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Optimal Management of a Multispecies Shorebird Flyway under Sea-Level Rise

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Abstract: *Every year, millions of migratory shorebirds fly through the East Asian–Australasian Flyway between their arctic breeding grounds and Australasia. This flyway includes numerous coastal wetlands in Asia and the Pacific that are used as stopover sites where birds rest and feed. Loss of a few important stopover sites through sea-level rise (SLR) could cause sudden population declines. We formulated and solved mathematically the problem of how to identify the most important stopover sites to minimize losses of bird populations across flyways by conserving land that facilitates upshore shifts of tidal flats in response to SLR. To guide conservation investment that minimizes losses of migratory bird populations during migration, we developed a spatially explicit flyway model coupled with a maximum flow algorithm. Migratory routes of 10 shorebird taxa were modeled in a graph theoretic framework by representing clusters of important wetlands as nodes and the number of birds flying between 2 nodes as edges. We also evaluated several resource allocation algorithms that required only partial information on flyway connectivity (node strategy, based on the impacts of SLR at nodes; habitat strategy, based on habitat change at sites; population strategy, based on population change at sites; and random investment). The resource allocation algorithms based on flyway information performed on average 15% better than simpler allocations based on patterns of habitat loss or local bird counts. The Yellow Sea region stood out as the most important priority for effective conservation of migratory shorebirds, but investment in this area alone will not ensure the persistence of species across the flyway. The spatial distribution of conservation investments differed enormously according to the severity of SLR and whether information about flyway connectivity was used to guide the prioritizations. With the rapid ongoing loss of coastal wetlands globally, our method provides insight into efficient conservation planning for migratory species.*

Keywords: coastal wetlands, conservation prioritization, East Asian–Australasian Flyway, ecological networks, global migrants, graph theory, maximum flow algorithm, migratory shorebirds

Gestión Óptima de una Ruta Migratoria de Múltiples Especies de Aves Costeras Sometida a Incremento del Nivel del Mar

Resumen: *Cada año, millones de aves costeras migratorias vuelan por la ruta migratoria Asia-Australasia de Oriente entre sus sitios árticos de reproducción y Australasia. Esta ruta incluye numerosos humedales costeros en Asia y el Pacífico que se usan como sitios de parada temporal donde las aves descansan y se alimentan. La pérdida de unos cuántos sitios de parada temporal por medio del incremento en el nivel del mar (SLR, en inglés) podría causar declinaciones poblacionales repentinas. Formulamos y resolvimos matemáticamente el problema de cómo identificar los sitios de paradas temporales más importantes para minimizar las pérdidas de poblaciones de aves a lo largo de rutas migratorias al conservar suelos que faciliten cambios orilla arriba de llanuras de marea en respuesta al SLR. Para guiar una inversión en la conservación que minimice la pérdida*

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de poblaciones de aves migratorias durante la migración, desarrollamos un modelo de ruta migratoria espacialmente explícito acoplado con un algoritmo de flujo máximo. Las rutas migratorias de 10 taxones de aves costeras fueron modeladas en el marco de la teoría de gráficos al representar agrupaciones de humedales importantes como nodos y los números de aves volando entre 2 nodos como bordes. También evaluamos varios algoritmos de asignación de recursos que requirieron sólo información parcial sobre la conectividad de rutas migratorias (estrategia de nodo, basada en los impactos del SLR en los nodos; estrategia de hábitat, basada en cambios de hábitat en los sitios; estrategia de población, basada en cambios de población en los sitios; e inversión al azar). El algoritmo de asociación de recursos basado en la información de rutas migratorias se desempeñó en promedio 15% mejor que las asignaciones simples basadas en patrones de pérdida de hábitat o conteos locales de aves. La región del Mar Amarillo sobresalió como la prioridad más importante para la conservación efectiva de aves costeras migratorias, pero sólo la inversión en el área no puede asegurar la persistencia de especies a lo largo de la ruta migratoria. La distribución espacial de las inversiones de conservación difiere enormemente de acuerdo a la severidad del SLR y dependiendo de si la información sobre la conectividad de las rutas migratorias se usó para guiar las priorizaciones. Con la continua y rápida pérdida de humedales costeros a nivel global, nuestro método proporciona conocimiento sobre la planeación eficiente de la conservación para especies migratorias.

Palabras Clave: Algoritmo de flujo máximo, aves costeras migratorias, humedales costeros, migrantes globales, priorización de la conservación, redes ecológicas, ruta migratoria Asia-Australasia de Oriente, teoría de gráficos

Introduction

Globally, 8,000–10,000 species are considered migratory (CMS 2011). There is accumulating evidence of population declines among migratory species around the world (Latham et al. 2008; Kirby 2011; Wilson et al. 2011), and 119 countries currently participate in the Convention on the Conservation of Migratory Species of Wild Animals to facilitate international collaboration for conservation of migratory species (CMS 2014). Spatially explicit conservation planning, however, has rarely been applied to migratory species, with the exception of a few recent efforts (Martin et al. 2007; Klaassen et al. 2008). Many migratory species rely on a few small areas as stopover sites during migration, and the loss of such bottleneck sites can cause sudden population declines (Myers 1983; McCulloch et al. 1992). Crucially, where flyways are constrained by bottlenecks, conservation investment to protect sites that are not themselves bottlenecks can be redundant (Iwamura et al. 2013). This raises a serious problem for applying existing prioritization techniques, which often assume a monotonic relationship between the area of conserved habitat and the conservation status of species or populations (Purvis et al. 2000).

