Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations

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Sea-level rise (SLR) will greatly alter littoral ecosystems, causing habitat change and loss for coastal species. Habitat loss is widely used as a measurement of the risk of extinction, but because many coastal species are migratory, the impact of habitat loss will depend not only on its extent, but also on where it occurs. Here, we develop a novel graph-theoretic approach to measure the vulnerability of a migratory network to the impact of habitat loss from SLR based on population flow through the network. We show that reductions in population flow far exceed the proportion of habitat lost for 10 long-distance migrant shorebirds using the East Asian–Australasian Flyway (EAAF). We estimate that SLR will inundate 23–40% of intertidal habitat area along their migration routes, but cause a reduction in population flow of up to 72 per cent across the taxa. This magnifying effect was particularly strong for taxa whose migration routes contain bottlenecks—sites through which a large fraction of the population travels. We develop the bottleneck index, a new network metric that positively correlates with the predicted impacts of habitat loss on overall population flow. Our results indicate that migratory species are at greater risk than previously realized.

1. Introduction

Anthropogenic habitat loss has precipitated a recent wave of extinctions [1,2]. For non-migratory species, increased extinction risk from habitat loss can be approximated by measuring the area of suitable habitat that has been lost [3]. This method currently underpins assessments of extinction risk [2,4], and global conservation prioritizations [5,6]. However, for migratory species, the impact of habitat loss depends not just on its extent, but also on where it occurs [7–10]. Estimating extinction risk simply from the extent of habitat lost could severely underestimate the vulnerability of migratory species. For example, the Rocky Mountain grasshopper Melanoplus spretus collapsed from some 15 trillion individuals to extinction because habitat loss was concentrated into a small region in which the species contracted during dry years [11].

Millions of shorebirds migrate annually from their Russian and Alaskan Arctic breeding habitats to the coasts of Southeast Asia and Australasia through the East Asian–Australasian Flyway (EAAF) [12,13]. These birds interrupt their journeys to rest and feed in intertidal habitats at staging sites across eastern Asia that can constitute significant bottlenecks for migration [14,15]. For example, over 45 per cent of all red knots Calidris canutus in the flyway use a single site in the Yellow Sea during their migration [15,16]. Habitat loss from sea-level rise (SLR) at...
such bottleneck sites could disproportionately impact popula-
tion persistence, but to our knowledge, the magnitude of
these effects has not been quantified in this or any other
migration system. Here, we estimate the vulnerability of
migratory routes for shorebirds to future loss of coastal habitat
through SLR across all the EAAF sites used by the birds [17].

To model the impacts of habitat loss on the migratory
shorebird populations, we estimate the flow of birds through
the network of habitat patches by applying an algorithm
widely used to solve the maximum flow problem, developed
to calculate the maximum amount of flow running through
complex networks (e.g. water in a pipeline system) [18].
There is growing interest in applying graph theory to ecologi-
cal phenomena, though its application has so far been limited
to analyses of network structure such as metapopulations
[19,20] and landscape connectivity [21,22]. Using our novel
application of graph theory, we estimate the impact of habitat
loss on the maximum flow capacity of migratory populations
(hereafter referred to as ‘population flow’) of 10 migratory
shorebird taxa using the EAAF [12,13]. Migratory pathways
are modelled using a graph consisting of nodes connected
by edges representing the flow of individuals along the migration
route (see figure 1 and electronic supplementary material). We
applied an algorithm quantifying the maximum flow that the
network could support, given any particular configuration of
habitat availability across the nodes.

2. Material and methods

(a) Network structure

In mathematical graph theory [23], a real-world network is
represented as a ‘graph’, a diagram consisting of points called
‘nodes’, joined by lines, called ‘edges’. In ecological applications,
nodes typically represent habitats or populations and edges
indicate a connection between any two nodes. Edges can have weights
direction to indicate population fluxes, colonization probabil-
ities or internode distances. Here, we represent a flyway as a
weighted directional graph, where each node represents a regional
group of internationally important shorebird sites. Each node has
an attribute indicating habitat loss from SLR and each edge has a
weight and direction representing the flux of birds between the
two nodes connected by the edge (figure 1). We constructed
graphs linking northward and southward migration routes, as
these often differ [24,25].

