSTANDING FROM THE USE OF NEW AND EMERGING TRACKING TECHNOLOGIES

The ability to track individual birds throughout their annual migratory cycle has the potential to link life cycle events to populations and population trends. Since the publication of Vickery *et al.* (2014), we have identified 216 papers related to the tracking of Afro-Palaeartic migrants (see Supplementary information for the complete reference list of tracking studies, Appendix S3). Before the current review, stable isotopes were frequently used to elucidate patterns of connectivity of Afro-Palaeartic migrants (e.g. Hobson *et al.* 2014) but their resolution and accuracy for this purpose is such that conclusions may be superseded by even preliminary tracking (Burgess *et al.* 2022) and they have provided no significant recent advances. Nonetheless, where it is necessary to assign individuals within a breeding population to divergent migratory groups, these methods may still be valuable, especially combined with other approaches (e.g. Liedvogel *et al.* 2014). In the future, recently developed 'genoscaping' methods may provide a higher-resolution alternative to isotopes for connectivity studies (e.g. Bay *et al.* 2021).

Tracking studies provide information on migration routes and strategies, and the location of wintering and stopover sites. This is fundamental information for conservation, helping to identify potential threats and drivers of decline (Rodríguez-Ruiz *et al.* 2019, Burgess *et al.* 2020), key sites to protect (Horns *et al.* 2016, Buechley *et al.* 2018, Salewski *et al.* 2019; also, Tonra *et al.* 2019), or to target detailed ecological studies. Almost half of these studies (101) were judged to have contributed significant information for conservation. Recent papers present extensive new information on routes (e.g. Trierweiler *et al.* 2014, Sara *et al.* 2019), stopovers (e.g. van der Winden *et al.* 2014, Salewski *et al.* 2019) and non-breeding areas (e.g. Willemoes *et al.* 2014, Finch *et al.* 2015, Ouwehand *et al.* 2016). They confirm that non-soaring migrants migrate on broad fronts to and from Europe (supported by a positive correlation between breeding and wintering longitudes (Briedis *et al.* 2020a, 2020b)), rather than

following narrow corridors such as those used by soaring migrants. They are also beginning to reveal some unexpected patterns. The first is the extensive mid-winter use of the Congo Basin and immediately adjacent areas by species such as Common Swift *Apus apus*, Common Cuckoo *Cuculus canorus* and European Nightjar *Caprimulgus europaeus* (Hewson *et al.* 2016, Evens *et al.* 2017, Åkesson *et al.* 2020), as well as some open country species such as Great Snipe *Gallinago media* and Corn Crake *Crex crex* (Klaassen *et al.* 2011, Green 2020). The second is the surprising western detour that many populations make from the Congo Basin area to West Africa on their spring migration (Åkesson *et al.* 2020, Willemoes *et al.* 2014, Norevik *et al.* 2019).

These studies have also advanced knowledge regarding the timing of annual events (e.g. Ouwehand & Both 2017, van Wijk *et al.* 2017, Briedis *et al.* 2018, Tomotani *et al.* 2019, Brlík *et al.* 2020) and patterns of connectivity between breeding and non-breeding populations (e.g. Hahn *et al.* 2013, Åkesson *et al.* 2020). Several species have been shown to move between multiple sites in the tropics during the non-breeding season (Åkesson *et al.* 2012, Willemoes *et al.* 2014, Koleček *et al.* 2016, 2018, Thorup *et al.* 2017), tracking food resources across rainfall gradients with small-scale (Montagu's Harrier *Circus pygargus* (Schlaich *et al.* 2016), Great Reed Warbler *Acrocephalus arundinaceus* (Koleček *et al.* 2018a, 2018b), Pallid Swift *Apus pallidus* (Norevik *et al.* 2019)) and/or larger-scale movements (e.g. Common Cuckoo, Red-backed Shrike *Lanius collurio* and Thrush Nightingale *Luscinia luscinia* (Thorup *et al.* 2017)). This dependence on multiple locations makes identification of site-level drivers difficult and means that the conservation of single sites may be of limited use except for some habitat specialists (e.g. Aquatic Warbler *Acrocephalus paludicola*).

Tracking studies can also provide insights into the timing of annual events (Lisovski *et al.* 2012, Briedis *et al.* 2018, Pedersen *et al.* 2018), as well as the dependencies and carry-over effects between them (Emmenegger *et al.* 2016, Briedis *et al.* 2017, Brlík *et al.* 2020). However, most studies actually suggest little or no linkage between timing of events early and late in the annual cycle, because of the buffering effects of variable non-breeding periods (Ouwehand *et al.* 2016, van Wijk *et al.* 2017, Briedis *et al.* 2018, Tomotani

et al. 2019, although see Briedis *et al.* 2020a, 2020). There may, however, be strong linkages between directly successive seasons (e.g. the timing of departure from the non-breeding grounds and arrival on the breeding grounds for European Pied Flycatcher *Ficedula hypoleuca* (Ouwehand *et al.* 2016) and breeding season conditions and overwinter survival for Alpine Swift *Tachymarptis melba* (Robinson *et al.* 2020)).