Migratory shorebirds of the East Asian–Australasian Flyway (EAAF) are global-scale migrants. They fly from breeding sites in Siberia or Alaska to Australasia every year (Bamford et al. 2008). They are the second most threatened group of migratory birds in the world; 40% of species in this group are in decline (Kirby 2011). Most shorebirds in the EAAF interrupt their journeys to rest and feed at stopover sites, often in coastal intertidal areas across Asia and the south Pacific (Kirby et al. 2008; Zharikov & Milton 2009; Amano et al. 2010). Higher mortality rates are reported during migration than other stages of the migratory cycle (Baker et al. 2004); thus, stopover sites are likely to be important conservation targets (Myers 1983; Myers et al. 1987; Weber et al. 1999). Many coastal areas in the region have been heavily exploited for agriculture, residential development, and development of transportation facilities (Amano et al. 2010; Rogers et al. 2010; Murray et al. 2014). Shorebirds are not only threatened by these local activities, but also by the global threat of sea-level rise (SLR), which can lead to inundation of intertidal areas (Galbraith et al. 2002; Kirby et al. 2008). Considering their dependence on coastal habitats as stopover sites during migration, the loss of these areas may cause disproportionate impacts on populations of migratory shorebirds. Proposed conservation actions to help shorebirds adapt to SLR include building artificial wetlands and allowing intertidal areas to shift inland (Galbraith et al. 2002; Hughes et al. 2005; Seavey et al. 2011).

Haig et al. (1998) outline 4 important guidelines for setting conservation priorities for migratory shorebirds: treat wetlands as a connected mosaic, deal with multiple species, develop species-specific migratory patterns, and develop spatially explicit models for population change. Previous work accounting for flyway structure when optimizing the efficiency of conservation actions relies on detailed information about energy intake rates, and its applications are restricted to individual-based models of animal movement (Klaassen et al. 2008). Moreover, although there is some work on the conservation of migratory birds at the population level (Esler 2000; Martin et al. 2007), previous work deals with relatively simple connections between breeding and nonbreeding habitats, ignoring flyway structure and the importance of stopover sites. Conservation prioritization schemes with connectivity for nonmigratory species often focus on spatial relations between habitat patches (Minor & Urban 2007; Moilanen et al. 2008) and do not directly quantify the impacts of losing stopover sites.

We developed a new approach to spatial conservation prioritization for migratory species that explicitly accounts for migratory connectivity that we based on a recently developed flyway model (Iwamura et al. 2013). We used spatially explicit flyway modeling to estimate the impacts of habitat loss through SLR on overall population size (Haig et al. 1998). The conservation investment we considered was protection of land behind the present intertidal area to allow upshore movement of wetland ecosystems in response to SLR as far as possible given the topography of each site.

We developed a method for allocating conservation investment in multispecies migratory flyways, compared results of this method with results based on rules of thumb, which required only partial information that is readily available, and estimated the performance of methods relative to methods that do not require flyway information. If there are large gains in efficiency by incorporating migratory connectivity, this places a premium on learning more about the structure of species' migratory networks when planning for their conservation.

Methods

Conservation Target

We prioritized investment in the 163 internationally important sites used by 10 shorebird taxa in the EAAF (Bamford et al. 2008). These taxa were selected because of their dependence on coastal wetlands during their migration and their relatively well-known migratory patterns (Iwamura et al. 2013). They were Bar-tailed Godwit (*Limosa lapponica menzbieri* and *L. l. baueri*), Curlew Sandpiper (*Calidris ferruginea*), Far Eastern Curlew (*Numenius madagascariensis*), Great Knot (*Calidris tenuirostris*), Grey-tailed Tattler (*Tringa brevipes*), Lesser Sand Plover (*Charadrius mongolus*), Red Knot (*Calidris canutus rogersi* and *C. c. piersmai*), and Terek Sandpiper (*Xenus cinereus*). These taxa are undergoing long-term declines in several regions around Australia (e.g., Wilson et al. 2011; Clemens et al. 2012; Minton et al. 2012).

Flyway Structure and Flow of Population

We defined a flyway structure as the migration routes of the birds from their breeding habitats in Siberia and Alaska to their nonbreeding habitats in Australasia. A flyway includes a series of stopover sites, coastal habitats in Asia where the birds can stop to feed. Each taxon uses a different suite of sites during migration and consequently has a different migration network structure. The flyway structure, cast as a spatial graph consisting of nodes and edges, was developed separately for each taxon with a combination of expert opinion and empirical data (Iwamura et al. 2013). Each node was defined as a geographical region that contained one or more individual sites at which birds may stop. The boundaries of individual sites were mapped via satellite images, digital elevation maps, and tidal ranges (Iwamura et al. 2013). The weight of edges represented how many individuals moved between nodes during their migration, and habitat loss at a node from SLR was expressed as the reduction in the weight of an edge connecting these nodes.

The loss of population was then calculated as reduced flow in each migratory network (Iwamura et al. 2013). Flyway population size was mathematically defined by the function describing the maximum flow (Goldberg & Tarjan 1988) for each taxon (Supporting Information). We used the extent of habitat loss at sites to estimate the loss of population flying between the clusters of important wetlands.

Conservation Objective

An objective function lies at the heart of the decision science approach to conservation prioritization (Possingham et al. 2006). Our conservation objective was to invest in upshore habitat protection that maximizes the fraction of each taxon's population remaining after SLR. The conservation investment would allow upshore movement of intertidal habitats by protecting currently supratidal areas predicted to become shorebird feeding habitat in the future.