A migratory network structure for each shorebird species
was constructed, based on the collective knowledge and experi-
ence of a group of experts who have worked in the flyway for
several decades [13,24]; see author list and acknowledgements
for a list of workshop members; electronic supplementary
material; figure 1). Estimates of network structure were founded
on a combination of count data, banding and flagging infor-
mentation, routes of birds fitted with satellite tags and geolocators
[12,13,24]. The experts were asked to conceptualize each node
as the smallest possible groups of internationally important
sites between which there is sufficient information to map
the migratory routes of each species in this study (figure 1a).
First, sites within a geographical region (e.g. China Seas, northeast
Australia) were clustered as groups, then the experts further cate-
gorized sites into finer scale groups (e.g. east coast of the Yellow
Sea, Gulf of Carpentaria) based on data about migratory patterns
for each taxon (see the electronic supplementary material). The

(b) Defining migratory networks

We selected 10 shorebird taxa using the EAAF that (i) have declin-
ing populations, (ii) depend principally on coastal habitats while on
migration, and (iii) have sufficiently comprehensive information
available for modelling the spatial structure of their migratory net-
works. These taxa were bar-tailed godwit (two subspecies treated
separately: Limosa lapponica menzbieri and Limosa lapponica baueri),
curlew sandpiper (Calidris ferruginea), eastern curlew (Numenius
madagascariensis), great knot (Calidris tenuirostris), grey-tailed tattler
(Charadrius mongolus mongolus and Charadrius mongolus stejnegeri)
banded plover (Charadrius mongolus mongolus and Charadrius mongolus stejnegeri
combined), red knot (two sub-species treated separately: Calidris canutus rogersi and
Calidris canutus piersna) and terek sandpiper (Xenus cinereus).
Barnard et al. [12] catalogued the locations of all sites supporting
more than 1 per cent of the flyway population of each taxon. For our
study taxa this comprises 163 individual sites, distributed across
Alaska, Russia, China, North Korea, South Korea, Japan, Philippines,
Vietnam, Thailand, Malaysia, Indonesia, Papua New
 Guinea, Australia and New Zealand.

Polygon data delineating the extent of each wetland were only
available for 76 sites (e.g. Wetland database for Ramsar sites,
World Database of Protected Areas, National Wetland Inventory for Australia). Where such data were not available, the extent of each wetland(20,160),(881,933)
proportional loss of flyway capacity and loss of habitat extent was much larger at the medium sea-level scenarios (figure 2). At 50 cm SLR, mean loss in population flow across the 10 taxa was only slightly higher than mean habitat loss (mean population flow loss = 0.181, mean habitat loss = 0.113, Welch two-sample tests: \( p = 0.012 \)), but the difference between these two values is much larger at 150 cm SLR (mean population flow loss = 0.494, mean habitat loss = 0.306, \( p = 0.004 \)).

In an optimistic scenario, where an upshore shift of intertidal habitat into all non-urban areas is assumed, the rate of predicted habitat loss unsurprisingly was smaller for all SLR scenarios (figure 4). However, the declines in population flow always remained higher than those predicted by habitat loss alone, and the patterns were generally similar to those when no compensation was assumed (figure 2). For some species such as great knot and terek sandpiper, magnification

Table 1. Estimated proportional loss of intertidal habitat through twenty-first century SLR. (Loss of intertidal habitat is shown for the internationally important sites for migratory shorebirds within each region across the flyway, and was calculated by dividing the sum of lost habitat by the total area of present intertidal habitat across the sites within each region.)