Tracking studies are also invaluable in understanding the strength of connectivity between breeding and non-breeding populations, with important implications for understanding declines and how to stem them (Cresswell 2014). The concept of connectivity can be defined in different ways but here we refer to a species as having low connectivity if individuals from the same breeding population spread over a large non-breeding area, resulting in different breeding populations sharing the same non-breeding area to a large degree. In contrast, a species has high connectivity if individuals from the same breeding population occupy a small non-breeding area (Finch *et al.* 2017), resulting in different breeding populations having different non-breeding areas. The results of studies in which multiple populations have been tracked (see Finch *et al.* 2017; also Prochazka *et al.* 2018, van Wijk *et al.* 2018) show that levels of connectivity vary greatly across species. However, breeding populations of most Afro-Palaeartic migrants show high levels of spread in non-breeding areas, with mean inter-individual distance between individuals from the same breeding population across all studies being 743 km (Finch *et al.* 2017), with the Common Nightingale *Luscinia megarhynchos* (Hahn *et al.* 2013) among the lowest so far (mean inter-individual distance in the non-breeding season for birds from three breeding populations of 484, 490 and 697 km), and Red-backed Shrike (2918 km on average, data from two breeding populations (Pedersen *et al.* 2019)) and Willow Warbler *Phylloscopus trochilus* (1734 km on average, data from two breeding populations (Lerche-Jorgensen *et al.* 2017)) among the highest.

Connectivity in migrant birds has important implications for their resilience to habitat change, habitat loss and climate change: low connectivity is associated with more generalist species able to exist in anthropogenically modified habitats, and susceptibility to outright habitat loss but resilience to climate change (Cresswell 2014, Finch *et al.* 2017, Patchett *et al.* 2018). It also has

implications for our ability to identify where population limitation occurs. Given almost all long-term monitoring of populations is on the breeding grounds and that many migrants are highly dispersed in winter, any localized reduction in carrying capacity in non-breeding areas, unless at an extremely large scale, e.g. drought in the Sahel (Peach *et al.* 1991), is unlikely to be detected in breeding trend data (Cresswell *et al.* 2020). This is because any impact is effectively diluted across the large breeding range and will be masked by the many individuals wintering in unaffected areas (Finch *et al.* 2017). This may mean we are less likely to pick up changes in survival rate driving population trends or to detect future effects of any African conservation interventions in Europe, or vice versa.

Tracking also potentially provides a means by which to link individual behaviour to population trends. Such studies remain rare because they require heavy non-archival tags that provide information on mortality events (Klaassen *et al.* 2014, Oppel *et al.* 2015, Ibanez-Alamo *et al.* 2019, Loonstra *et al.* 2019). For example, Common Cuckoos in the UK follow two different southward migration routes associated with different levels of mortality to a common non-breeding area in western Central Africa. The proportion of birds in local breeding populations using the less successful route correlated with the extent of population decline (Hewson *et al.* 2016), suggesting a role of conditions encountered during the migration and/or the pre-migratory fattening period in the UK. A second study on Egyptian Vulture *Neophron percnopterus* (Buechley *et al.* 2021) highlights variation in survival in time and space with lower survival during periods of migration, and on the northerly breeding grounds, compared with sub-Saharan Africa, and for birds originating from eastern compared to western Europe.

The growing MOTUS network of automated radio receiver stations in Europe (Taylor *et al.* 2017) has huge potential for linking demography and migration of smaller species, as do future developments in space-based radio tracking, which allow increasing miniaturization of non-archival tags (Jetz *et al.* 2022). The MOTUS system allows a large number of tags to be deployed with the receiver array serving as a 'virtual mist net' registering any passing bird over a large area. The system has been used to track Barn Swallows *Hirundo rustica* to assess survival over relatively

short time periods (Evans *et al.* 2020) and carry-over effects of breeding on autumn migration (Imlay *et al.* 2021). Solar-powered nano-tags allowing individuals to be tracked across their entire life and an extensive receiver network along the flyway could allow partitioning of mortality across routes and major parts of the annual cycle, as well as help to identify key stopover sites, as it has done in the Neotropical–Nearctic flyway (e.g. Gómez *et al.* 2017).