Thus, the objective function was to find $\mathbf{x} = (x_1, \ldots, x_n)$, a vector of investments at each of the migratory sites that solves the following problem:

$$\max_{j} \sum_{i} f_i(\mathbf{x}, L) \text{ such that } \sum_{j} x_j \leq B \text{ and } x_j \leq y_j \; \forall j, \quad (1)$$

where $f_i(\mathbf{x}, L)$ is the fraction of the population of taxon i that is expected to persist given an investment plan of $\mathbf{x}$ and the vector of habitat losses across all sites L, x_j is the investment at site j, y_j is the maximum investment possible at site j, and B is the total budget available for conservation investment. The maximum investment at each site is constrained by the amount of habitat predicted to become available for protection in future within the site.

Resource Allocation Strategies

We compared 5 different strategies (which we refer to as flyway, node, habitat, population, and random) for spatial conservation prioritization to examine the importance of having information on migratory routes. In the flyway strategy, all available information about the flyway structure (Iwamura et al. 2013) was used to maximize the proportional increment in population flow across the 10 taxa. In the node strategy, investment was directed to the most vulnerable nodes (i.e., where the loss of population through habitat loss is the highest). This strategy simulated a condition in which one knows something about the rates of habitat loss but not about the way in which the sites are connected with each other by migration. In the habitat strategy, sites that maximize the total intertidal area were prioritized, and it was assumed that nothing was known about network structure. This strategy invested in sites of high potential for habitat expansion and of low protection cost. In the population strategy, investment was allocated to minimize population loss at a wetland level without considering network structure. In the random strategy, investment was allocated randomly to sites where new habitat could form by upshore shifts of wetlands.

In the flyway strategy, investment in bottleneck sites was prioritized to maintain population flow through the network (Iwamura et al. 2013). It thus avoided redundant investments in sites that would not affect the population flow through a network. We used a greedy algorithm to find the best flyway strategy because it often performs almost as well as more complex algorithms, though it is not guaranteed to provide the optimal solution (Pressey et al. 1997; Wilson et al. 2006). In our case, the solution to Eq. (1) is given by the iterative greedy algorithm (see Fig. 1 for step-by-step algorithm):

$$\max_j \sum_i f_i(\mathbf{x}_j, L), \tag{2}$$

where $\mathbf{x}_j = \mathbf{x} + (0, ..., 0, \Delta x_j, 0, ..., 0)$ and $f_i(\mathbf{x}_j, L)$ is the fraction of the population of taxon *i* that survives given additional units of investment Δx_j to site *j*. The population flow of the flyway network for the taxon *i* at the investment of $\mathbf{x}_j$ is calculated by applying the maximum flow algorithm (Iwamura et al. 2013).

By focusing investment on the most vulnerable stopover node, the node strategy aimed to maintain a population flow as much as possible without explicit information about migratory routes. We also applied a greedy algorithm to the node strategy:

$$\max_j \sum_i g_i(\mathbf{x}_j, L), \tag{3}$$

where $\mathbf{x}_j = \mathbf{x} + (0, ..., 0, \Delta x_j, 0, ..., 0)$ and $g_i(\mathbf{x}_j, L)$ is the increment of intertidal area within the node, which has the highest habitat loss rate among all the nodes of taxon *i* with the additional investment Δx_j to site *j*.

In the habitat strategy, neither nodes nor edge information was used; thus, it was akin to a traditional prioritization framework. The greedy algorithm was applied to solve

$$\max_j \sum_i h_i(\mathbf{x}_j, L), \tag{4}$$

where $\mathbf{x}_j = \mathbf{x} + (0, ..., 0, \Delta x_j, 0, ..., 0)$ and $h_i(\mathbf{x}_j, L)$ is the increment of intertidal habitat of taxon *i* with the additional investment Δx_j to site *j*.

In the population strategy, investment was allocated in proportion to the abundance of birds at each site. Estimates of bird numbers at each site, taken from Bamford et al. (2008), were used but information about flyway structure was not. In this allocation, we assumed a linear relationship between area loss through SLR and habitat loss and applied a greedy algorithm to represent investment according to population size:

$$\max_j \sum_i k_i(\mathbf{x}_j, L), \tag{5}$$

where $\mathbf{x}_j = \mathbf{x} + (0, ..., 0, \Delta x_j, 0, ..., 0)$ and $k_i(\mathbf{x}_j, L)$ is the increase of population of taxon *i* with the additional investment Δx_j to site *j*.

SLR and Conservation Cost

Mean global sea level is predicted to rise from 90 to 200 cm by 2100 (Vermeer & Rahmstorf 2009). We considered 6 SLR scenarios (50, 100, 150, 200, 250, and 300 cm). Habitat loss estimates from SLR (Iwamura et al. 2013) were used to predict reductions in coastal habitats and in the extent of upshore shift of these wetlands (the latter were the conservation investment opportunities). The extent of habitat loss through SLR at each of the 163 wetlands was based on a digital elevation map that included bathymetry and tidal range, and the current extents of tidal flat were estimated using global wetland data sets and remotely sensed images obtained from Google Earth (see Iwamura et al. 2013).

Conservation cost has important implications for spatial conservation prioritization (Naidoo et al. 2006). Because agriculture is the most prevalent driver of habitat loss at a global scale, potential rent from agriculture is often used as a surrogate for conservation cost (Carwardine et al. 2008). We used a global data set of foregone profit from agricultural production (Naidoo & Iwamura 2007) to estimate the opportunity cost of protecting coastal areas into which habitat for migratory shorebirds is predicted to expand as a result of SLR.