<table>
<thead>
<tr>
<th>no. sites</th>
<th>50 cm</th>
<th>100 cm</th>
<th>150 cm</th>
<th>200 cm</th>
<th>250 cm</th>
<th>300 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Russia</td>
<td>8</td>
<td>0.133</td>
<td>0.184</td>
<td>0.328</td>
<td>0.401</td>
<td>0.492</td>
</tr>
<tr>
<td>Yellow Sea</td>
<td>34</td>
<td>0.225</td>
<td>0.280</td>
<td>0.428</td>
<td>0.546</td>
<td>0.744</td>
</tr>
<tr>
<td>Japan</td>
<td>39</td>
<td>0.216</td>
<td>0.280</td>
<td>0.428</td>
<td>0.546</td>
<td>0.744</td>
</tr>
<tr>
<td>East China Sea (incl. Philippines)</td>
<td>6</td>
<td>0.161</td>
<td>0.280</td>
<td>0.428</td>
<td>0.546</td>
<td>0.744</td>
</tr>
<tr>
<td>Southeast Asia</td>
<td>11</td>
<td>0.387</td>
<td>0.457</td>
<td>0.524</td>
<td>0.619</td>
<td>0.728</td>
</tr>
<tr>
<td>southwest Australia</td>
<td>7</td>
<td>0.261</td>
<td>0.528</td>
<td>0.699</td>
<td>0.867</td>
<td>0.977</td>
</tr>
<tr>
<td>northeast Australia</td>
<td>11</td>
<td>0.071</td>
<td>0.144</td>
<td>0.225</td>
<td>0.322</td>
<td>0.343</td>
</tr>
<tr>
<td>northwest Australia</td>
<td>17</td>
<td>0.062</td>
<td>0.137</td>
<td>0.293</td>
<td>0.567</td>
<td>0.834</td>
</tr>
<tr>
<td>southeast Australia</td>
<td>15</td>
<td>0.222</td>
<td>0.486</td>
<td>0.768</td>
<td>0.921</td>
<td>0.977</td>
</tr>
<tr>
<td>New Zealand</td>
<td>11</td>
<td>0.159</td>
<td>0.329</td>
<td>0.490</td>
<td>0.652</td>
<td>0.811</td>
</tr>
<tr>
<td>Alaska</td>
<td>1</td>
<td>0.399</td>
<td>0.451</td>
<td>0.490</td>
<td>0.523</td>
<td>0.560</td>
</tr>
<tr>
<td>total</td>
<td>163</td>
<td>0.131</td>
<td>0.224</td>
<td>0.350</td>
<td>0.450</td>
<td>0.542</td>
</tr>
</tbody>
</table>
4. Discussion

Migratory routes often include staging sites where migrants can rest and feed, and the loss of such sites can cause severe ‘bottleneck’ effects on migratory populations [14,31,32]. That is, sudden declines in population flow can be triggered by small amounts of overall habitat loss owing to migratory connectivity [11,14,33]. By developing a method to estimate the amount of population flow travelling through a migratory route subject to habitat loss, we have shown that these effects can be very large across an assemblage of declining long-distance migrants. Importantly from a conservation perspective, the flyway-wide consequences of habitat loss through SLR differ dramatically among the taxa we studied, even though they all use the same geographical region. This is because of variation in the specific patterns of connectivity among sites as well as the absolute extent of habitat loss at the sites used by each taxon. This variation demonstrates that understanding the pattern of migratory connectivity is essential for correctly predicting population declines resulting from habitat loss in migratory species.

SLR threatens to inundate the intertidal habitats upon which migratory shorebirds depend [34,35], but SLR has been relatively understudied in comparison with other drivers of habitat loss such as land conversion and reclamation [33]. This is perhaps because the human consequences are preventable in the short term, and also because the magnitude of SLR was previously underestimated as a result of ice-sheet melting being excluded from SLR models [27,28]. Our results, viewed...
through the lens of the most recent SLR predictions, suggest that we could witness dramatic collapses of population flow caused by intertidal habitat loss for at least some of the migratory shorebird species in this flyway within a few decades.

By applying the maximum flow algorithm to migratory species, we have built a simple framework in which to estimate the consequences of habitat loss for migratory populations. The newly introduced bottleneck index shows strong correlation with the loss in population flow especially for low to medium SLR scenarios (figure 3). This indicates that habitat loss within a bottleneck node, i.e. a node through which a large proportion of the population passes, can drive large overall declines in population flow, even if only a small fraction of total habitat is lost. Reductions in flyway capacity were strongly positively related to the bottleneck index (figure 3), suggesting that we could begin to estimate the vulnerability of particular migration routes to habitat loss in data-poor situations where a formal connectivity analysis is not possible. Importantly, this index is only based upon information gleaned locally from sites (i.e. how much of the population passes through a site and how much habitat will be lost) and does not require formal models of how individuals traverse an entire network. Our discovery emphasizes the importance of incorporating migratory connectivity into estimates of habitat loss impacts, and also provides an approach to estimate the vulnerability of migratory populations to local habitat loss.