In summary, in recent years there has been a dramatic increase in the number of species that have been tracked with valuable insights into routes, stopovers, carry-over effects and connectivity. However, these studies still only relate to a small fraction of migrant species and populations (Guilherme *et al.* 2022). Marked biases exist towards more westerly breeding populations and larger-bodied birds. Greatest conservation value will be achieved by combining tracking studies (e.g. Guilherme *et al.* 2022), integrating them with field studies (e.g. Blackburn & Cresswell 2015, 2016a, 2016b) and undertaking them in a hypothesis-driven way (e.g. increasing and decreasing European populations).

RECENT ADVANCES IN KNOWLEDGE AND UNDERSTANDING FROM FIELD STUDIES OF MIGRANT BIRDS IN SUB-SAHARAN AFRICA

Several recent studies in the non-breeding season have collected empirical data relating to the distributions, movements and habitat associations of migrant birds. The biggest advances made since 2014 (Adams *et al.* 2014) have been in two areas, although in both cases the findings relate to a relatively small number of species (between two and 12). First, several studies have highlighted the importance of certain tree species on the non-breeding grounds (e.g. Zwarts *et al.*, 2015; Zwarts & Bijlsma 2015); and secondly, some studies have suggested that anthropogenic land cover change may not always be detrimental to overwintering Afro-Palaeartic migrants (e.g. Blackburn & Cresswell 2015, 2016a, 2016b).

It has long been recognized that a large proportion of migrant birds that cross the Sahara spend the winter in the Sahel region (Moreau 1972). Numbers decline as one travels south – although large numbers have recently been estimated in West African mangroves (Zwarts *et al.* 2014)

– and recent studies have attributed this to birds' preferences for a relatively small proportion of the tree and bush species available in the Sahel region (Zwarts *et al.*, 2015; Zwarts & Bijlsma 2015). Migrants were absent in 69% of all tree species present, favouring thorny trees such as *Faidherbia albida* and other acacias that are adapted to high grazing/browsing pressure through mechanical (thorns), rather than chemical, defence and so support relatively high invertebrate abundance. The main exception is the berry-bearing *Salvadora persica*, long known to be favoured by migrant birds, such as *Sylvia* warblers, that are at least partially frugivorous during the non-breeding season (Stoate & Moreby 1995, Fransson *et al.* 2008, Iwajomo *et al.* 2017).

Conditions in the Sahel have long been known to have an impact on survival and population trends of migrant birds (e.g. Winstanley *et al.* 1974, Peach *et al.* 1991, Norman & Peach 2013). Droughts have an immediate impact upon food availability, and a longer-lasting effect on vegetation cover and species composition in the region (Zwarts *et al.* 2009). Severe losses of woody cover in the dry northern Sahel since the 1960s, caused by drought, cutting, grazing and fire, may equate to the loss of habitat for 300–400 million migrant birds (Zwarts *et al.* 2015, 2018), something likely to be exacerbated by climate change (Simkins 2019).

Similarly, further south in the Sudan savannah and Guinea forest zones, various warbler species show preferences for taller trees compared with their immediate surroundings (Mallord *et al.* 2016, Awa II *et al.* 2018, Willemoes *et al.* 2018), while certain groups of tree species such as acacias (Willemoes *et al.* 2018) are often favoured. In some cases, individual tree species can be important: for instance, Wood Warblers *Phylloscopus sibilatrix* at a stopover site in the Sudan savannah strongly preferred *Terminalia leocarpa*, accompanied by a marked avoidance of other more common species, e.g. *Vitellaria paradoxa* and *Azadirachta indica* (Mallord *et al.* 2016), also highlighting the importance of native trees (Douglas *et al.* 2014).

To the extent that they can be considered habitat generalists (Cresswell 2014, Ivande & Cresswell 2016), migrant birds may be unlikely to be limited by the availability of suitable habitat on the wintering grounds in Africa. This may be particularly the case for open country species such as

Whinchat *Saxicola rubetra* (Hulme & Cresswell 2012, Blackburn & Cresswell 2015, 2016a, 2016b), which may tolerate some agriculture-related habitat change, but less so for species more reliant on wooded habitats (Jones *et al.* 1996, Vickery *et al.* 2014). However, species preferring open woodlands may exhibit some resilience to loss of tree cover, e.g. Wood Warbler (Mallord *et al.* 2016, 2018, Awa II *et al.* 2018, Buchanan *et al.* 2020, Jarret *et al.* 2021) and possibly other migrant species that prefer moderate forest cover, e.g. Willow Warbler (Thorup *et al.* 2017, Willemoes *et al.* 2018).