Performances and Budgets

We determined the performance of each investment strategy at varying budget levels, calculated as a fraction of the cost of purchasing all the land available. Budget levels from 10% to 90% were examined at 10% increments. In 2010 the Convention of Biological Diversity set a target to protect 17% of the terrestrial and 10% of marine and coastal areas by 2020 (Anon 2010). A budget of 10–30% therefore seems reasonable to achieve target protected area coverage in the future (James et al. 2001), and we focused on the consequences of resource allocation strategies for this range of budget levels. The performance of a strategy was evaluated as the fraction of the original population flow supported in the network after a budget was consumed.

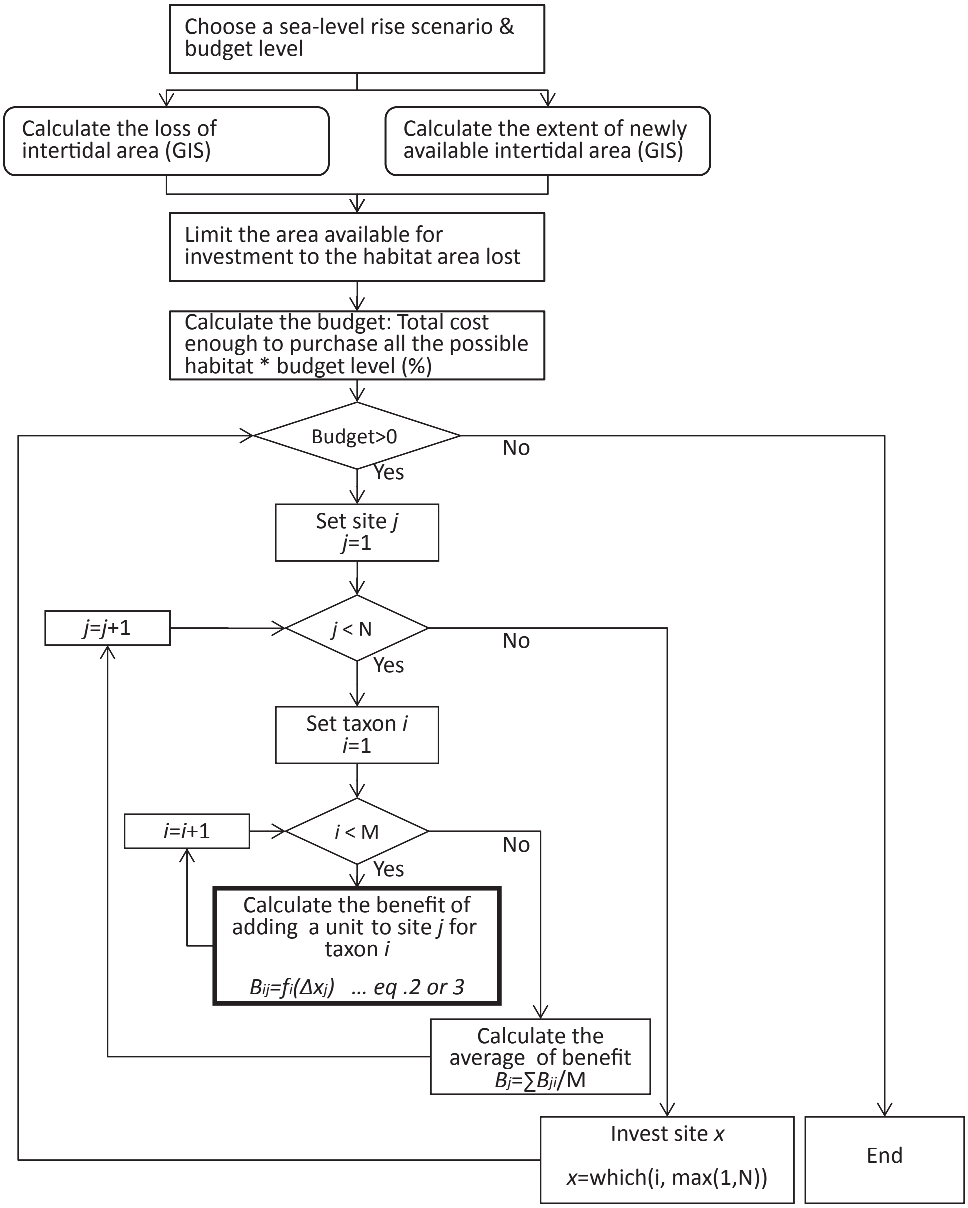

Figure 1. Resource allocation algorithm of the flyway strategy for conserving migratory shorebirds in East Asian–Australasian Flyway (N, total number of sites, in this case 163; M, number of taxa, in this case 10; Δx_j, investment in site j). Investment is allocated to maximize average population persistence across the 10 taxa. The investment is repeated until the budget is consumed. The rectangle with a heavy line is the calculation of the benefit of investment.

Results

Without any conservation investment, average population flow for all 10 taxa dropped to 82% at 50 cm SLR and to 10% at 300 cm SLR (Fig. 2). Investment to protect upshore habitat resulted in the retention of much larger population flows for any given SLR scenario, though the magnitude of this improvement varied markedly among investment strategies (Fig. 2). Random investment produced the poorest results; there was a roughly linear increase in retained population flow as investment increased. The other strategies performed as expected; retention of population flow increased as use of information about migratory connectivity increased for a given budget (Fig. 2).