Upshore movement of intertidal habitats in response to SLR would greatly reduce the magnitude of population declines (compare figure 2 with figure 4). Facilitating such movements, therefore, seems a critical conservation tool to protect migratory shorebirds from the impacts of habitat loss through SLR. In reality, the optimistic scenario is less likely to eventuate during the timeframe of the predicted rises in sea level we study here, given that the realization of such new habitat will depend on appropriate sediment patterns and coastal development regimes as well as a concomitant shift in food resources. Furthermore, managed realignment to allow existing intertidal habitat room to move upshore requires careful coastal zone planning and restriction of development footprints [36].

Our analysis does not incorporate the capacity of birds to change their migratory routes in response to environmental change. Such changes certainly do occur in nature [37,38], however, the occurrence of apparently sub-optimal migration routes suggests that flyways are rather constrained [39]. Some long-distance migrants (e.g. bar-tailed godwit) follow extremely tight flight schedules suggesting little room to adapt to major changes in flyway condition [40]. Our new framework for analysing migratory networks could incorporate changes in migratory routes by dynamically modifying the capacity of edges [41], provided the necessary data to parametrize such models were available. In addition to SLR, other aspects of climate change such as changes in temperature and patterns of storm activity could directly impact migratory species. For example, a temporal mismatch between migration times and peak abundance of food resources has been associated with population decline in migratory pied flycatchers *Ficedula hypoleuca* [42].

We have also assumed that the carrying capacity of each site is presently saturated—further field data would allow for variable carrying capacity to be incorporated into future analyses, perhaps by building spatially explicit population models [43]. Recent developments in remote sensing methodology have made it possible to derive satellite-derived estimates of habitat quality [44], and such data could be useful for estimating carrying capacity of intertidal wetlands across large areas. Varying

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**Figure 4.** Reductions in habitat extent and maximum population flow for 10 shorebird taxa, assuming upshore shifts of intertidal habitats. The loss of habitat extent (solid line) and loss of population flow (broken line) both rise with increasing sea levels, although the latter always equals or exceeds the former. Species vary in the degree to which the impact of habitat loss is magnified by migratory connectivity (the area between the two curves). Error bars indicate the highest and lowest range of losses in population flow from 1000 iterations.
habitat quality among sites can fundamentally affect how they are used by migratory shorebirds, for example, a site might act only as a minor feeding area prior to a continuing journey to a nearby location, or it might be a major staging area at which significant weight gain occurs and without which the migration would be impossible [32]. Thus, the population impact of losing habitat at a site depends on its quality and ecological context, and while such data are not yet available across the EAAF, it would be fruitful to incorporate habitat quality and context into future analyses.

Compensation of habitat loss by upshore shifts of intertidal areas would greatly reduce the net area of lost habitat, but it has a less predictable impact upon population flows (figure 4). Our results suggest that some species, such as the great knot, will still show large population declines even when full compensation is assumed. This is because many sites along highly developed coastlines, such as large areas of Japan and the Republic of Korea, cannot move upshore at all, thus compensation physically cannot occur. Species relying on sites in such areas for their migration will be those most vulnerable to SLR impacts. Moreover, SLR is not the only driver of intertidal habitat loss in the region, with several large estuaries in East Asia having been reclaimed over the past few decades [16]. This suggests that these species are more likely to experience sudden declines of population flow in future, even though they are currently relatively abundant. As such, careful monitoring of the populations of such species seems appropriate.

Severe declines in migratory shorebirds are becoming apparent around the world, with perhaps the most severe of those in the EAAF [16,45,46]. Intertidal habitats at staging sites in eastern Asia are diminishing rapidly in both area and quality. For example, a single reclamation project in the Yellow Sea recently removed 110 km² of shorebird habitat [16]. Our results (figure 2 and figure 4) indicate that developments around existing habitats severely affect the adaptability of migratory flyways against the threats from SLR. Unless steps are taken to allow the upshore movement of coastal ecosystems, it seems likely that SLR will compound such losses and cause accelerating population declines in migratory shorebirds.

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