Other migrants are highly mobile and able to track variation in resource abundance over wide areas. Montagu's Harriers track the abundance of grasshoppers (Trierweiler *et al.* 2013, Augiron *et al.* 2015, Schlaich *et al.* 2016) and changes in food availability can alter the migratory behaviour of Iberian-breeding White Storks *Ciconia ciconia* (Gilbert *et al.* 2016), and the foraging strategies of Eurasian Reed Warblers *Acrocephalus scirpaceus* (Vafidis *et al.* 2014).

In conclusion, we have greatly advanced knowledge for a small number of migrant species, but overall understanding of non-breeding ecology and distribution remains poor. We know of only 31 papers published since 2014 based on newly collected empirical data from the wintering grounds in sub-Saharan Africa, 12 of which are based on data from just three studies (distribution of migrants in the Sahel, Whinchats in Nigeria and Wood Warblers in Ghana). Overall, they show a preference for a small number of tree species, and apparent resilience to anthropogenic land-use change, especially loss of trees. However, it is important to emphasize that many of these studies represent a small subset of migrant bird species. This work is challenging and expensive and if the goal is to gather information to conserve these birds, we suggest that the return on investment of this area of work is low and unlikely to change.

RECENT ADVANCES IN KNOWLEDGE AND UNDERSTANDING FROM THE USE OF SURVEY AND DEMOGRAPHIC DATA FROM THE EUROPEAN BREEDING GROUNDS

The abundance of common breeding bird species in Europe is monitored under the PECBMS

(<https://pecbms.info/>), with additional data from schemes collated under Birds in Europe/European Red List of Birds (ERLoB; BirdLife International 2017a, 2017b). Demographic data are collected by standardized mist-netting across 20 countries under the European Constant Effort Site (Euro-CES) scheme. The spatial and temporal resolution of these data mean that they can be used to explore both large-scale and local-scale patterns in population trends and demography across species ranges. Studies include quantifying large-scale changes in abundance and demography across European breeding grounds, identifying within- and between-species variation in population trends and demography, examining the role of environmental processes on the breeding and non-breeding grounds on population declines and considering the nature and impact of changes in the timing of arrival and breeding on European breeding grounds.

Detailed exploration of changes in abundance and demography of migrant birds across European breeding grounds has highlighted differences at both regional and site levels. Growing evidence suggests that sites where migrants are doing well are also the sites where residents are doing well in the UK (Ockendon *et al.* 2012, Balmer *et al.* 2013, Morrison *et al.* 2013, 2016) and at the European level (Morrison *et al.* 2021). Analysis of one species (Willow Warbler) in Great Britain has shown that, although declines may be driven by poor conditions outside the breeding grounds, they could be addressed by targeted actions to improve productivity at poor breeding sites. However, in the long term, halting and even reversing survival-driven population declines are also likely to require environmental protection across non-breeding ranges (Morrison *et al.* 2016, 2021).

Survey and demographic data have also been used to quantify the role of environmental processes on the breeding and non-breeding grounds on population declines including spring temperature (Meller *et al.* 2018), breeding habitat types (Sullivan *et al.* 2015) and degree of habitat modification, e.g. through agriculture (Jørgensen *et al.* 2016, Sander-son *et al.* 2016, Gamero *et al.* 2017, Knaus 2018, Moreno-Zarate *et al.* 2021).

Studies relating European breeding bird data to large-scale habitat and environmental processes in Africa have failed to find any clear regional patterns (e.g. Ockendon *et al.* 2014, Jørgensen

et al. 2016, Halupka *et al.* 2017, Beresford *et al.* 2019). This failure may reflect marked spatial variation in environmental change in Africa, limited information about non-breeding and habitat requirements (e.g. Mallord *et al.* 2016, 2018, Beresford *et al.* 2019, Buchanan *et al.* 2020), and the large non-breeding area that individuals from a population may occupy (Finch *et al.* 2017).

Long-term demographic data have also provided insight into the effects of phenological change on migrant populations (Samplonius *et al.* 2021). Several studies in the UK and elsewhere have linked population trends to long-term datasets on timing of arrival, departure or egg laying and shown that those species that are least flexible exhibit the most negative population trends (Møller *et al.* 2008, Newson *et al.* 2016, Franks *et al.* 2018). Although changes in breeding ground temperature may impact the timing (Ockendon *et al.* 2013) or success (Arlt & Part 2017) of nesting attempts, there is little evidence of the importance of phenological changes on the breeding grounds. For example, for three insectivorous passerines, carry-over effects from passage regions had consistently stronger impacts on breeding phenology than breeding climate (Finch *et al.* 2014). For example, in Wood Warblers, a failure to advance breeding to match the advancement in peak prey (caterpillar) emergence did not impact on subsequent productivity, suggesting no marked effect of phenological mismatch (Mallord *et al.* 2017), and that individuals take advantage of alternative food types. Similarly, a UK-wide multi-species study found no latitudinal variation in the timing of peak nestling demand relative to peak caterpillar biomass for any of the three species studied (Burgess *et al.* 2018).