The flyway strategy retained 70–90% of the starting population flow with an investment of 50–60% of the budget required to purchase all habitat at all the SLR scenarios (Fig. 2). The benefit of having spatially explicit information about migratory routes was particularly great when the budget was small. It performed 2–4 times better than the other resource allocation strategies that did not use the full flyway information when the budget level was 10–30% of the total cost (Fig. 2). Whereas the difference in performances between the flyway strategy and the habitat or population strategy remained significant until the budget was very high, the benefit of full flyway information lessened at medium budget levels (40–60% of the total cost) in comparison with the node strategy. As the budget level approached 100% of what was needed

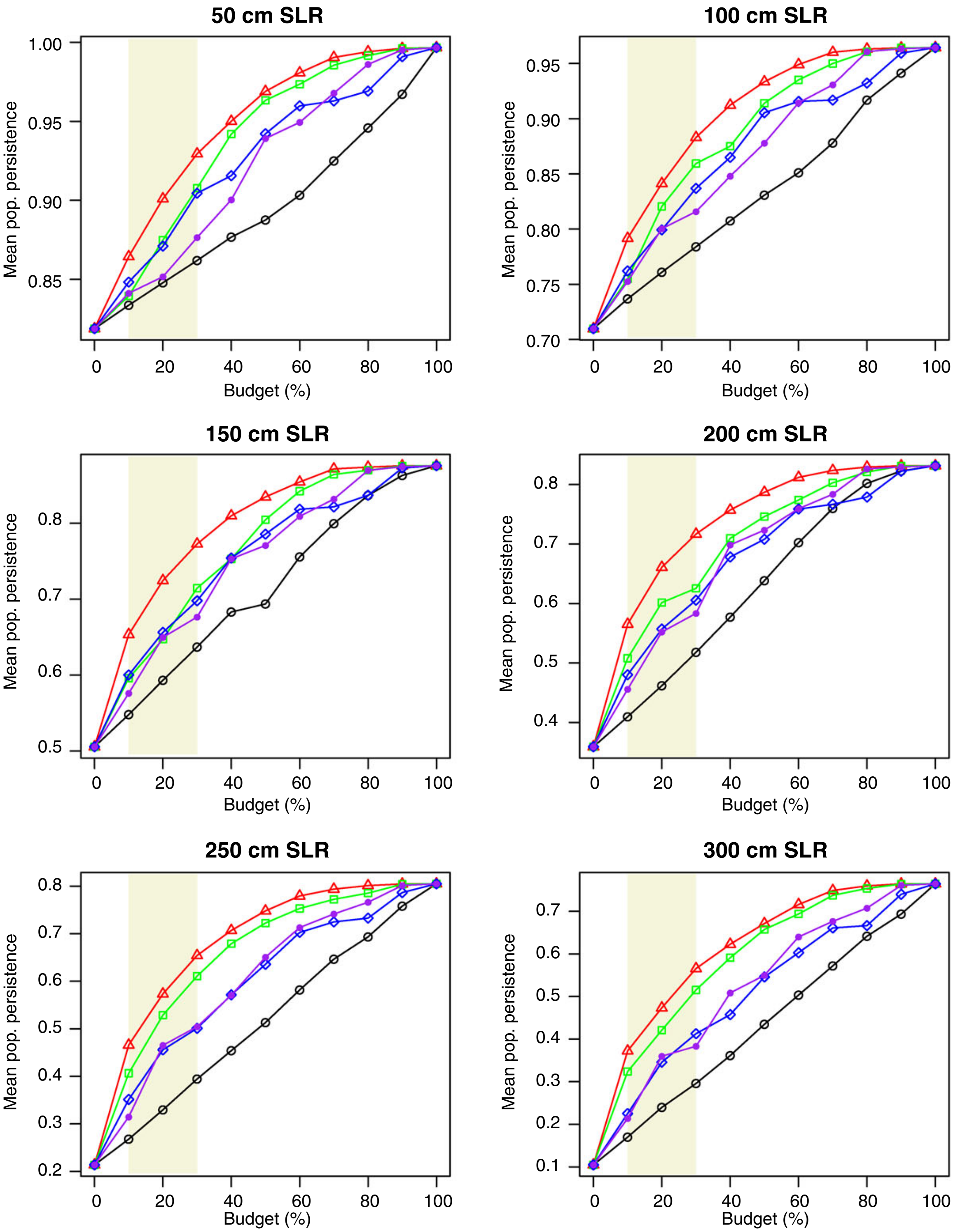

Figure 2. Comparison of the performances of resource allocation algorithms of conserving migratory shorebirds in the East Asian–Australasian Flyway based on the flyway (red, full information of flyway structure and bottleneck), node (green, node-level information), habitat (blue, change in habitat at each site), population (purple, change in population at each site), and random resource investment (black) strategies under the 6 sea-level rise (SLR) scenarios (50–300 cm). The x-axis is the budget relative to the total cost of purchasing all available intertidal area under each of the SLR scenarios. The y-axis indicates the level of population flow averaged across the 10 taxa. Because the size of a wetland is often smaller after SLR than its current extent, population flow can still be substantially lower than its present magnitude even with full investment. Plausible budget levels that represent 10–30% of the cost to protect all potential habitats are shaded.

to protect all sites, the performances of the strategies inevitably converged.