In summary, studies of large-scale survey and demographic data from the breeding grounds to identify demographic drivers of migrant population declines yield complex results that differ between species, populations, regions and habitats. Rainfall in the wintering grounds continues to emerge as an important factor and phenological mismatch is apparent in some insectivorous migrant birds but there is little evidence that this is linked to population trends. Importantly, for some species, recovery may be possible through targeted action to improve productivity on the breeding grounds, even if the drivers of their population trends are operating elsewhere.

RECENT ADVANCES IN KNOWLEDGE AND UNDERSTANDING FROM THE USE OF REMOTE SENSING OF LAND COVER CHANGE IN SUB-SAHARAN AFRICA

Rapid change in land use and land cover in sub-Saharan Africa is well documented. Recent assessments show an increasing area of agricultural land under 'shifting agriculture' (Curtis *et al.* 2018, Faour *et al.* 2018), particularly in more northerly zones and countries (Knauer *et al.* 2017, Schulte to Bühne *et al.* 2017, Potapov *et al.* 2021) with associated large-scale tree loss (e.g. Fensholt *et al.* 2015, Zomer *et al.* 2016). Long-term changes to wetland habitats are also apparent throughout the Sahel and tropical Africa, although these vary between countries and regions (Moser *et al.* 2014, Schroeder *et al.* 2015). Determining the extent to which these changes are linked to changes in migrant bird populations is compromised by the lack of basic empirical information on distribution and habitat use of these species in the non-breeding season (e.g. Beresford *et al.* 2019). Fourteen studies have been published since 2014 that have related migrant bird population trends to remote-sensed land cover, using either the Normalized Difference Vegetation Index (NDVI; $n = 12$) or tree cover data ($n = 2$).

The recent studies examine whether declines of migrants could be related to land cover changes in Africa using NDVI as a measure of vegetation development or primary productivity, and have produced mixed results (e.g. Ockendon *et al.* 2014). A number use over-simplistic single environmental parameters across the entire African continent in which vegetation phenology varies enormously (Beresford *et al.* 2019) and/or lack crucial information on non-breeding distribution and species-habitat relationships (e.g. Howard *et al.* 2020).

Only one study has incorporated known species-habitat relationships (Mallord *et al.* 2016) with remote sensed data on land cover and land cover change (from Hansen *et al.* 2013), first, to quantify optimal habitat across an Afro-Palaearctic migrant's non-breeding African range and, secondly, to estimate the change in cover of such habitat over time (Buchanan *et al.* 2020). This suggested that between 2000 and 2014, there was a 47% increase in the extent of optimal open

woodland habitat for this species with the degradation of pristine forest. Hence, while our understanding of land cover change in sub-Saharan Africa has increased greatly, our ability to relate these changes to habitat availability for and/or population trends of migrant birds has not. This area of research is constrained by our lack of knowledge about the distribution, abundance and species–habitat relationships of most migrant birds in the non-breeding season and unless this knowledge gap is addressed, such large-scale analyses will remain of limited value for conservation.

HOW MUCH CAN THESE RECENT ADVANCES INFORM CONSERVATION ACTION?

Ultimately, any research into migrant declines might usefully be turned into conservation action. Key to this is the identification of stage(s) in the

annual cycle where an action can cost-effectively increase populations. The cost-effectiveness of any conservation action, measured as money and/or effort, is always likely to be an S-shaped function, where a small amount of resource makes no difference, and a large amount of resource sees diminishing returns (the ‘conservation investment function’, e.g. based on decision analysis, see Valero 2021; Fig. 4a). The function shape will vary according to the strength of the relationship between investment and the population response and will be species- and stage-specific (Fig. 4b).

For example, western Ortolan Bunting populations may currently have the steepest relationship between change in population and amount of conservation investment on passage, where hunting is the main driver of population declines (Jiguet *et al.* 2019), whereas for Whinchats the steepest relationship is likely to be on the breeding grounds (Bastian & Feulner 2015). Hence, when a