Whereas the flyway strategy always outperformed the other resource allocation strategies, the node strategy performed reasonably at a wide range of budget levels and might be a good rule of thumb if information about flyway connectivity is not available. For example, the node strategy retained 90% of starting population flow with an investment of 50–70% of the total budget needed to purchase all sites (Fig. 2 & Supporting Information). This strategy was, however, not very efficient when the budget was very small under low SLR. The habitat strategy protected twice the population flow of the random strategy when the budget was smaller than 60%, but its performance gap was lower at higher budget levels (Fig. 2). The population strategy did not perform any better than the habitat strategy, except at a budget over 60%.

The Yellow Sea, Southeast Asia, northeast Australia, southeast Australia, and the East China Sea region were the highest priorities for conservation on the basis of the flyway investment strategy (Fig. 3). The Yellow Sea region was the single most important priority at low- to medium-SLR scenarios (Fig. 3) because this area attracted more investment when the budget was higher (Fig. 4). Other strategies based on population information (node and population) also prioritized the Yellow Sea region (Supporting Information). The spatial distribution of investment priorities was strongly affected by the choice of SLR scenarios. At higher SLR scenarios, more of the budget was invested at sites in northeast Australia than the Yellow Sea (Fig. 3). Southeast Asia became an important investment priority under very high SLR scenarios (250 and 300 cm).

Although the overall amount of population flow retained was rather similar for the flyway and node strategies, the spatial distribution of the investments differed markedly at low budget levels (Fig. 4). Under a 100-cm SLR scenario, the node strategy resulted in prioritization in Southeast Asia instead of northeast Australia when the budget was small (Fig. 4), a result that diverged markedly from the flyway strategy. Both flyway and node strategies resulted in prioritization of areas in the Yellow Sea region, whereas the habitat strategy prioritized areas there only at higher budget levels (Fig. 4). Multiple SLR scenario analyses showed that only the flyway strategy prioritized areas in the Yellow Sea region when budgets were small at 50 cm SLR and that the difference between strategies decreased as SLR increased (Supporting Information).

Discussion

Our results suggest that redundancy in conservation investments is potentially an acute problem when planning for the conservation of migratory species. In our case study with the EAAF, the efficiency of investment in habitat protection was greatly improved by spatially explicit knowledge about the structure of a migratory flyway, and the spatial distribution of the investments varied substantially according to the strategy used to guide the investment. The flyway strategy, which prioritized conservation investment based on information on flyway routes to maximize retention of overall population flow, always outperformed other strategies (Fig. 2). It did so by concentrating investment in a few bottleneck sites and avoiding redundant investments that did not contribute to maintaining overall population flow (Fig. 4). Information about migratory routes was particularly important when the budget was small (Fig. 2), a likely scenario in coastal areas where competition with other land uses is invariably intense (Dasgupta et al. 2009; Kirwan & Megonigal 2013).

The Yellow Sea stands out as the single most important investment target under the flyway strategy, where the aim is to maintain population flow for 10 taxa affected by habitat loss from SLR (Fig. 3 and 4). Given that a large proportion of migratory shorebirds within the EAAF use stopover sites in the Yellow Sea, it is likely that this region acts as a migratory bottleneck (Barter 2006; Rogers et al. 2010; Minton et al. 2012). In the habitat strategy, only a limited amount of investment was directed to the Yellow Sea, which reflected relatively low levels of habitat loss through SLR in this region. Even though the population strategy suggested heavy investment in the Yellow Sea, its overall performance was not as efficient as the habitat strategy under small budgets. This shows how important it is to evaluate investments based on overall flyway structure to avoid redundancy. Investing solely in the most vulnerable regions might not conserve migratory species under global change.

Southeast Asia and northeast Australia also emerged as key priorities for investment in habitat protection, but the relative importance of these regions differed greatly depending on the magnitude of SLR and budget size (Fig. 3 and 4). Large geographic variation in the relative amounts of habitat loss under different SLR scenarios (Iwamura et al. 2013) may explain why investments in these regions are so sensitive to the choice of SLR scenario. Investment in these regions also changed according to the size of budget (Supporting Information). This instability suggests that a more dynamic resource allocation process will be needed to cope with the uncertain threats from SLR in Southeast Asia and northeast Australia.

The node strategy, which prioritizes investment in a node (a group of wetland sites defined based on expert opinion) where habitat losses are highest, may be a useful rule-of-thumb strategy when explicit knowledge about migratory pathways is lacking (Fig. 2). The habitat strategy performed reasonably well for low SLR scenarios, but was inefficient at >150 cm SLR (Fig. 2). This is because investment in some areas becomes redundant