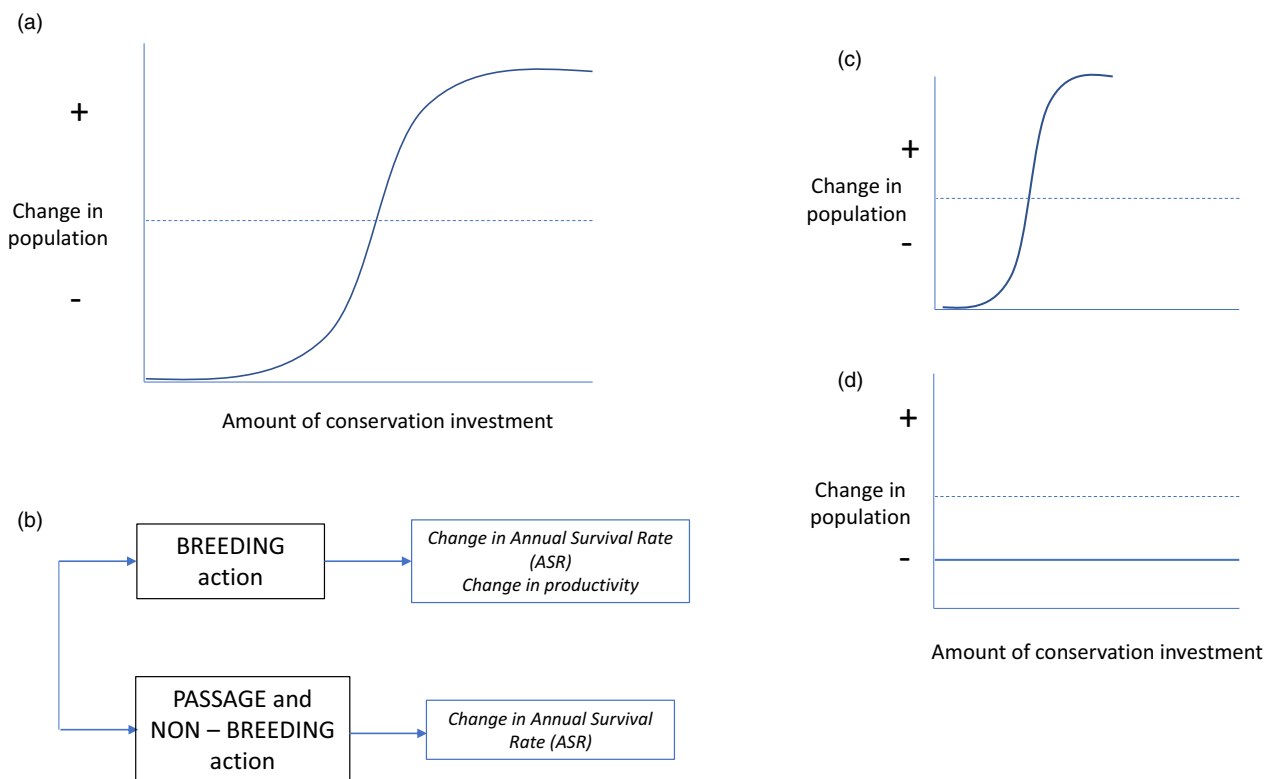


Figure 4. (a) The relationship between investment and population response (the conservation investment function). (b) The crucial stages in any conservation decision analysis to determine which stage would give the best return for any conservation investment to address the decline of a migrant species. The success of any intervention will depend, first, on how ecologically relevant it is to a given population and, secondly, on the ease of implementation. Even if the stage at which the drivers of decline are operating is known, variation in the ease of implementation can result in very different functional relationships (c, d).

conservation investment increases population size, its ranking among all possible interventions will depend on the steepness of the slope and the absolute change in population, relative to other possible interventions at other stages in the annual cycle. How many other species may benefit from this intervention is also relevant but challenging to assess. There are at least two important sources of uncertainty that affect these relationships. The first is whether the actions taken will actually reverse species' declines. A second uncertainty is linked to the ease of implementation. For example, the underlying causes of the population declines of Corn Crakes and European Turtle Doves in the UK are well established (Green *et al.* 1997, Browne & Aebischer 2004). These declines are associated with changes in farming practices reducing productivity, and conservation investment has been provided for both species. In the Corn Crake, the declines were caused by high chick mortality through mowing of their grassland habitat (Green *et al.* 1997, Tyler *et al.* 1998). Payments were made to farmers to alter the mowing regimen (Green *et al.* 1997), increasing UK populations (cf. Fig. 4b; Wotton *et al.* 2015). In the European Turtle Dove, the declines were linked to a changing food supply and shifts in diet from wild to cultivated seeds (Browne & Aebischer 2003, 2004). However, a large amount of investment, especially in terms of management interventions within UK government agri-environment schemes (Dunn *et al.* 2015), has not resulted in population recovery (cf. Fig. 4c) (Woodward *et al.* 2020). Differences in population response are also likely to be the result of differences in the ease of implementation. Corn Crakes are geographically confined to a relatively small area in the UK, so that management can be targeted precisely. European Turtle Doves are more widespread and the precise cause of the decline is less certain. Understanding whether the failure of a particular conservation intervention is due to the nature of the action, or its implementation, will be important in terms of replicating the measures more widely. Ordering the various potential conservation interventions, therefore, depends fundamentally on a reasonable quantification of how population changes arise from variables that are amenable to conservation action, and the cost of influencing these variables. For example, habitat quality in terms of retained larger trees on the non-breeding grounds in Guinea savannah landscapes across Africa is likely to be