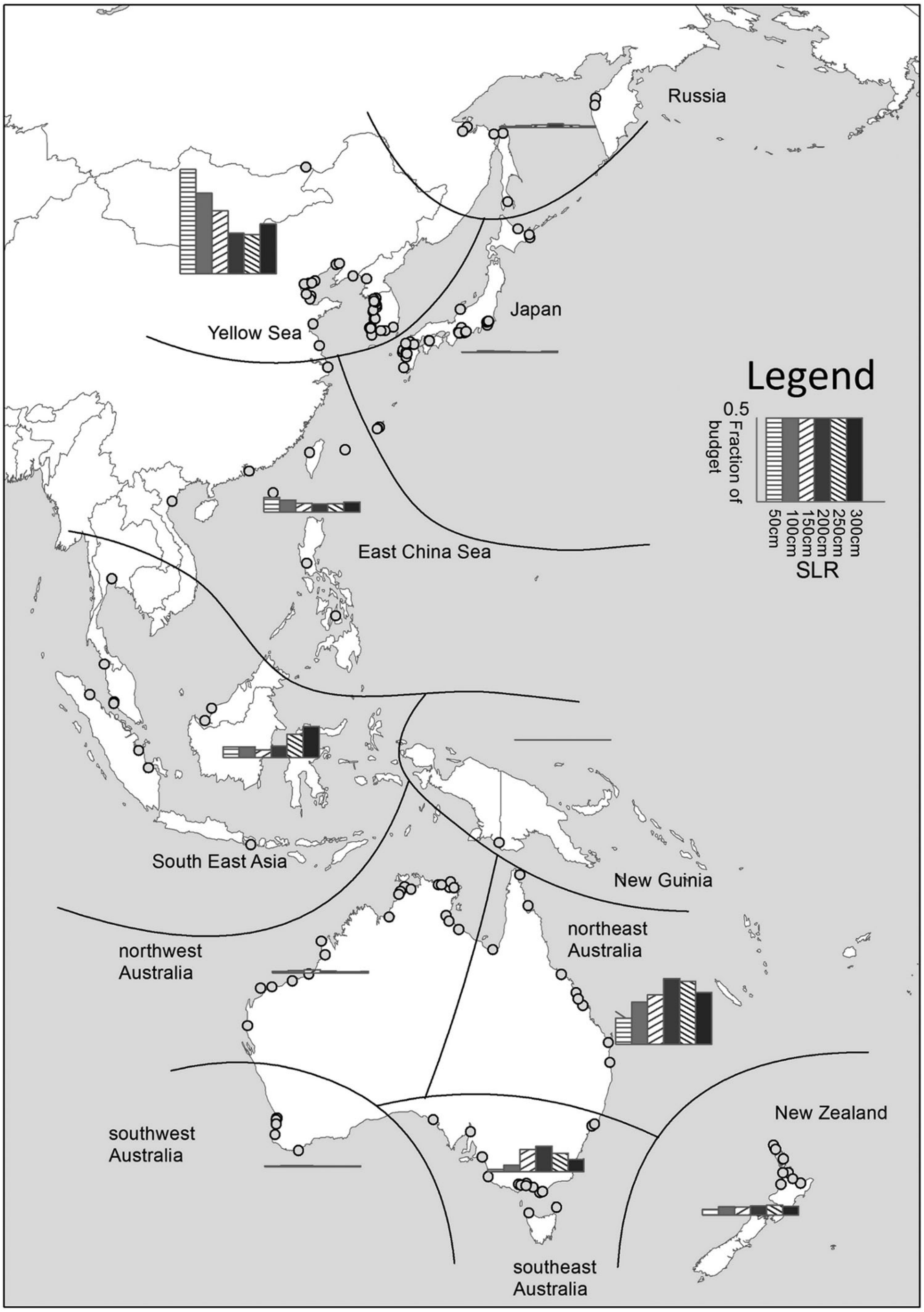

Figure 3. Spatial investment patterns of the flyway strategy aimed at conserving migratory shorebirds in East Asian–Australasian Flyway for 6 sea-level rise (SLR) scenarios (50, 100, 150, 200, 250, 300 cm). The results shown here are at the 20% budget level. Investments in coastal sites are summarized regionally (black lines, regional boundaries; these are different from the nodes of flyways and are for presentation purposes only). Graphs indicate regional investments (y-axis) at the different SLR scenarios (x-axis).

due to the bottlenecked structure of the EAAF (Iwamura et al. 2013). The node strategy was meant to maintain a coherent migratory flyway by protecting the most vulnerable node without complete flyway information. This strategy provided a marked improvement over the habitat or population strategies when the SLR was >150 cm and was close to the performance of the flyway strategy under some conditions (Fig. 2). The spatial distribution of conservation investments differed from the flyway strategy at lower budget levels (Fig. 4 & Supporting Information).

Our results highlight the importance of information about connectivity when designing conservation plans for migratory species. Detailed empirical information about flyway structure is, however, largely unavailable for migratory shorebirds (Webster et al. 2002), and species could potentially change migratory routes (Rakhimberdiev et al. 2011) or the timing of migration (Gunnarsson et al. 2006) over time in response to habitat loss. We did not investigate the consequences of such changes for the sake of simplicity, but further development of our method to incorporate migration dynamics

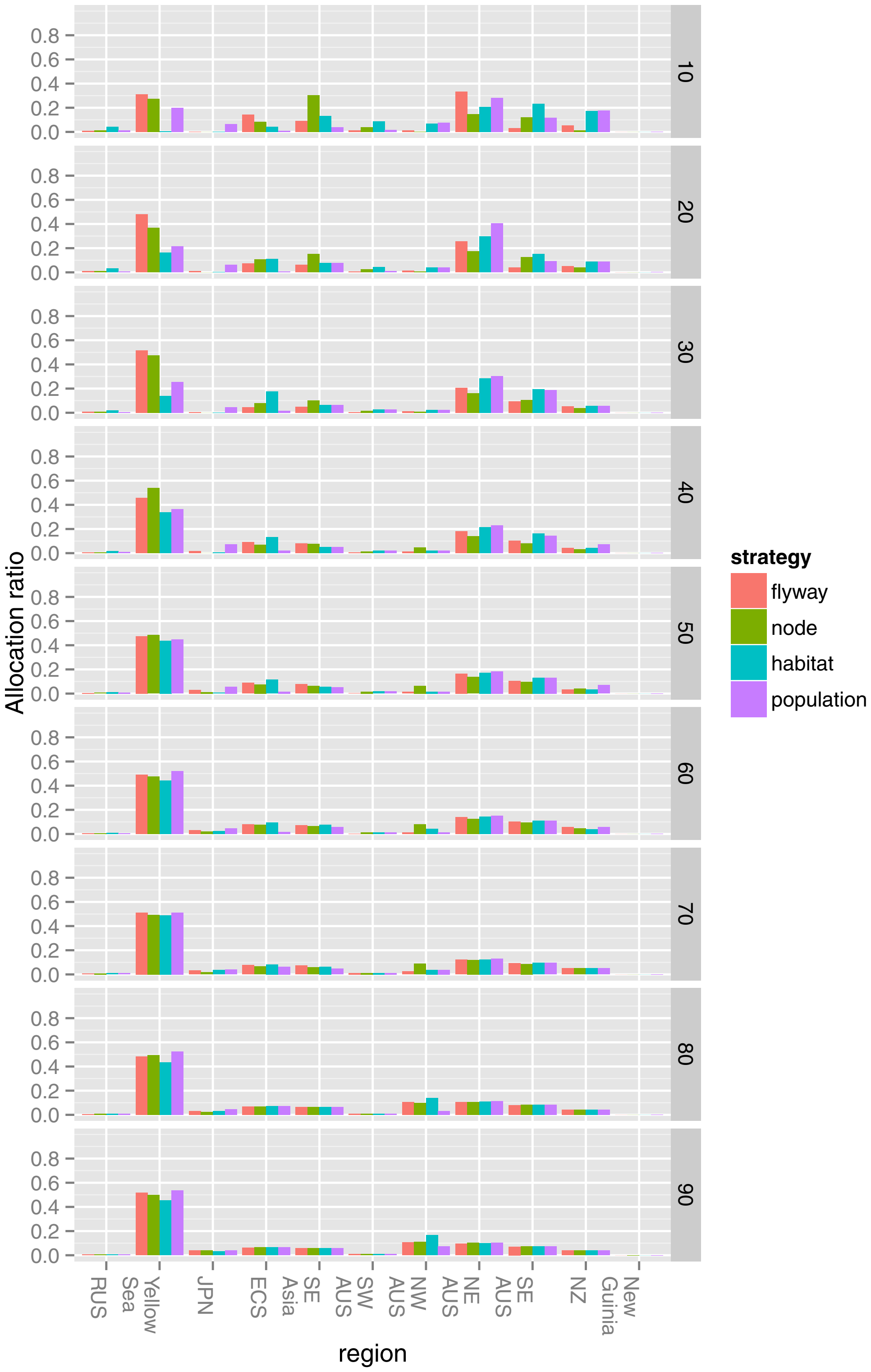

Figure 4. Regional investment across the East Asian–Australasian Flyway under each strategy aimed at conserving migratory shorebirds (red, flyway; green, node; blue, habitat; purple, population; strategies defined in legend of Fig. 2; RUS, Russia; JPN, Japan; ECS, East China Sea; AUS, Australia; NZ, New Zealand). The y-axis indicates the ratio of investment per budget level. Numbers to the right of graphs indicate the budget levels (10–90%). The results under 100 cm sea-level rise (SLR) are shown. The results at different SLR scenarios are in the Supporting Information.

would be interesting. Spatial and temporal variation in migratory routes means that empirical data collection can be time consuming and expensive, but in the meantime advances in optimal migration modeling offer statistical methods for constructing flyway models based on knowledge of energy intake requirements and physiological information about flight range capacity (Klaassen et al. 2008; Bauer et al. 2010). We also simplified our model by assuming a linear relationship between the area of a site and the population size supported there and that each site is currently at carrying capacity. Although little empirical information exists, it would be interesting to explore departures from these assumptions, which could change the relative priority of large sites. Use of remote sensing to measure activity of benthic fauna might possibly provide a way of measuring relative carrying capacity across many sites (Matthews 2011). Combined with detailed maps of intertidal areas (Murray et al. 2012), such sources of information could radically improve conservation investment strategies.

We investigated only the impacts of SLR on coastal habitats for migratory shorebirds, and it must be borne in mind that there are many other threats operating in this flyway. Increasing human populations in coastal regions are creating widespread conflict with coastal conservation goals (Kirwan & Megonigal 2013), and land use change and coastal reclamation constitute an emerging conservation crisis, especially in the Yellow Sea (Amano et al. 2010; Rogers et al. 2010; Murray et al. 2014). With the prospect of exacerbated threats to coastal ecosystems through future SLR (Dasgupta et al. 2009), our results can be updated once region-wide information is available. Importantly, our approach can readily be modified to direct conservation investment under any type of threat in migratory networks.

Several international frameworks to conserve migratory species have formed around the world (CMS 2011; Murray & Fuller 2012). Our results show that existing habitat-based approaches to conservation prioritization may not work well for migratory species because of the risk of making redundant investments due to spatial dependencies caused by migration between sites. This means that knowledge (or at least good models) of migratory connectivity may be crucial in correctly guiding conservation prioritization for many migratory species. Most notably, stopover sites that link breeding and nonbreeding areas can be extremely spatially limited but crucial for the continued functioning of migration networks and hence important priorities for conservation. Once the functional significance of such areas is understood, there is more scope for avoiding redundant conservation investments. Our approach could in principle be used to allocate investment in habitat protection for any migratory species where the spatial structure of the migration is reasonably well understood.

Acknowledgments

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Supporting Information

Supplementary method for calculating flyway population (Appendix S1), the performances of allocation strategies (Appendix S2), and the prioritization patterns under SLR scenarios (Appendix S3) are available on-line. The authors are solely responsible for the content of these materials.

Literature Cited

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