important for many Palaearctic migrant populations (e.g. Mallord *et al.* 2016) as well as resident species. Tree and natural habitat retention or management could be encouraged through direct payments or indirect incentives to landowners (Brown *et al.* 2021). The costs and population consequences of this, relative to conservation action on the breeding grounds (Mallord *et al.* 2012), would require establishment of a functional relationship between levels of investment and population response. Each relationship is straightforward, but it requires ornithologists and conservationists working in countries throughout a particular migrant species' range to make such empirical measurements. The complexity arises because there are many stages in the annual cycle of a migrant, and many possible conservation actions, whose implementation will be dependent on geographical, political and socio-economic factors, which will be different for each species.

The key question in the context of this review is, therefore, have we modelled sufficient conservation investment functions to be able to start halting and ultimately reversing migrant population declines effectively? The answer remains no, partly because we are still limited by the lack of studies of how migrant populations are affected by conditions during passage and on the non-breeding grounds. As Figure 3 shows, we lack complete annual cycle data on most populations, and for those species that are well studied (e.g. Common Cuckoo, European Turtle Dove, Whinchat, European Pied Flycatcher, Wood Warbler), knowledge is restricted to a very limited number of populations. Perfect knowledge across the flyway may not be necessary; for example, population recovery may be possible through increasing productivity/survival at stages where implementation is easiest, even if the drivers of decline are operating at other stages (Morrison *et al.* 2021), although this remains untested.

SUMMARY AND CONCLUSIONS

Despite considerable efforts, there has been rather limited progress in identifying the causes of migrant bird declines, linked, in no small part, to the complexity of the system and the diversity of species involved. The 'full annual cycle approach' (Marra *et al.* 2015) is often viewed as key to understanding a system. Although possible for a species such as the American Redstart *Setophaga*

ruticilla, with relatively low non-breeding dispersion, it is rarely possible for species with high non-breeding dispersion, which is often the case in the Afro-Palaeartic system. This is particularly true where non-breeding grounds are in remote and often politically unstable areas, as is the case for many migrants (Guilherme *et al.* 2022). There are examples where individual species have been linked to specific (or, at least, flyway) populations, confirming that hunting pressure is unsustainable and the probable cause of population declines and/or lack of recovery, e.g. Ortolan Bunting and European Turtle Dove.

We argue that there is an urgent need to shift from diagnosing declines to trialling potential solutions, based on the best available evidence, combined with monitoring and adaptive actions. The escalating scale of Afro-Palaeartic bird declines suggests that conservation action cannot await the outcome of future research investment focusing purely or largely on diagnosis. This review may be used to identify valuable policy-based and/or land-based experiments. Such experiments, if effectively monitored, could help to indicate where the steepest parts of the 'population response and conservation investment' curve are (Fig. 4), in the absence of full prior understanding of such relationships, to support decision analysis.

The substantial advances in recent knowledge from tracking, and particularly results relating to dispersion, are important in this context. In the broadest terms, these show that individuals from the same population may spread over a large non-breeding area, leading to breeding populations sharing the same areas extensively during passage and the non-breeding season (low connectivity). This suggests that (1) any one site that is conserved will only benefit a very small fraction of the overall population, although any suitable habitat site will conserve some individuals of many breeding populations; (2) land-sharing solutions may be more effective than purely site-based conservation; (3) any local changes in Africa may affect many European populations, and these local changes will be averaged across many breeding sites, making it difficult to pick up changes in survival rate on the non-breeding ground driving population trends, or to detect future effects of any localized African conservation interventions; and (4) if factors driving declines of species do operate on non-breeding grounds, they must do so at a relatively large scale to have significant impact on any one breeding

population (e.g. climate change or large-scale land use change).

Hence, the degree of connectivity and number of sites required by a species helps to identify general principles for conservation action and approaches. There are a smaller number of species, often specialists, that migrate along defined routes and bottlenecks (e.g. Aquatic Warbler (Salewski *et al.* 2013) and Ortolan Bunting (Jiguet *et al.* 2016)), that rely on a small number of key sites and may benefit from targeted site-based conservation action at multiple sites across the flyway. Although a relatively small number of species may benefit from widespread small-scale site-level interventions, a significant proportion of migrants are widely spread on the non-breeding grounds. These species (e.g. Whinchat (Blackburn *et al.* 2017) and Great Reed Warbler (Lemke *et al.* 2013)) may be best served by broad landscape-scale conservation action, e.g. land sharing solutions (Green *et al.* 2005) and nature-based solution approaches (Seddon *et al.* 2020).

On the breeding grounds, work to understand the habitat conditions associated with good sites for key species may help to identify the sorts of habitats to replicate and/or scale up and implement targeted action to boost productivity (Morrison *et al.* 2021). On non-breeding grounds where implementing management action is challenging, there is great potential in monitoring the benefits, for both migrant and resident birds, of aid and development initiatives that are linked to enhancing, for example, tree cover to improve livelihoods (Le Houérou 1977, Bizikova *et al.* 2015, Graves *et al.* 2019). These range from large-scale initiatives, such as The Great Green Wall for the Sahara and the Sahel Initiative (GGWSSI or Great Green Wall GGW (FAO 2014, Bozzano *et al.* 2014, <https://www.greatgreenwall.org>)), to smaller-scale projects – e.g. The Acacia Operation Project (Bozzano *et al.* 2014); Bocage system (Girard 2008); Zai pits (Sawadogo 2011, Danjuma & Mohammed 2015); and Ecovillages (ANEV 2015, <http://www.Ecovillages.sn/>, GENSEN 2015) that often adapt traditional agricultural practices to grow native trees and shrubs (Berrang-Ford *et al.* 2011). The extent to which they will benefit biodiversity, and indeed climate, depends to a very great extent on the number and species of trees planted and surviving, and their provenance (Douglas *et al.* 2014, Seddon *et al.* 2020). However, very few of these initiatives currently include biodiversity monitoring (though see Stout *et al.* 2018,

Delaney *et al.* 2020) and integrating such monitoring could provide valuable evidence on ways to enhance benefits for biodiversity, climate and local people.

We also urge greater collaboration and integration between research projects and programmes, sites, geographical regions and scientific disciplines. In the case of tracking, for example, the most significant advances for conservation will be made by combining tracking studies and using them in combination with other approaches in a hypothesis-driven way. This will reveal generalities and differences between, for example, migration routes and wintering locations between western and eastern Europe or increasing and decreasing European populations (see, for example, Guilherme *et al.* 2022). Pooling data will also allow the identification of 'hotspots' or 'regions' used by multiple species and populations.

In summary, if we are to stem the declines of migrant birds, we need to use the scientific knowledge we have to start to act rather than wait for complete knowledge and understanding. This means identifying and evaluating potentially valuable policy and land-based 'natural experiments', where possible guiding their establishment in ways to yield the best understanding. We need to connect bird and land-use researchers along the flyway, for research to be carried out and understood and applied locally, involving local communities where possible. This will demand a much larger scientific capacity and a new scientific literacy within policy encompassing biodiversity, human development, business and industry. Soberingly, we need to recognize that the decline of widespread relatively common species may carry a stronger warning about the health of our natural world than the decline of rare and threatened species, and to afford them a higher priority.

We dedicate this review to Japheth Roberts, a brilliant young biologist from Ghana whose life was tragically cut short by illness. He made a major contribution to RSPB and Ghana Wildlife Society work in Africa – an area of work we highlight as a key ongoing priority. The review drew on discussion and insights generated at a workshop in Cambridge in 2019 generously funded by the Cambridge Conservation Initiative collaborative fund CCC-05-18-003 and RSPB and co-organized by J.V. and Susana Requena. We are grateful to all attendees for their invaluable input: Guy Anderson, Phil Atkinson, Olivier Biber, Claire Bissel, Graeme Buchanan, Malcolm Burgess,

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Juliet Anne Vickery: Writing – original draft. **John W. Mallord:** Writing – original draft. **William Adams:** Writing – original draft. **Alison E. Beresford:** Writing – original draft. **Cristiaan Both:** Writing – original draft. **Will R. L. Cresswell:** Writing – original draft. **Ngoné Diop:** Writing – review and editing. **Steven Ewing:** Writing – original draft. **Richard Gregory:** Writing – original draft. **Catriona Morrison:** Writing – original draft. **Fiona Sanderson:** Writing – original draft. **Kasper Thorup:** Writing – original draft. **Rien van Wijk:** Writing – original draft.

CONFLICT OF INTEREST

The authors have no conflicting interests.

ETHICAL APPROVAL

None.

Data Availability Statement

All data are available in the Supplementary Material.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Summary of our understanding of factors impacting Afro-Palaeartic migrants on their breeding, non-breeding and staging grounds.

Table S2. Widespread and common European long-distance and short-distance migrants.

Appendix S3. Complete list of tracking references.